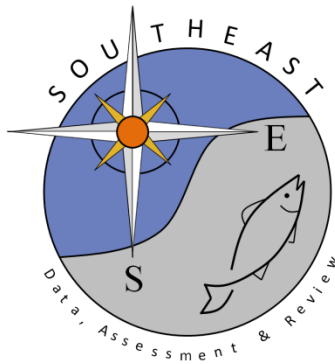


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Determining the stock boundary between South Atlantic and Gulf of Mexico managed stocks of Cobia, *Rachycentron canadum*, through the use of telemetry and population genetics

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Executive Summary

The most recent stock assessment for Atlantic and Gulf migratory group cobia, SEDAR 28, established a management boundary between the two groups at the Florida/Georgia border and recommended additional data collection including electronic tagging to provide greater resolution of the major stock boundary/mixing zone in the southeastern United States. We partnered with charter anglers to capture and place acoustic transmitters in 143 cobia between South Carolina, Georgia, and the east coast of Florida, making use of the rapidly expanding network of receiver arrays in this region. We additionally collected genetic samples in these areas to complement previous analyses and provide a more comprehensive view of cobia stock structure. Tagging occurred in four regions: South Carolina, Georgia, central Florida, and south Florida and analyses were informed by these initial tagging locations.

Generally, overall detection of telemetered fish was high (91%) and provided 4,120 detection days for movement analysis. The telemetry results suggested two major groups of cobia in the study area; a South Carolina/Georgia group and a central Florida/south Florida group. South Carolina/Georgia fish had largely overlapping geographic ranges and migratory patterns were similar based on network analysis of detection data. Cobia tagged in these regions were present in South Carolina and Georgia coastal receiver arrays during April-November and completely absent during December-March, suggesting a movement into areas where receivers are not present (i.e., offshore) during winter. No cobia tagged in this region were detected moving into coastal Florida. Central Florida and south Florida also had largely overlapping geographic ranges and movement patterns with each other. Most cobia tagged in this region displayed resident behavior with a minimal amount of exchange with South Carolina/Georgia as well as the Florida Keys and Gulf of Mexico. In addition to the previously described genetically distinct population segment within estuarine South Carolina waters, genetic analysis agreed with telemetry data suggesting two major groups; South Carolina-Central Georgia and central Florida-south Florida with a mixing zone occurring north of Cape Canaveral to southern Georgia. Genetic analysis is consistent with the acoustic data, suggesting that a low level of gene flow/movement occurs between the two offshore groups along the Atlantic Coast.

The results of this project agree with the external tagging and genetic analysis used in SEDAR 28 and do not refute the current management boundary at the Florida/Georgia border. Because long-term tags acoustic tags were used, we expect to collect additional migratory data from these cobia over the next 2-3 years. These results provide a highly valuable data source that will be directly incorporated into a stock identification workshop for Atlantic and Gulf cobia in spring 2018.

Introduction

Cobia are a popular recreational sportfish that seasonally inhabit inshore and offshore habitats along the south Atlantic and Gulf of Mexico coasts of the United States as well as most of the world's warm oceans. In the United States, cobia are managed under the Coastal Migratory Pelagic Fishery Management Plan (FMP) established in 1983 (GMFMC and SAFMC, 1983). The current management boundary between South Atlantic and Gulf of Mexico stocks is the Georgia/Florida border.

Statement of Problem

Cobia were initially managed as a single stock throughout the Gulf of Mexico and the South Atlantic with joint management authority shared by the Gulf of Mexico Fishery Management Council and South Atlantic Fishery Management Council. Amendment 18 to the FMP (GMFMC and SAFMC, 2011) established separate Gulf and Atlantic migratory groups based on clear differences in growth rate and maximum age in fish from each region (Burns et al. 1998, Franks et al. 1999). The amendment, which took effect in January 2012, set annual catch limits (ACLs) and established accountability measures that are triggered when harvest exceeds the ACL as required under the Magnuson-Stevens Fishery Conservation and Management Act. Amendment 18 initially set the stock boundary between the South Atlantic and Gulf of Mexico migratory groups at the Dade/Monroe County line in Florida, based on a long-held belief that cobia in the southeast US overwinter and mix in the Florida Keys before migrating north in the South Atlantic and Gulf of Mexico (Williams, 2001). Subsequent genetic analysis (Darden, 2012) disputed that stock boundary and tag recapture analysis suggested that the major boundary or mixing zone between groups more likely occurs around Cape Canaveral on the east coast of Florida (Perkinson and Denson, 2012). However, because sample sizes of genetic and tagging data were low along the coasts of Georgia and northeast Florida and stock assessment scientists were hesitant to split the east coast of Florida into multiple management regions, amendment 20B to the FMP placed the new stock boundary at the Florida/Georgia line. This demarcation may or may not be representative of the true biological boundary or mixing zone between stocks. In addition, Darden et al. (2014) identified discrete population segments (DPSs) among cobia that seasonally aggregate in both the Chesapeake Bay and the southern sounds in South Carolina (St. Helena, Port Royal, and Calibogue). These DPSs are included in the Atlantic Migratory Group but how they relate to the overall stock structure in the southeastern United States is not completely clear.

Following SEDAR 28, research recommendations from both the data and review workshops indicated a need for a more integrated tagging program including the use of electronic tagging. The review workshop recommended forming partnerships with the fishing industry and suggested that, "Industry participation rates might be high if information is provided back to participants, and their collaboration improves stock assessment and fishery management." Based on these recommendations and the need for greater data resolution, we partnered with recreational anglers to capture and implant cobia with acoustic transmitters to evaluate movements and delineate stock structure along coastal Florida, Georgia, and South Carolina. Acoustic telemetry technology allows researchers to collect additional migratory data points that

are not available through traditional tagging methods and has become a viable method for tracking long distance cobia migrations due to rapid expansions of collaborative acoustic telemetry networks. These telemetry data were paired with the collection and analysis of additional genetic samples to comprehensively evaluate the stock structure and boundaries of cobia along the southeastern United States coast. Our project specifically addressed **CRP Program Priorities:**

1d: increasing the amount of at-sea observations and data collection opportunities through the use of acoustic transmitters and genetic fin clip collection, and **1e:** providing improved life history information (migration patterns, habitat use, degree of estuarine fidelity) for an important recreational finfish.

Objectives

The overall goal of our project was to utilize acoustic telemetry and population genetics to determine the biological stock boundary between Gulf of Mexico and South Atlantic stocks of cobia. Our specific objectives were to:

1. Employ charter boat captains and recreational fishermen in Florida, Georgia, and South Carolina to capture live cobia for implantation of 50 long-life acoustic transmitters in each state.
2. Collect transmitter observation data semi-annually from the coastal and estuarine VEMCO receiver arrays in the Atlantic Cooperative Telemetry Network (ACT) and Florida Atlantic Coast Telemetry (FACT) network.
3. Collect 100 cobia genetic tissue samples in each state via cooperating anglers and project staff and analyze genetic data.
4. Collect water temperature data from SECOORA's (Southeast Coastal Ocean Observing Regional Association) data portal.
5. Integrate data and evaluate recapture patterns in relation to genetic population patterns, water temperature and current data, and cobia size/maturity; and
6. Disseminate findings.

Methods

Acoustic Telemetry

Passive acoustic telemetry utilizes an array of submerged acoustic receivers deployed to continuously and autonomously record the presence of fish implanted with acoustic transmitters. The acoustic telemetry portion of this project relied on the ever-expanding network of submerged acoustic receiver arrays throughout the study area and beyond. The Florida Atlantic Coast Telemetry (FACT) and Atlantic Coastal Telemetry (ACT) Networks are organized as part of a regional-scale cooperative network of passive acoustic receiver arrays maintained by several marine research organizations along the South Atlantic coast. As of 2018, the FACT Network consists of over 900 acoustic receivers deployed in a variety of habitats including coastal rivers, open estuarine waters, tidal inlets, beachfronts, offshore reefs, wrecks, and sand shoals (Figure 1). The core FACT array was established in 2008 and covers 875 km of all Florida's east coast

from Jacksonville down into the Florida Keys. Membership in FACT has grown markedly in recent years with additional arrays now deployed in the Everglades, Florida Keys, Bahamas (Eleuthera, Andros Island, Bimini, and Grand Bahama), Jacksonville and Georgia. FACT currently has 42 partner groups including the Florida Fish & Wildlife Conservation Commission, Georgia Dept. of Natural Resources, Kennedy Space Center, US Navy, many research Universities along the East Coast, and several independent marine research organizations.

The ACT Network was established in 2006, primarily as a means for monitoring Atlantic and Gulf Sturgeon migration, and extends from Georgia to Maine. As is the case with FACT, the ACT Network has expanded rapidly from 15 researchers at inception to currently include 120 researchers working with over 85 different species. GADNR and SCDNR are currently each maintaining coastal arrays as part of the FACT and ACT networks with large clusters of receivers along the Georgia and South Carolina coasts, including but not limited to Brunswick, Gray's Reef, Port Royal Sound, Charleston, and northern South Carolina (Figure 2) (<http://dnr.sc.gov/marine/receiverstudy/methods.html>). This network includes natural and artificial reef, shipping channel, and sand bottom locations. In addition to these coastal arrays, several hundred riverine and estuarine receivers are deployed throughout all major South Carolina waterways; including several areas in close proximity to identified cobia inshore aggregations. Additional acoustic arrays exist in the Gulf of Mexico (integrated Tracking of Aquatic Animals of the GOM-iTAG) and Mid-Atlantic that are able to detect tagged cobia that leave our study area.

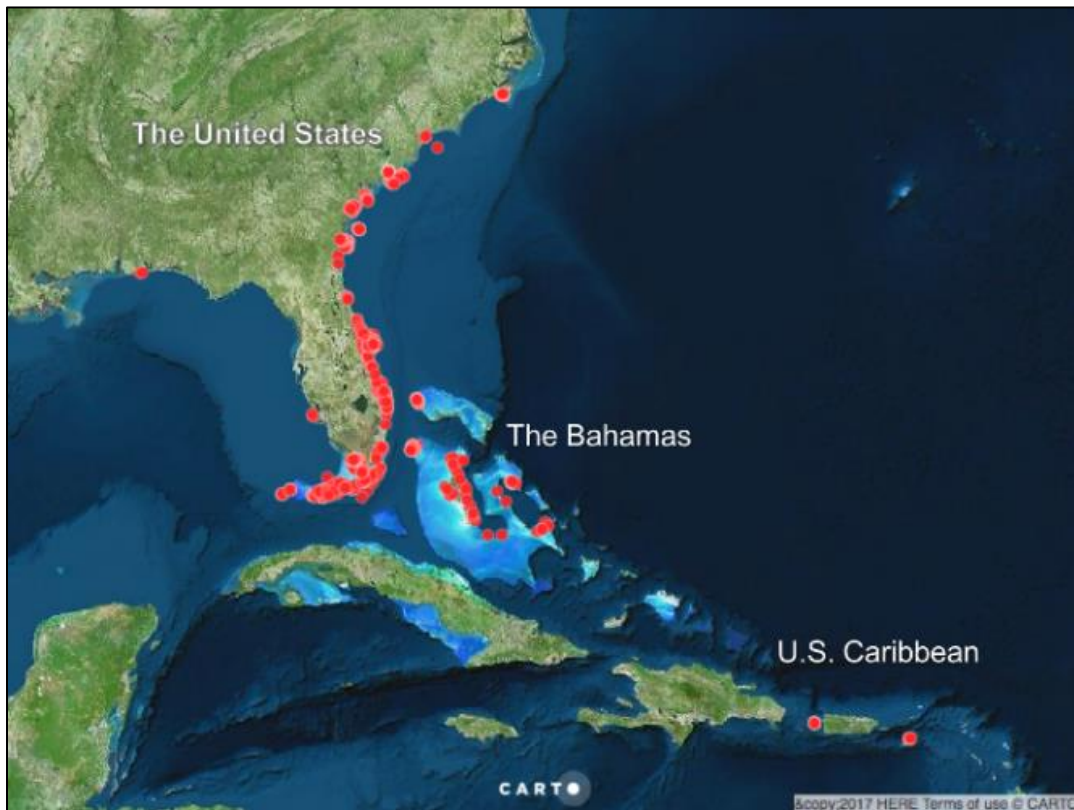


Figure 1. Overview of all current Florida Atlantic Coast Telemetry Network receiver arrays from NC-FL and the Caribbean.

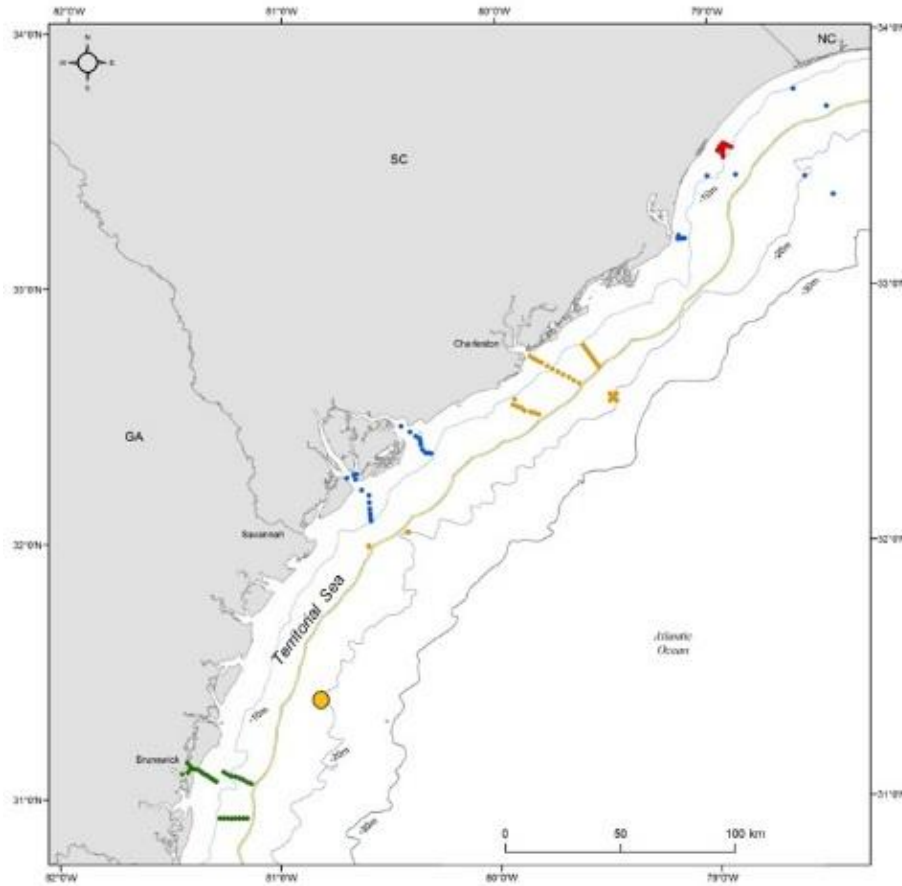


Figure 2. Florida Atlantic Coast Telemetry Network receiver arrays in coastal South Carolina and Georgia.

Cobia were captured, implanted with acoustic transmitters (V16-4H, Vemco Inc.) and released. The acoustic transmitters were programmed to emit a 69-kHz ultrasonic “ping” every 90 seconds with a signal that is specific to the individual transmitter. If the animal passes within range (300-800 meters, depending on depth and oceanographic conditions) of a receiver, the ping is recorded (a detection) and therefore an animal’s relative location at a specific point in time is known. By evaluating detections over time with multiple animals, we can evaluate migratory patterns of the overall tagged group. The size of the cobia involved allowed us to use a larger acoustic transmitter with a battery life of 4-5 years, meaning that each transmitting cobia will provide data well beyond the end of this specific project.

Tagging

Project staff in both South Carolina and Florida relied on existing relations with charter captains and commercial fishers who were willing to participate through previous work with cobia and other species. We also recruited additional captains to participate in the project to expand our geographic range and increase sample sizes. Charter guides that devoted a trip to tagging efforts were compensated \$300 a day and \$150 for each cobia successfully tagged. Charter guides who donated fish as part of other ongoing charters were compensated \$150 for each cobia. Fishing trips targeted cobia near artificial/natural reefs offshore, locations inshore that are known spawning sites in South Carolina, and nearshore zones that typically produce cobia. Cobia were

landed via hook and line using either dead bait, live bait, or artificial lures throughout the water column. A total of 143 cobia were implanted with acoustic transmitters (hereafter referred to as “tagged”) during the project. Cobia tagging was clustered in four main locations throughout the study area due to availability of fish, participating charter captains, and staff: inshore and offshore (defined hereafter as any location seaward of coastal landmasses and not within the interior of an estuary) locations in South Carolina, offshore locations in Georgia, offshore locations around Cape Canaveral, Florida (hereafter referred to as “Central Florida,” and offshore locations near Jupiter, Florida (hereafter referred to as “South Florida”) (Figure 3). One additional cobia was tagged in Jacksonville, FL. Tagging duties were split geographically among project collaborators for logistical reasons. South Carolina Department of Natural Resources (SCDNR) staff were responsible for all tagging in South Carolina and Georgia. Kennedy Space Center (NASA) Ecological Program staff were responsible for tagging in Central Florida and FWC staff were responsible for tagging in South Florida.



Figure 3. Locations and number of cobia tagged in South Carolina, Georgia, and Florida.

Cobia were transported, ventral side up, to a v-shaped fish cradle. Two methods for respiration were used: a modified bilge pump and tubing apparatus pumped seawater into the mouth and across the gills of the cobia or the cobia’s head and gills were kept submerged in saltwater during the procedure. Both methods allowed constant respiration during the surgical procedure, and based on high redetection rates, were successful. Fork and total length, as well as sex (in the case of males that readily expressed milt) was recorded for each fish. Transmitters were surgically implanted into the peritoneal cavity. A small incision approximately 20 to 25 mm long was made

adjacent to the midventral line between the pelvic girdle and vent to insert the acoustic transmitter. The incision was then closed with 1-2 interrupted sutures and VetBond cyanoacrylate adhesive (Figure 4). These methods typically allowed for quick recovery and robust condition at the point of release. Following the surgical procedure, cobia were fitted with two nylon dart tags inserted into the dorsal pterygiophores to alert anglers to the presence of the internal transmitter and to ask them to release the cobia upon capture. A small 10x10 mm sample of tissue was taken from the anal fin of each fish for genetic analysis. Cobia were then transferred to the water, revived until able to swim off under their own power, and released. Most surgical procedures were completed in 5-10 minutes.



Figure 4. Suture applied to cobia following insertion of acoustic transmitter.

Overall, cobia tagged had a mean FL of 862 mm with a minimum FL of 625 and a maximum of 1,245. Cobia were primarily tagged during 2016-2017 (Table 1). Six fish were released during 2014-2015 at Cape Canaveral as proof of concept and were included in analysis. Tagging efforts in South Carolina and Georgia primarily occurred in May/June (Figure 5). In central Florida, tagging occurred largely in March or during summer upwelling events in July and August that brought cooler water and cobia into nearshore waters. In south Florida, tagging efforts were spread out over March-July, with a peak in March.

Table 1. Number of acoustic tags implanted in cobia in South Carolina, Georgia, and Florida during the project from 2014-2017.

Year	Tagged Cobia (#)
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2014	1
2015	5
2016	110
2017	27

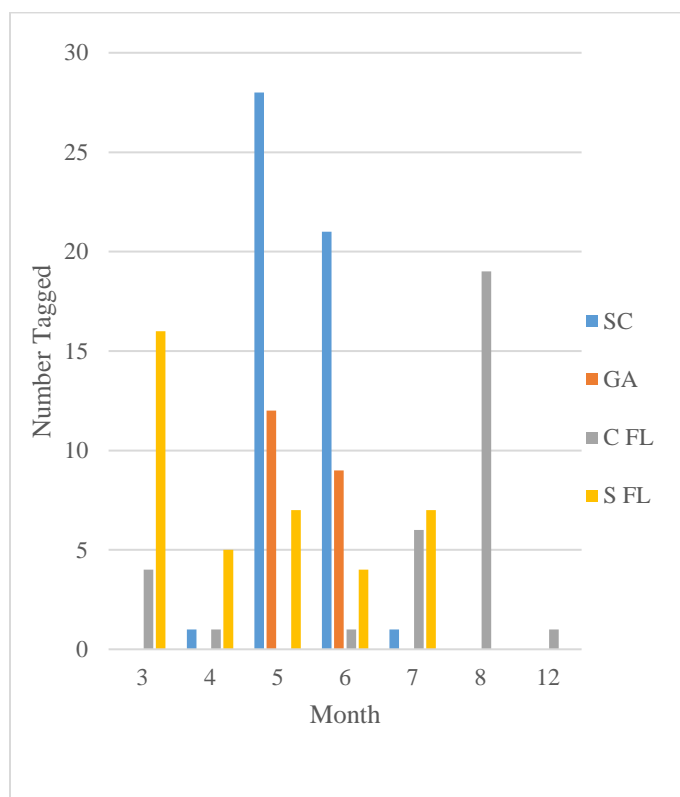


Figure 5. Acoustic tagging of cobia by state, region, and month during 2014-2017.

As a cooperative research project, one of the primary goals was to involve charter guides in the data collection process. Because these guides spend countless hours on the water searching for cobia, their knowledge and experience helped us to increase our tagging sample size in an efficient manner. Over 2016-2017, a total of 24 charter guides in South Carolina, Georgia, and Florida participated in the study. Collectively, they were chartered for a total of 44 trips and were used to tag 90 of 143 cobia (additional fish were tagged by project staff). Project funds were used to pay charter guides \$13,200 for trip fees and an additional \$13,500 for tagged fish. In total, \$26,700 were transferred to the private sector for these services. Additionally, project staff have remained in contact with participating guides to provide ongoing updates on the results of this project. Each guide will receive a personalized summary of project results along with information specific to the fish that they helped tag. Through this outreach, we hope to maintain strong relationships with anglers who will remain vested in the science and management process into the future.

Receiver Downloads

Receivers maintained by project partners in South Carolina, Georgia, and Florida were downloaded between 2-4 times per year and made up the bulk of all cobia detections. In addition to our downloads, we received detection data from the United States Navy, Gray's Reef National Marine Sanctuary, Florida Atlantic University, the University of Miami, the University of Florida, The University of North Carolina, and the University of South Alabama. Detection data were edited to a uniform template and maintained in a relational database (Microsoft access).

Several methods of validating data have been employed in telemetry-based studies to ensure the accuracy of detections (e.g. Bijoux et al. 2013; Young et al. 2016). In this study, detection data for tagged fish were validated before analysis by applying four rules: (1) removal of any detections before the date of surgery, (2) removal of any detections after a tag's published expiration date or after a known harvest date, (3) removal of detections that exceed a maximum swim velocity, specifically detections that occur within one hour at receiver stations over 10.5 km apart (2.9 meters/second), and (4) removal of continuous detections on a single receiver station for 2 months or more. In addition, a series of detections reported from Mobile Bay, Alabama were eliminated because the salinity and water temperature at the time of detection were deemed out of the physical tolerances for cobia and a large number of tagged individuals (red drum) were present in the estuary, suggesting that tag interference may have led to false detections.

Environmental Data

Daily sea surface temperatures at the time of each detection were determined using mosaic netCDF datasets available from the Southeast Coastal Ocean Observing Regional Association (SECOORA). The datasets provided a mean daily temperature to a resolution of 1x1 km square. Python script was used to extract temperature data from the mosaic datasets for each individual detection using a combination of station location and date in ArcGIS (ESRI) 10.5.1 software.

General Linear Models

General linear models (GLM) were used to model latitude and longitude as a function of sea surface temperature, month and year of detection, tagging location, and fork length (Table 2). Candidate models for the response variable that differed 3 or less from the model with the lowest AICc score were furthered explored using GLM with Restricted Maximum Likelihood (REML) estimation. When main effects were significant, Least Squares Mean (LSM) post hoc tests were used to compare differences between groups. Analyses were conducted using SAS[®] Enterprise 7.1 software.

Table 2. Predictors used in the generalized linear mixed-effects models (GLMM) for location. (c): categorical variable

Location	Biotic and abiotic factors
(response variable)	(predictor variables)

Latitude	Sea Surface Temperature
Longitude	Month (c)
	Year (c)
	Tagging Location (c)
	Fork Length
	Tag ID (c) (<i>random effect</i>)

Network Analysis

To quantify spatial relationships throughout the study area, we developed directed movement networks, where each node represents an area and the tie between them an associative link. Directed movements were defined as the number of individuals that moved between two locations. Due to the unequal distribution of receivers and the potential bias for overestimation of movement in areas of high receiver density, all receiver locations within a tenth degree were combined to form a single node and detections were binned into daily presence or absence at each node. This matrix was used to create directed networks for the tagged population by month.

Network level metrics were calculated for each observed network to examine how the structure of the network changes over time. Network metrics include: (1) density, the proportion of actual ties out of potential ties between all nodes (2) degree centralization, the proportion of actual directed ties out of potential directed ties and (3) average path length, average number of steps along the shortest path for all possible pairs of nodes.

Visualization was achieved using a theoretical layout based on 100 random permutations, resulting in a layout based on the relationship between areas, not geographic location. Locations more closely related are closer together, while dissimilar areas are repelled. Arrows indicate direction of movement and line thickness indicate number of movements between locations. For ease of interpretation, nodes are colored according to geographic location (Figure 6).

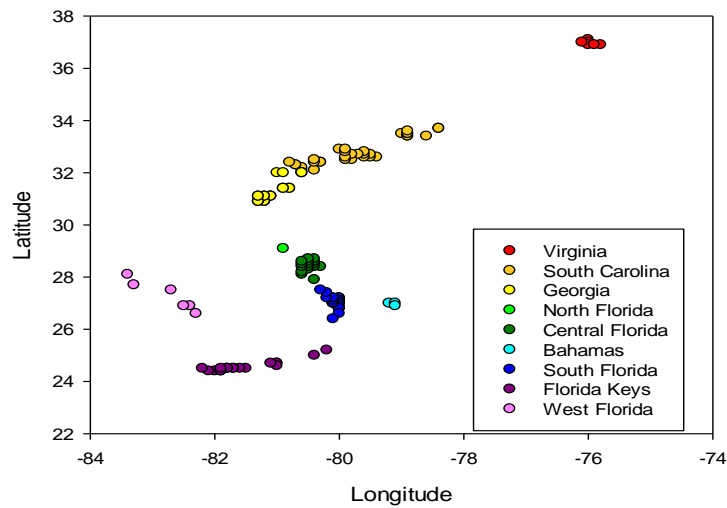


Figure 6. Latitude, rounded to the nearest 10th of a degree, where cobia were detected.

Genetic Analysis

Small tissue samples were collected from the anal fin at the time of tagging and stored in a sarcosyl-urea preservation solution (8M urea, 1% sarcosyl, 20 mM sodium phosphate, 1 mM EDTA). The sarcosyl-urea preservative simultaneously stabilizes DNA and serves as a preliminary cell lysis solution. All DNA isolation, microsatellite amplification, and genotyping methods followed previous work on cobia from our group (Darden et al. 2014). Briefly, DNA was isolated from all samples using a metal bead isolation procedure. Ten polymorphic microsatellite loci were then amplified via polymerase chain reaction (PCR) in three multiplexed groupings. These loci have been optimized and multiplexed previously, and were used by our lab to document both global and local population structure in cobia. PCR was conducted in 11 μ L reactions with 1x HotMaster buffer with 2.5 mM Mg^{2+} , 0.2 mM dNTPs, 0.3 units HotMaster *Taq* polymerase (5 Prime, Inc.), 0.5 mM $MgCl_2$, 0.20 mg/mL BSA, 0.3 μ M forward and reverse primers, and 1 μ L of 1:10 diluted DNA template. Individual primer concentrations differ among loci and are given in Darden et al. (2014). Forward primers for all loci were labeled with WellRED fluorescent dyes (Beckman Coulter, Inc.). Thermal cycling for PCR used a modified 60°C touchdown protocol (from Renshaw et al. 2006) consisting of an initial denaturation step at 94°C for 2 min, followed by 34 cycles of denaturing at 94°C for 30s, annealing at 60°C, 57°C, and 54°C (7, 7, and 20 cycles, respectively) for 1 min, and extension at 64°C for 2 min, followed by a final extension step at 64°C for 60 min (as in Darden et al. 2014). Both size standards (Genome Lab DNA Size standard kit 400) and reaction products were separated with a Beckman CEQ 8000 (Beckman Coulter, Inc.), with fragment size analysis performed with CEQ8000 software. All chromatograms were scored manually by two independent readers. Discrepancies between readers were resolved in conference, or samples were rerun to obtain an unambiguous genotype for all individuals.

As researchers at SCDNR initiated a cobia stock enhancement research program in 2004, the genetic samples collected for this project were also screened for hatchery individuals in the sampled populations. We utilized a maximum likelihood parentage approach as implemented in CERVUS 3.0.3 (Kalinowski et al. 2007) to provide a statistical evaluation of parentage taking into account mutation rates and population allele frequencies. The power of the loci suite to correctly identify hatchery fish as well as individual fish is high, with average parent-pair and identity non-exclusion probabilities of 1.7×10^{-7} and 7.8×10^{-12} , respectively, suggesting very low probabilities of incorrectly identifying hatchery fish or individuals. Parentage simulations ($n=20$) were run with known sex parentage analysis using allele frequencies from individuals collected from 2007 to 2009 ($n=1,407$). All simulations were conducted with 10,000 offspring, 8 candidate parent pairs (with all parents sampled), 95% genotyping, low mistyping error (0.01) and mutation (0.001) rates. Critical delta scores were determined using 99% confidence for the relaxed criteria and 99.9% for the strict criteria. Parentage analyses for the juvenile samples were conducted with the modal simulation file from the simulation runs. All parental assignments were designated at the strict confidence level (99.9%). All hatchery-born fish were removed from the dataset prior to further analysis.

All remaining individuals were subjected to sibship analyses as implemented in the software Colony 2.0.6.4 (Jones & Wang 2010) to identify any potential large family groups within the dataset that could confound further genetic structure analyses. Two simulations were run using settings of polygamous breeding, weak prior, updating allele frequencies, no genotyping error, and FPLS likelihood method for a medium run length. Any identified duplicate samples were removed from the dataset prior to further analyses. Results were evaluated for consistency among runs for individual fullsib relationships as well as family sizes present.

Standard population genetic statistical analyses were applied to the resulting sample dataset. Population genetic structure throughout the collection range was assessed via AMOVA analyses in Arlequin 3.5.1.2 (Excoffier et al. 2005), pairwise F_{ST} -style statistics calculated in GenAlEx 6.5 (Peakall & Smouse 2006, 2012), and with the clustering algorithms implemented in STRUCTURE 2.3.4 (Pritchard et al. 2000). Iterative AMOVA (R_{ST} -based) analyses were conducted to evaluate areas of genetic discontinuity in the data set with all potential location groupings under a two population scenario, and was followed up by limited evaluations of potential three population scenarios guided by the initial analyses. Pairwise comparisons of sample locations were conducted initially at the smallest geographic scale and locations were combined sequentially to represent the smallest number of homogenous groupings. Estimates of F_{ST} , G_{ST} , G'_{ST} (Nei), G''_{ST} , and D_{EST} were initially calculated to verify consistency across metrics; as patterns of all estimates were consistent, only F_{ST} metrics are reported. The clustering model assignment employed in the program STRUCTURE using a hierarchical approach with the assistance of the web-based software Structure Harvester 0.6.94 (Earl et al. 2012) was used to identify the most appropriate number of distinct populations (K) of each run. Simulations were run using the locprior parameter, with five replicates for each K , the length of the burn-in period = 10,000, and number of Markov chain Monte-Carlo reps after burn-in = 10,000. Sites that were strongly assigned to one population were removed from the data set and STRUCTURE was run iteratively until $K=1$ was the most appropriate assignment for each cluster.

Results

Summary Statistics

The number of cobia tagged with acoustic transmitters during the course of the project was 143. Of those, three were determined to have died or shed their tag and have been excluded from analysis. Of the remaining 140, 128 have been detected to date (91%). After the detection validation process, tagged cobia were detected a total of 95,950 times. Individual fish detections ranged from 2 to 5,080 (mean of 750 ± 90 detections). The first detection occurred on 12/15/2014 and the last detection included occurred on 11/5/2017. The time between first and last detections for individual fish varied from less than one day to 749 days (mean of 307 ± 15 days). Individual fish were detected on receiver stations between 1 and 109 days (mean of 17 ± 2 days). A total of 372 receiver stations within the ACT, FACT, and iTAG networks have been visited by tagged cobia to date.

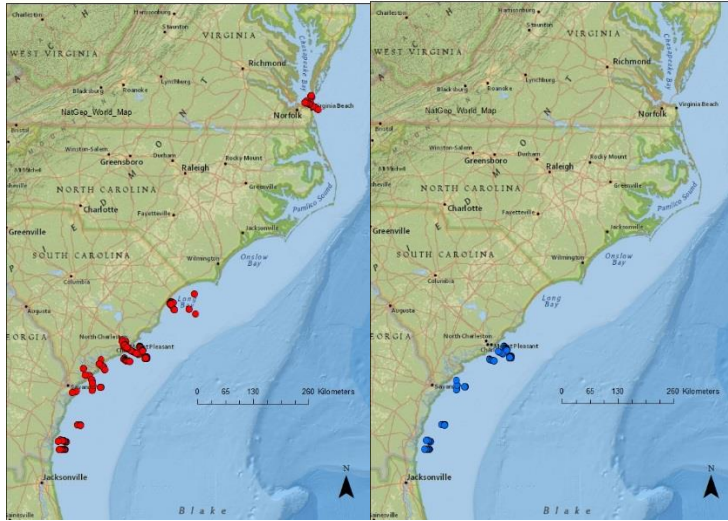
In addition to the high detection rate of tagged cobia, year to year redetection rates were high as well. The six cobia tagged as proof of concept in 2014 and 2015 were detected for several years following tagging and three of them (50%) were detected during recent downloads in 2017. Cobia tagged in 2016 were detected at a relatively high rate during 2017 (63/110, 57%) highlighting that acoustic telemetry is an effective tool to track annual patterns in cobia migration and could potentially be useful in providing yearly mortality estimates with sufficient sample sizes and long-term tagging datasets.

Geographic Extent of Detections

Tagged cobia were detected over a very wide geographic area, from the Chesapeake Bay in the north to the Florida Keys in the south, a minimum straight-line distance by water of 2,704 km. Additionally, two cobia that were tagged in south Florida moved into the Gulf of Mexico north of Tampa Bay and another cobia tagged off south Florida was detected off Grand Bahama to the east.

South Carolina: Fifty-one cobia were tagged in South Carolina waters during 2016-2017. Cobia detections from this group occurred from Chesapeake Bay ($n=2$) to Brunswick, Georgia. No cobia tagged in South Carolina were detected on receivers in Florida. Tagged cobia were detected over a 1,162 km range (Figure 7).

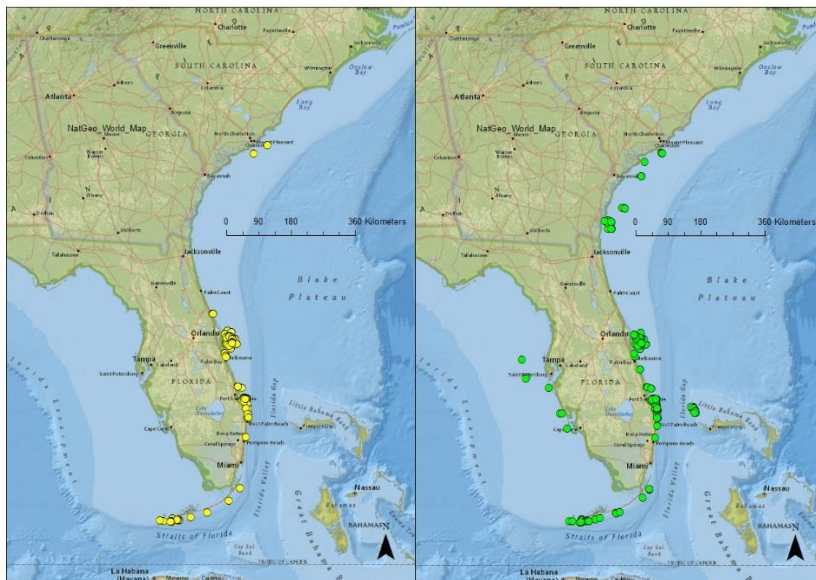
Georgia: Twenty-one cobia were tagged in Georgia during 2016-2017. Cobia were detected as far north as Charleston, SC and as far south as Brunswick, GA. No cobia tagged in Georgia were detected by receivers in Florida. Tagged cobia were detected over a 306 km range (Figure 8).



Figures 7 and 8. Detection extent of cobia tagged in South Carolina (left) and Georgia (right).

Central Florida: Thirty-one cobia were tagged in Cape Canaveral during 2014-2016. Cobia were detected from Charleston (n=1) to the Florida Keys (n=6). Tagged cobia were detected over a range of 1,283 km (Figure 9).

South Florida: Thirty-nine cobia were tagged in the St. Lucie/Jupiter area during 2016-2017. Cobia detections occurred from Charleston, SC (n=1) and Georgia (n=3), to the Florida Keys (n=7). Additionally, 2 cobia tagged were detected in the Gulf of Mexico as far north as Tampa and another cobia was detected off a University of Miami array in Grand Bahama. Tagged cobia were detected over a range of 1,745 km (Figure 10).

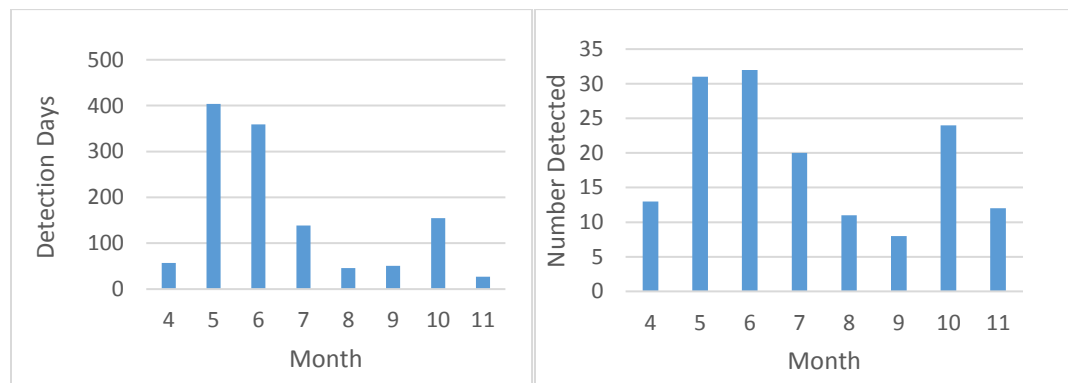


Figures 9 and 10. Detection extent of cobia tagged in central (left) and south (right) Florida.

General Movement and Temporal Patterns

One potential concern of an acoustic telemetry project utilizing pelagic animals is the ability to detect movements given limited receiver array coverage within 30 km and a relative lack of coverage in locations 30 or more km offshore. Despite these concerns, the number and range of animals detected during this project made it clear that individual cobia cover large areas, making them an excellent candidate for acoustic telemetry research. Because of the large number of cobia tagged ($n=143$) and the large geographic extent of tagging efforts, we describe general movement observations by tagging location. Raw detections have been collapsed into detection days (only one detection per station per day from each fish used in analysis) to remove biases associated with large numbers of detections from an individual fish and to provide a more meaningful metric for comparisons.

South Carolina: The majority of tagging efforts in South Carolina occurred during the spring/summer of 2016 (36/49, 73%) providing more than a year of detection data to infer movement patterns. Cobia were present within South Carolina and Georgia receiver arrays from April through November. No cobia tagged in South Carolina were detected by a receiver from December through March in any year. Detection days peaked in May and June, when cobia are traditionally most available to anglers on inshore aggregations and nearshore artificial reefs. Another small peak occurs during October, a month that is not traditionally associated with cobia abundance in South Carolina (Figures 11 and 12). Most cobia (46 of 49, 94%) tagged in South Carolina were detected at some point during the project period.



Figures 11 and 12. Detection days (left) and number detected (right) by month of cobia tagged in South Carolina.

Overall, detection numbers of tagged fish were sufficient so that seasonal patterns were apparent. Fish tagged in the southern South Carolina off Port Royal Sound ($n=26$) were frequently detected moving from central to southern South Carolina or into Georgia during October and November ($n=14$). The following spring, fish from this tagging location were frequently first detected off Georgia or southern South Carolina ($n=9$). In September-November following the first year of tagging (2016) in southern South Carolina, mean daily latitude of detected cobia drops sharply with a similar magnitude of sharp increase the following April-May (Figure 13). These detections suggest that some cobia move south as waters cool and back north into Georgia and South Carolina as they warm in the spring. Despite the apparent north/south trend, cobia have not been detected moving into coastal Florida. The pattern of north/south movement was

not as apparent with fish tagged off Charleston (n=10). Most of these fish were last detected near Charleston in the fall and first detected near Charleston in the spring following tagging. While fish tagged within Port Royal Sound (n= 15) were detected throughout South Carolina and Georgia, most (13/15) were tagged in the spring of 2017 and therefore seasonal movement patterns are not yet available.

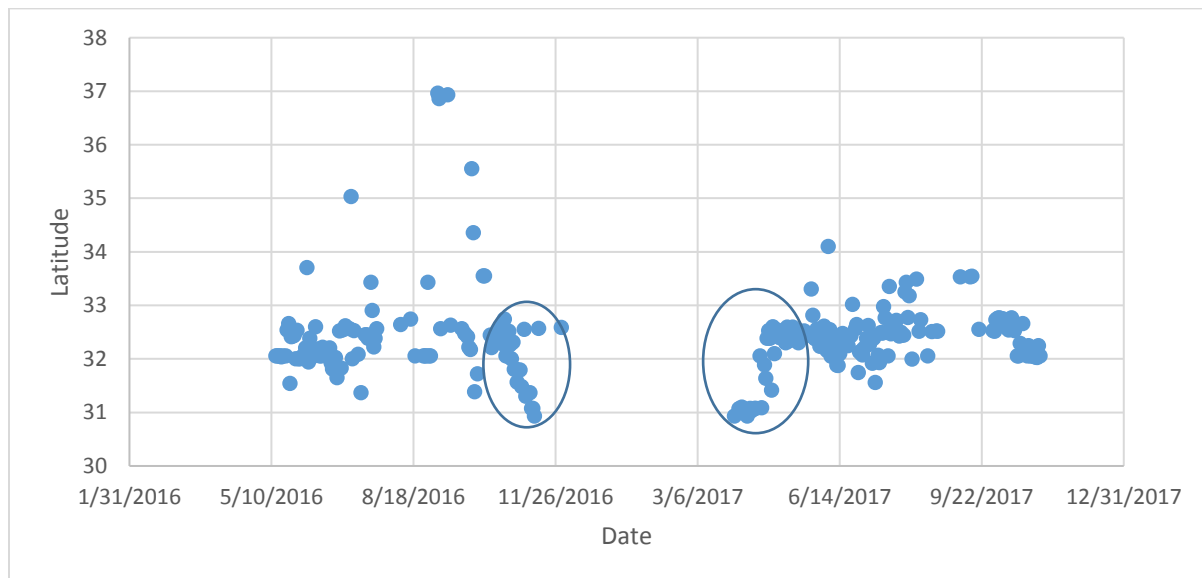


Figure 13. Mean daily latitude of cobia tagged in southern South Carolina.

Cobia were detected moving south in the fall and again north in spring as water temperatures approached 23° and 21°C, respectively. Movements during summer were not as unidirectional. Cobia often moved north to south and south to north several times during May-September, covering as much as 1000 km during a five month period. Cobia #19071 provides a good example of this sporadic movement. This fish was detected off Brunswick, GA during April of 2017 and then detected approximately 250 km to the north off Charleston, SC one month later, spending the next month moving north, south, east, and west among Charleston area receivers. It was next detected 140 km to the south on an artificial reef off Hilton Head, SC in early June where it spent two weeks. Two weeks later it was detected 280 miles to the north off Garden City, SC. After no detections for two months, it was again detected off Garden City, before gradually moving south to Hilton Head during October/November. Despite these sporadic in-season movements by a portion of cobia (32%), there was a general trend of movement from south to north during the middle of the summer. Cobia detections in southern South Carolina peak in May and June and decrease during mid-summer (Figure 14). The peak in central South Carolina lasts until July, while the peak in northern South Carolina (where no cobia were tagged) occurs during July-August. Another peak occurs during October in all three regions, as noted above. This general trend of increased detections suggest that while cobia are likely to move both north and south during the summer, more cobia utilize the northern coast during midsummer through the early fall.

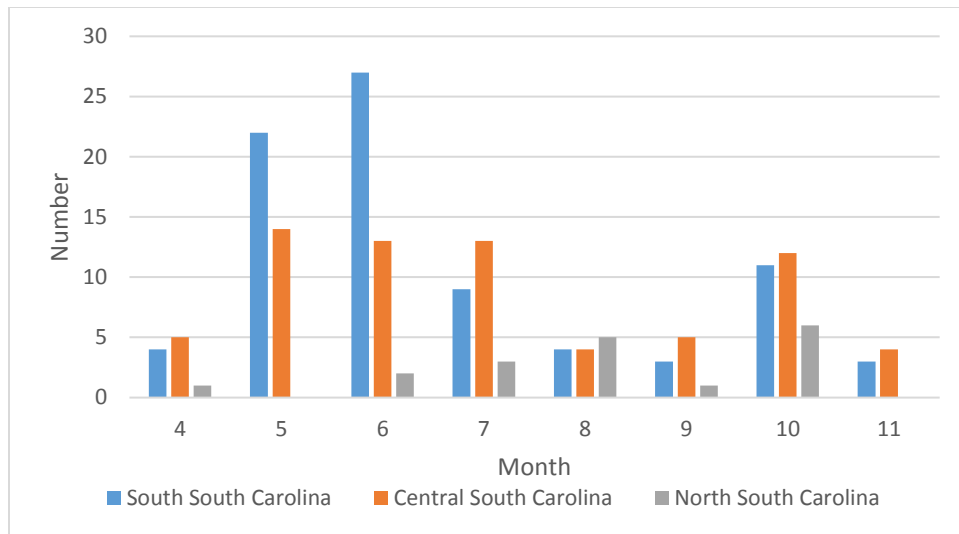


Figure 14. Location of detections within South Carolina by month of cobia tagged in South Carolina.

A subset of South Carolina cobia are known to utilize estuarine sounds in the southern portion of the state as spawning grounds (Lefebvre and Denson, 2012) and this subset is part of a genetically distinct population segment (Darden et al., 2014). We observed the utilization of inshore (defined here as within the bounds of an estuary, as opposed to outside an inlet) habitats by cobia that were tagged both in inshore and offshore locations. A total of 17 cobia tagged in South Carolina were detected on receivers in inshore South Carolina locations. Only 4 of 36 cobia tagged in offshore locations were detected on inshore receivers, while 13 of 15 cobia tagged in inshore locations were detected inshore. The majority of inshore tagging (n=13) occurred in summer 2017, so these fish are expected to provide data for the next three years. Four of the cobia detected in inshore locations were detected in multiple estuaries with three of four having been at large for more than one year. Seven of 15 cobia tagged in inshore locations were detected moving between inshore and offshore locations during the summer, travelling up to 400 km before moving back into inshore waters. No cobia tagged outside of South Carolina were detected on inshore South Carolina receivers.

In addition to the cobia that were detected in inshore South Carolina waters, two cobia tagged offshore of Hilton Head, SC in May of 2016 were detected within the Chesapeake Bay. A69-1901-19032 was tagged at the Betsy Ross Reef on 5/13/2016. After detections on several SC receivers moving north, it was detected on a receiver in the Chesapeake Bay on 6/4/2016. It was also detected in the Bay during July and September. Its last detection of 2016 occurred 20 days later off Brunswick, GA, approximately 1,000 km to the south. The following year, the same fish was briefly detected within St. Helena Sound, SC before moving back into the Chesapeake Bay in May. Another cobia, A69-1901-19092 spent May-October of 2016 exclusively offshore of South Carolina with regular detections each month. The following spring, it was briefly detected offshore of Charleston, SC in April before being detected in the Chesapeake Bay in May and June.

Cobia tagged in South Carolina were detected on virtually every offshore receiver in South Carolina and Georgia that was operational during the study period. The Hilton Head Reefs

Array, which were comprised of the Betsy Ross Reef and Hilton Head artificial reefs, were visited by 35 of 51 cobia tagged in South Carolina (Figure 15). These reefs are well known hot spots for cobia anglers and 26 of the South Carolina cobia were tagged in close proximity to these reefs, meaning that some detections occurred immediately following the tagging event. However, after removing the first week of detections for all fish tagged in proximity to this array in order to mitigate location bias, the receivers still detected a total of 35 SC-tagged cobia. Additionally, 11 cobia that were detected on this array in 2016 were also detected in 2017, providing evidence of site fidelity. Eleven cobia (of 25) tagged at other South Carolina locations have been detected on this array, underscoring the location's importance as cobia habitat. The group of arrays covering offshore locations near Charleston, SC (Stono Line, Dewees Line, Charleston Shipping Channel, and Charleston Mid Shelf) were also frequented by a high percentage of cobia tagged in the Charleston area (8/10), offshore of Hilton Head (16/26) and inside Port Royal Sound (6/15). Other frequently visited arrays include Port Royal Sound and the Brunswick, GA shipping channel.

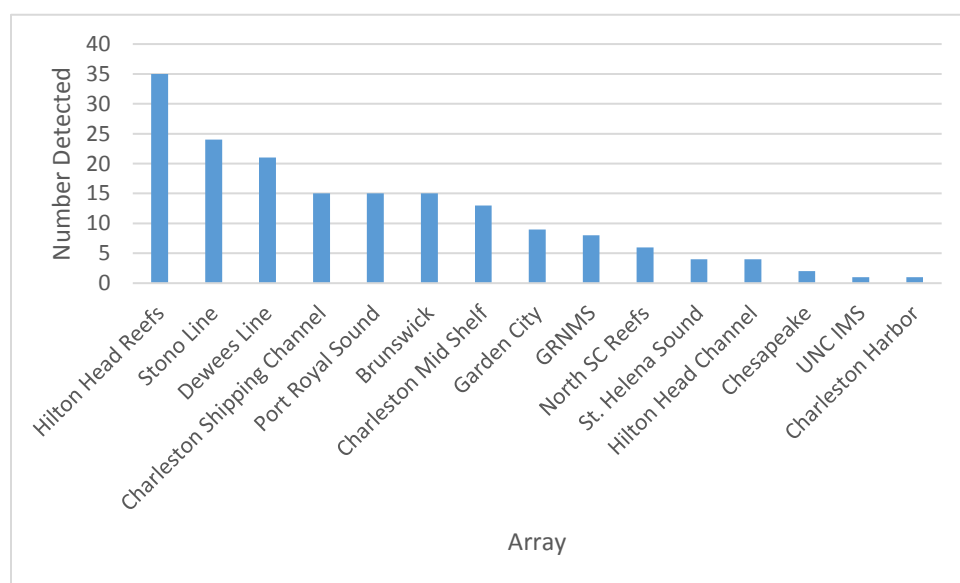
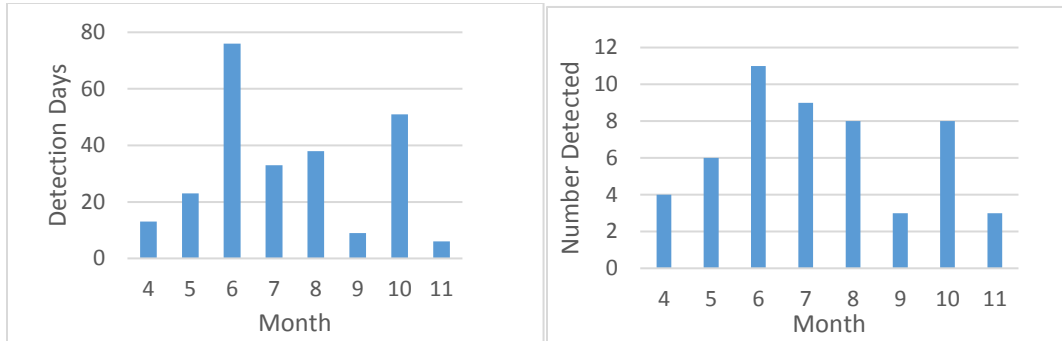


Figure 15. Acoustic array locations utilized by cobia tagged in South Carolina in order of number of cobia detected

Georgia:

The majority of cobia tagging in Georgia occurred in 2016 (15/21, 71%), allowing analysis of 12-16 months of detections for most fish. Almost all, 20 of the 21 (95%), cobia tagged in Georgia waters were detected at some point during the study period, even though none were tagged within 30 km of a receiver. While a higher proportion of Georgia fish were detected, those fish did not generate as many detections as those tagged in South Carolina. Altogether, Georgia fish accounted for 249 detection days (12.5 per detected fish) vs 1,238 in South Carolina (27.5 per detected fish). They were detected on 53 unique stations (7.9 per fish) vs 141 from South Carolina cobia (11.7 per fish). The relative lack of detections as compared to South Carolina-tagged fish made evaluating temporal patterns more difficult, although all tagged cobia in both locations are theoretically at-large and should continue to provide data.

Seasonal availability of Georgia fish was similar to South Carolina fish, with tagged cobia present within Georgia and South Carolina arrays during April-November and completely absent during December-March (Figures 16 and 17). Detection days and the total number of cobia detected peaked in June and remained high through July and August with another peak in October. The pattern of cobia moving gradually north during the summer was not as apparent with Georgia fish as those tagged in South Carolina (Figure 18).



Figures 16 and 17. Detection days (left) and number detected (right) by month of cobia tagged in Georgia.

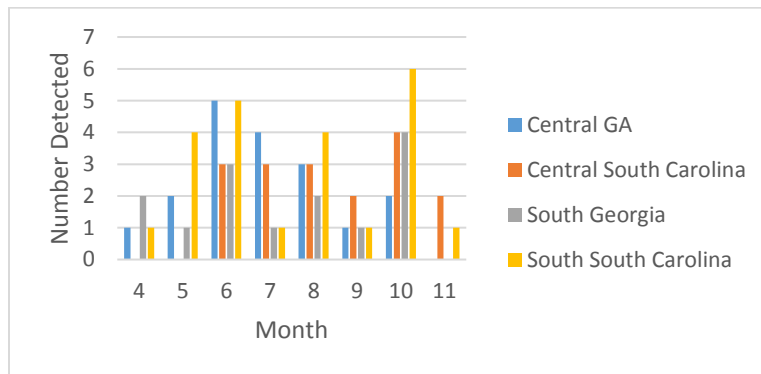


Figure 18. Location of detections from cobia tagged in Georgia by month.

Detections occurred most frequently on the two major arrays off Georgia: Grays Reef National Marine Sanctuary, approximately 45 km offshore of central Georgia and the Brunswick gates extending 28 km offshore of southern Georgia as well as the Hilton Head Reefs array located approximately 35-50 km north of the tagging locations for most Georgia cobia. No cobia tagged off Georgia were detected in an inshore location (Figure 19).

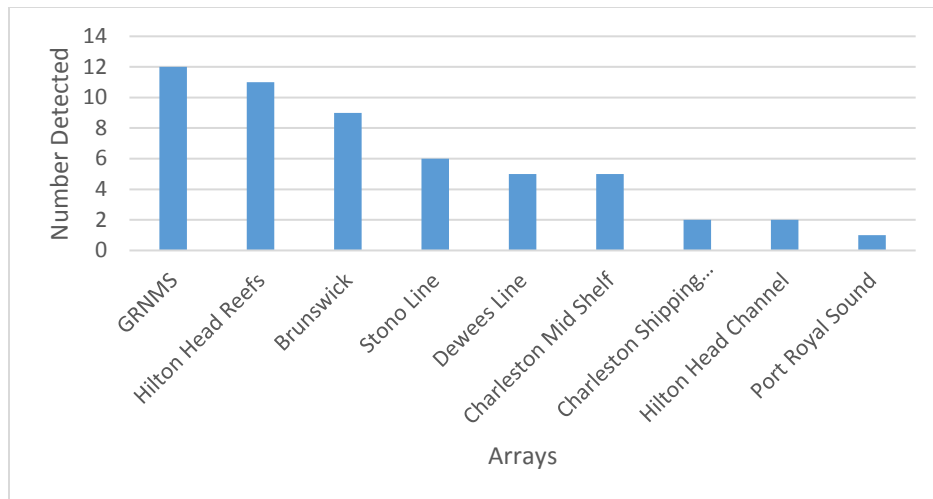


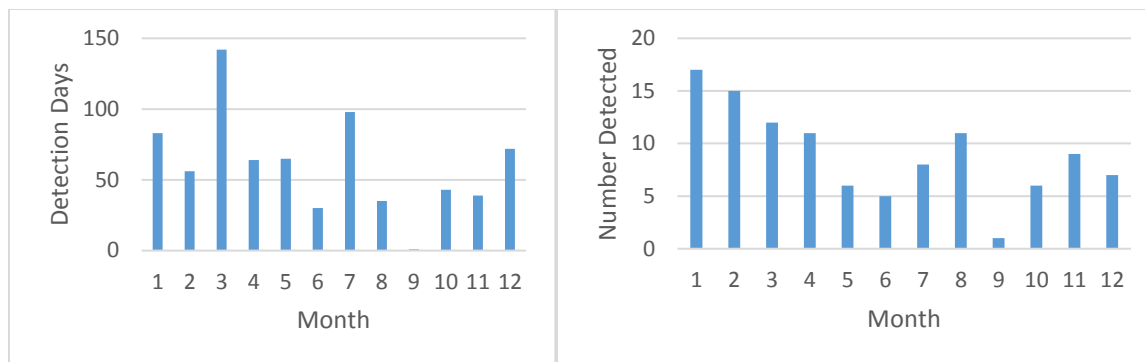
Figure 19. Arrays utilized by cobia tagged in Georgia.

Central Florida:

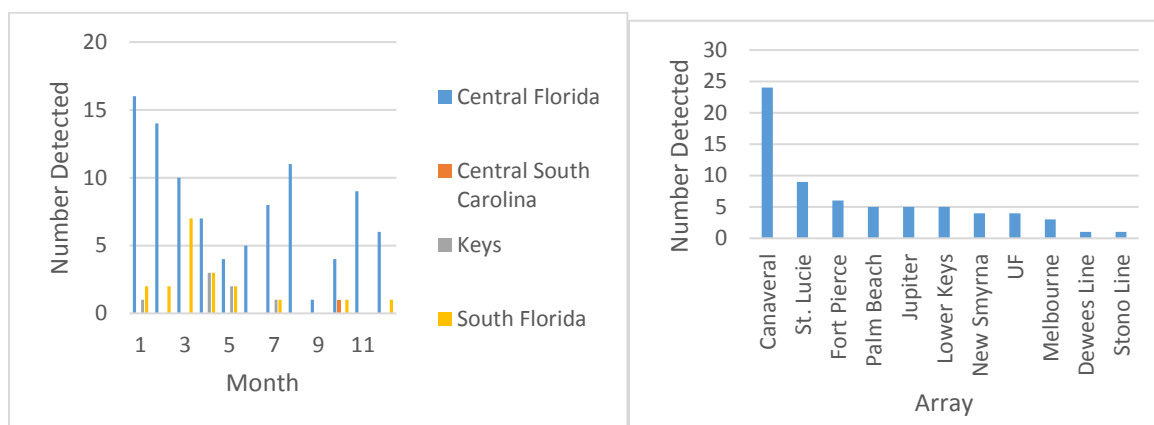
The first cobia was tagged offshore of Cape Canaveral as pilot data for this project in December 2014 along with an additional 5 fish in 2015. As a result, the longest-term movement data comes from this region. Two cobia tagged in December 2014 and July 2015, have accounted for 140 and 132 detection days, respectively which is more than all 21 cobia tagged in Georgia.

Altogether, 25 of 31 cobia tagged off Cape Canaveral have been detected and produced 735 detection days (29.4 days/detected fish). They have been detected on 154 unique receivers to date (6.2 stations/detected fish). Unlike those tagged in South Carolina and Georgia, cobia tagged in this region were detected during every month of the year (Figures 20 and 21). Detections peaked during January and February and were lowest during summer and early fall. Many of the cobia tagged in this region appear to be largely “resident” fish, as 19 of the 25 detected fish were only detected between the central Florida and South Florida receiver arrays throughout the year (Figures 22 and 23). These fish were typically present in the array off of Cape Canaveral during late fall and winter and moved roughly 150 km south during spring in to St. Lucie/Jupiter area. Most of these fish were again detected off Cape Canaveral during July-August, before largely eluding detection during September-October and returning in late Fall.

While long-range movements for most of the Cape Canaveral cobia were not detected, a total of six were detected in the lower Florida Keys array. The pattern of movement was similar for five of the six fish: they were detected in the arrays near Cape Canaveral during winter, then moved down the coast past St. Lucie/Jupiter in early spring. Those five then arrived in the Florida Keys during either April or early May; one other cobia was detected in the Keys during January. No further detection info is available for these fish yet, although one was recaptured by an angler offshore of Fort Pierce, FL in December 2017. In addition to the Florida Keys fish, one cobia tagged off Cape Canaveral in June 2017 was detected offshore of Charleston, SC in October 2017. No other detections for this fish have been recorded.



Figures 20 and 21. Detections days (left) and number detected (right) of cobia tagged in central Florida by month.



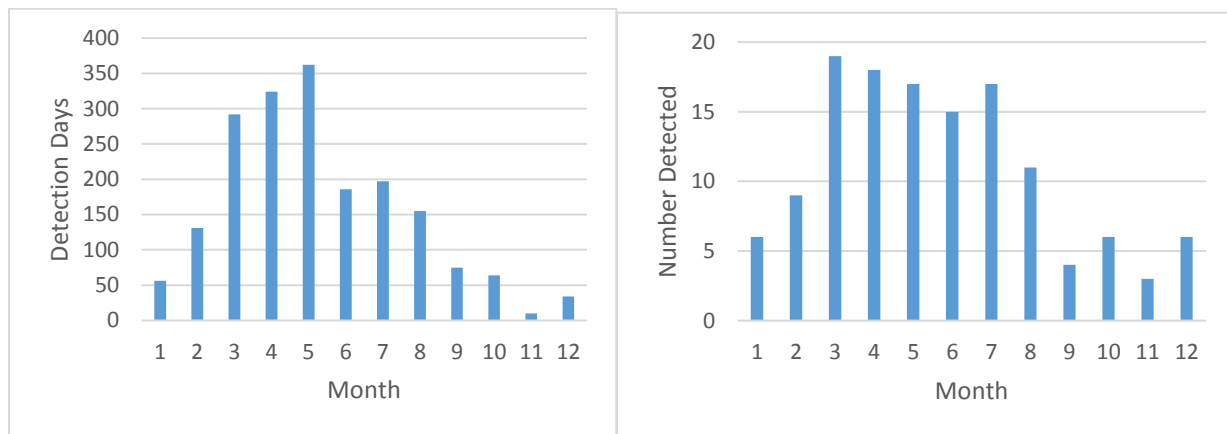
Figures 22 and 23. Location of detections of cobia tagged in central Florida by month.

South Florida:

Most of the tagging efforts in south Florida occurred during 2016 (n=34) with an additional five fish tagged in 2017, allowing us to analyze detections over a period of roughly 18 months for most fish. One cobia tagged in this region was determined to have died or shed the tag following the tagging process due to continuous detections at a receiver site over a period of greater than six months. Overall, 36 of 38 (95%) cobia have been detected to date and cobia tagged offshore of St. Lucie/Jupiter accounted for the largest number of detection days of any area (n=1,898, 52.7 detection days per detected fish). Individual cobia had as many as 225 detections days. Cobia tagged in this area also were detected on the largest number of individual stations (n=204), with a mean of 5.7 stations per detected fish.

As in Canaveral, tagged cobia were detected in every month of the year, with a peak in March-May and fewer in late fall and early winter (Figures 24 and 25). The most popular locations were a series of receiver stations just offshore of St. Lucie Inlet, FL which detected up to 70% of all cobia. Cobia tagged in this region can be defined by one of two movement behaviors: one group was largely resident while another group was more likely to travel longer distances. The resident group accounted for the majority of tagged fish and were either only detected within south Florida (n=15) or a combination of south Florida and central Florida (n=10), a distance of

roughly 150 km (Figure 26). Another seven cobia were detected in the Florida Keys, a distance of roughly 400 km. Similar to some central Florida-tagged fish, cobia were detected moving into the Keys in April and May, with two fish also detected in September. Two of the cobia that were detected in the Florida Keys were later detected in the Gulf of Mexico as far north as offshore of Tampa Bay, approximately 800 km, by late May. One was detected in the Gulf as late as September, before moving through the Keys and south Florida to overwinter around Cape Canaveral. Only four cobia tagged in this area were also detected in either South Carolina or Georgia with one detected off South Carolina during October of both 2016 and 2017 and another off South Carolina and Georgia in October of 2016. The remaining two more were detected moving into Georgia during May before immediately returning to south Florida in June. One of the cobia detected in Georgia also spent December 2016-March 2017 in the area around Grand Bahama before being detected offshore of Cape Canaveral. There was no overlap between cobia that traveled to the Florida Keys and Gulf of Mexico and those that traveled to Georgia and South Carolina.



Figures 24 and 25. Detection days (left) and number detected (right) of cobia tagged in south Florida by month.

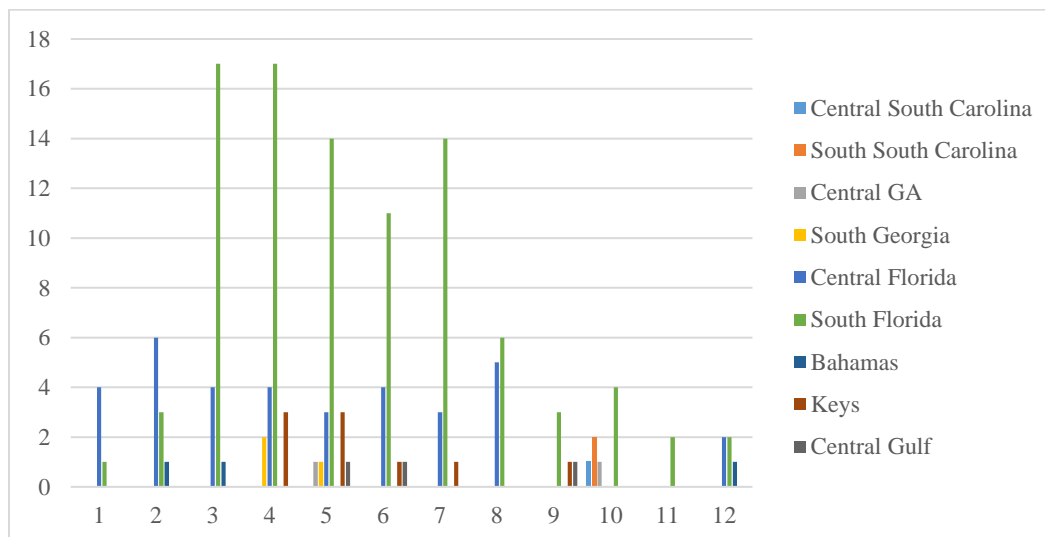


Figure 26. Location of cobia tagged in south Florida by month.

Recaptures

To date, 14 of the 143 cobia tagged for this project have been recaptured by anglers. All but one of these recaptures occurred in the state of Florida and 12 of those were harvested (Table 3). One cobia was recaptured and released in Port Royal Sound, SC during June 2017. Regulatory changes in the cobia fishery over the last few years have likely changed the amount of effort and harvest that have occurred on cobia stocks in the southeastern US and affected the amount and source of returns from our tagged fish. In the region from GA through NY, the cobia fishery was closed to harvest in federal waters on June 20, 2016 and remained closed through the end of the year. Harvest in this region remained closed throughout 2017 while the fishery has remained open in Florida waters for the duration of the project. Most of the recaptures occurred in proximity to where acoustic detections had previously occurred. However, one recapture occurred approximately 45 km offshore of Jacksonville, FL in an area where receiver coverage is non-existent. Another was captured 60 km offshore of Tampa Bay and was not detected moving through the Florida Keys or up the Gulf Coast of Florida. These recaptures provide additional information about the movement of individual cobia. Anglers were provided a reward (either \$25 or a t-shirt) and information about the tagged cobia. Transmitters were recovered from 8 of the 12 cobia harvested cobia.

Table 3. Reported recaptures of acoustically-tagged cobia.

Transmitter	Date	Location	State
A69-9001-19024	9/26/2016	Offshore Cape Canaveral	Florida
A69-1601-54497	5/13/2017	Hillsborough Inlet	Florida
A69-9001-19114	6/11/2017	Port Royal Sound	South Carolina
A69-1601-54494	5/9/2017	Offshore Stuart	Florida
A69-9001-19012	4/3/2017	Offshore West Palm	Florida
A69-9001-19044	11/12/2016	Offshore Fort Pierce	Florida
A69-1601-54499	2/19/2017	Offshore Tarpon Springs	Florida
A69-9001-19013	3/12/2107	Offshore St. Lucie	Florida
A69-1601-54498	9/14/2017	Offshore Sebastian	Florida
A69-9001-20111	6/4/2017	Offshore Cape Canaveral	Florida
A69-9001-19006	12/3/2017	Offshore Fort Pierce	Florida
A69-9001-19008	8/6/2016	Offshore Cape Canaveral	Florida
A69-9001-19056	12/17/2017	Offshore Jacksonville	Florida
A69-1601-54488	12/12/2017	Ft. Pierce	Florida

Sea Surface Temperature

Each detection event was assigned a sea surface temperature (SST) that coincides with the location and time of detection using the methods described above. Mean temperatures at detection were lowest for cobia tagged in central Florida, followed by South Carolina, south Florida, and Georgia (Table 4).

Table 4. Mean sea surface temperatures (SST) at time of detection of cobia tagged in four regions.

Tagging Location	Mean SST (C)
South Florida	27.3
Central Florida	25.2
Georgia	27.5
South Carolina	26.7

Cobia were detected at SSTs that ranged from a daily average of 18.7 to 32.3° C, with the vast majority of detections occurring between 20-30° C (Figure 27). The water temperature profile of different locations within the study area differed drastically. At the Betsy Ross Reef, the most visited receiver location for cobia tagged in South Carolina, the period during which SSTs remained in the range of 20-30° C lasted from mid-April through November (Figure 28). This coincides with the period when cobia tagged in South Carolina were detected. At Cape Canaveral, FL, SSTs remained within this range for virtually the entire year (Figure 29) and cobia were detected year-round. Here, summer upwelling events lead to temporary decreases in nearshore water temperatures in August of 2015/2016. Many of the cobia tagged in this region were captured during these events and charter captains reported large numbers of cobia following giant manta (*Mobula birostris*) on the surface in nearshore waters when temperatures decreased by 2-3°C. The detection data appears to validate this trend as Cape Canaveral area receivers saw an increase in cobia detections during August (Figure 30).

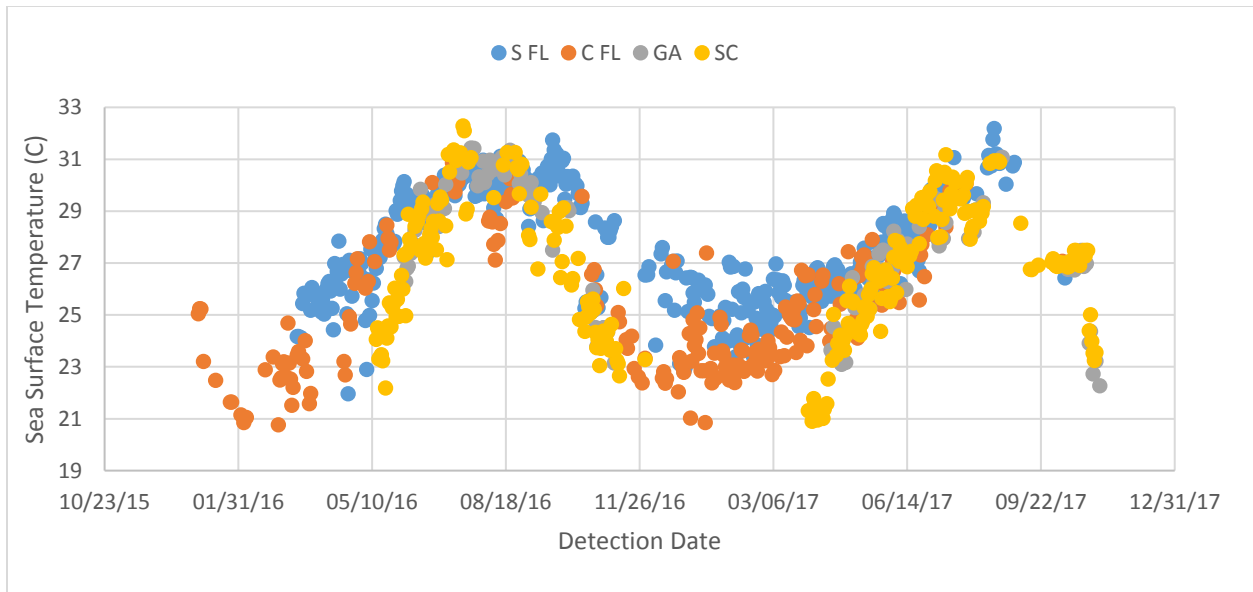
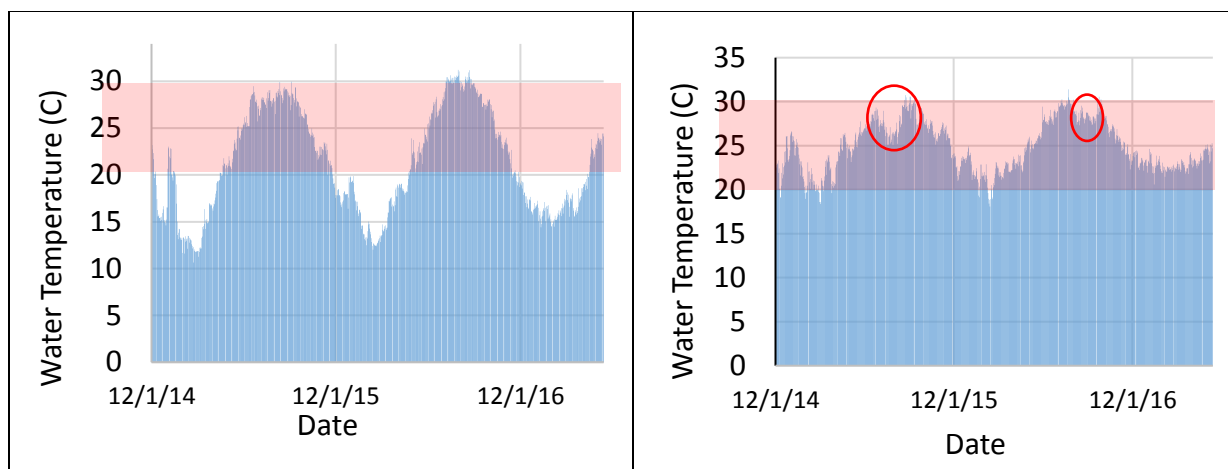


Figure 27. Mean daily sea surface temperatures at detection locations for cobia tagged in four locations.



Figures 28 and 29. Temperature profiles at the Betsy Ross Reef (left) and nearshore Cape Canaveral (right). Red circles indicate an upwelling event with decreased sea surface temperatures.

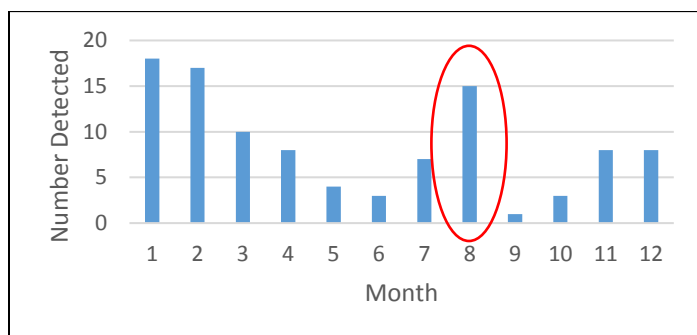


Figure 30. Number of cobia detected in Cape Canaveral arrays by month.

General Linear Models

Latitude and longitude were documented for 128 cobia for 1-109 days each from 2014-2017 (Table 5). Extended exploration of candidate models using GLM with REML revealed that for latitude, the AICc of the alternate candidate models differed by >3 from the model with the lowest AICc score. Therefore, all alternate candidate models for latitude were discarded and the original candidate model with the lowest AICc score was retained. For longitude, two models with AICc score <3 are presented. GLM revealed varying influences of sea surface temperature, year and month detected, and tagging location on detection location (Table 5). Length was not a significant variable in any selected model. Sea surface temperature and month appeared in the best fit models, demonstrating the importance of these variables in the north-south and east-west movements of cobia.

Sea Surface temperature

Cobia were detected at temperatures ranging from 18.3-32.4 C (**Error! Reference source not found.**), with 50% of recorded locations between 25.1 and 28.5 C (Figure 31). Sea surface temperature was a significant predictor of latitude ($p < .0001$) and longitude (Model A: $p = .0083$ and Model B: $p = .0058$). In the best fit models, temperature is negatively related to latitude with a slope of -0.2141 (0.09 SE) and positively related with longitude with a slope of 0.0169 (0.006

SE, Model A; 0.0177 slope, 0.006 SE, Model B). Thus, cobia were more often detected closer to shore at warmer water temperatures, and less often in lower latitudes as water temperatures decreased.

Tagging Location

The spatial effect of tagging location was a significant predictor of latitude ($p < .0001$). Fish tagged in Florida were detected significantly further south compared to fish tagged in Georgia (differences of least squares mean: $t_{(3972)} = -25.26$, $p < .0001$) and South Carolina (differences of least squares mean: $t_{(3972)} = -36.23$, $p < .0001$). Latitude of fish tagged in Georgia and South Carolina were not significantly different (differences of least squares mean: $t_{(3972)} = -1.33$, $p = 0.5462$). Tagging location was selected in one of the final model for longitude, but was not significant (Model B: $p = .1079$).

Month

The temporal effect of month was a significant factor for the prediction of latitude ($p < .0001$) and longitude (Model A: $p < .0001$ and Model B). Fish are predicted to be significantly further south in February, March, and April, followed by a northward migration, peaking in September before returning south (Figure 12). Some of this trend may be driven by the lack of any detections by northern tagged fish (i.e., SC and GA) during December-March. Fish are predicted to be significantly further inshore in April and May, followed by an ocean-ward migration and residence in offshore water for the rest of the year (33).

Year

The temporal effect of year was a significant variable for the prediction of longitude in both selected models (Model A: $p = .0011$ and Model B: $p = .0017$). However, not all years were significantly different from each other, and the result may be an artifact of tagging effort. In model A for longitude, only 2016 and 2017 were significantly different, with tagged fish located closer to shore in 2016 than 2017 (differences of least squares mean: $t_{(3969)} = -3.88$, $p < .0001$). In model B for longitude, only 2015 and 2016 were significantly different from 2017, with tagged fish located closer to shore in 2015 (differences of least squares mean: $t_{(3969)} = -2.15$, $p = .0315$) and 2016 (differences of least squares mean: $t_{(3969)} = -3.76$, $p = .0002$) compared to 2017.

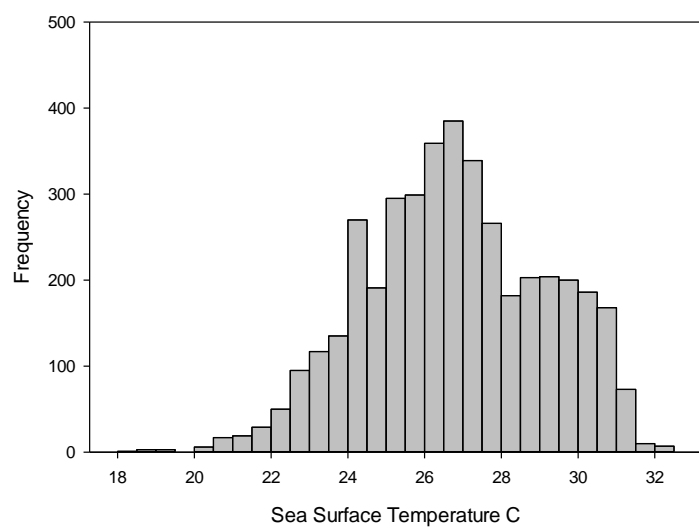


Figure 31. Frequency of cobia detections at sea surface temperatures.

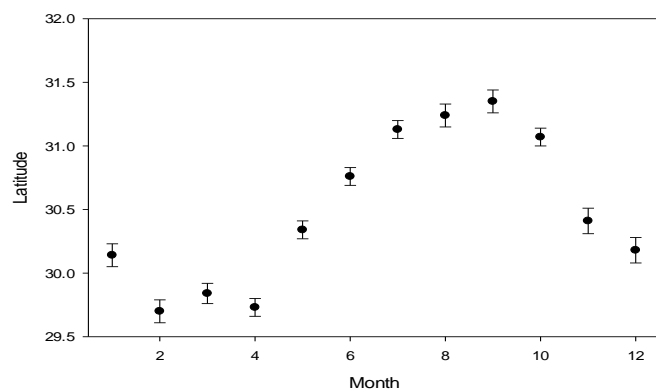


Figure 12. Mean latitude of cobia detections per month. Numbers are presented as the mean response (estimate marginal mean, EMM \pm SE) for each month adjusted for all other variables in the model.

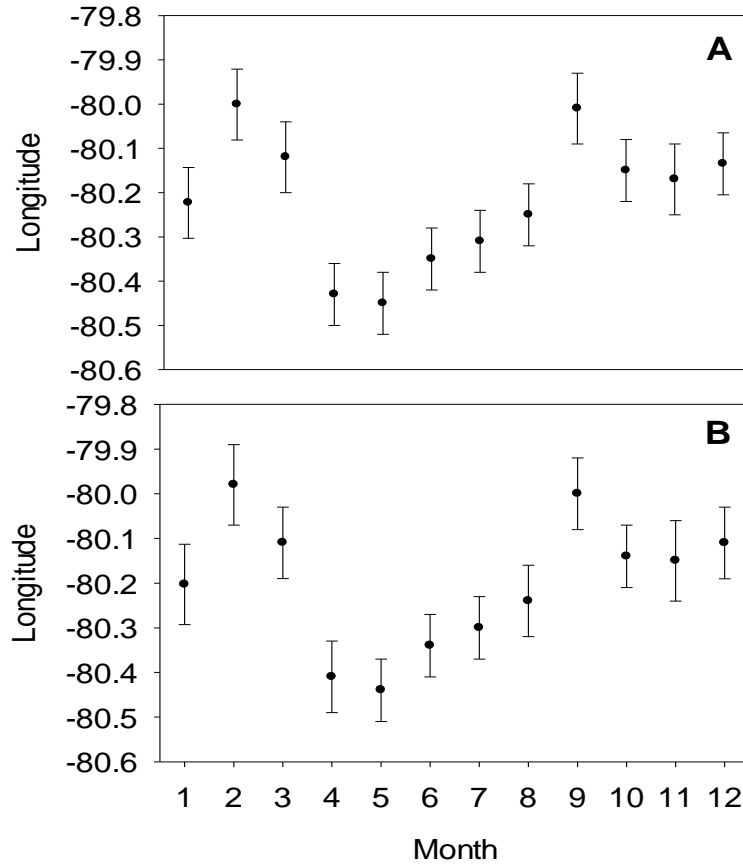


Figure 33. Mean longitude of cobia detections per month. Numbers are presented as the mean response (estimate marginal mean, $EMM \pm SE$) for each month adjusted for all other variables in the model A and B.

Table 5. Best fit model based on lowest corrected Akaike information criterion (AICc) values and significance of main effects specified in the GLMM model for daily location of cobia.

Index	Effects	df	F	P
Latitude	Sea Surface Temperature (C)	1, 3972	458.57	<0.0001
	Month Detected	11, 3972	55.08	<0.0001
	Tagging Location	2, 3972	762.35	<0.0001
Longitude (A)	Sea Surface Temperature (C)	1, 3969	6.98	0.0083
	Year Detected	3, 3969	5.40	0.0011
	Month Detected	11, 3969	22.60	<0.0001
Longitude (B)	Sea Surface Temperature (C)	1, 3969	7.63	0.0058
	Year Detected	3, 3969	5.07	0.0017
	Month Detected	11, 3969	22.78	<0.0001
	Tagging Location	2, 3969	2.23	0.1079

Network Analysis

Network metrics were calculated for networks by month (*Table*). In general, average path lengths increased with more nodes, and when paired with lower average densities, like April, May, and June, it suggests that networks got larger during the summer months (*Table 6*). Centralization values were low, ranging from 0.006-0.0453, suggesting a single network framework with one central area does not represent movement of cobia along the Atlantic coast.

If cobia move randomly along the Atlantic coast, we expect the network to be uniform. However, the networks suggest heterogeneous spatial use with some exchange. Minimal exchange, limited to 1-3 fish, across the Florida/Georgia border was observed April, May, June and October (*Figure 34*). In general, cobia moved more freely within subgroups consisting of Georgia/South Carolina and central/south Florida/Florida Keys. Network density was lowest in September and November, when complete segregation of cobia into discrete units occurred. Due to minimal detections of tagged fish

in SC and GA during the winter months, networks from December-March do not reflect movement within those areas, and instead solely focus on Florida.

Table 6. Network metrics for cobia movement by month.

Month	Number of nodes	Density (D) Mean \pm SD	Centrality (In)	Centrality (Out)	Path Length Mean \pm SD
January	28	0.16 \pm 0.69	0.0088	0.0082	3.6 \pm 1.9
February	24	0.24 \pm 0.93	0.0052	0.0057	2.3 \pm 0.9
March	31	0.28 \pm 1.18	0.0091	0.0066	2.5 \pm 1.0
April	57	0.10 \pm 0.65	0.0048	0.0041	3.6 \pm 1.5
May	74	0.10 \pm 0.94	0.0006	0.0006	4.1 \pm 1.9
June	61	0.10 \pm 0.58	0.0065	0.0061	4.0 \pm 2.1
July	54	0.11 \pm 0.70	0.0036	0.0032	4.4 \pm 2.4
August	39	0.13 \pm 0.67	0.0051	0.0045	3.3 \pm 1.5
September	36	0.08 \pm 0.46	0.0051	0.0057	2.5 \pm 1.3
October	49	0.12 \pm 0.46	0.0089	0.0095	3.3 \pm 1.5
November	31	0.08 \pm 0.34	0.0369	0.0453	2.4 \pm 1.1
December	23	0.20 \pm 0.61	0.0131	0.0112	2.6 \pm 1.3

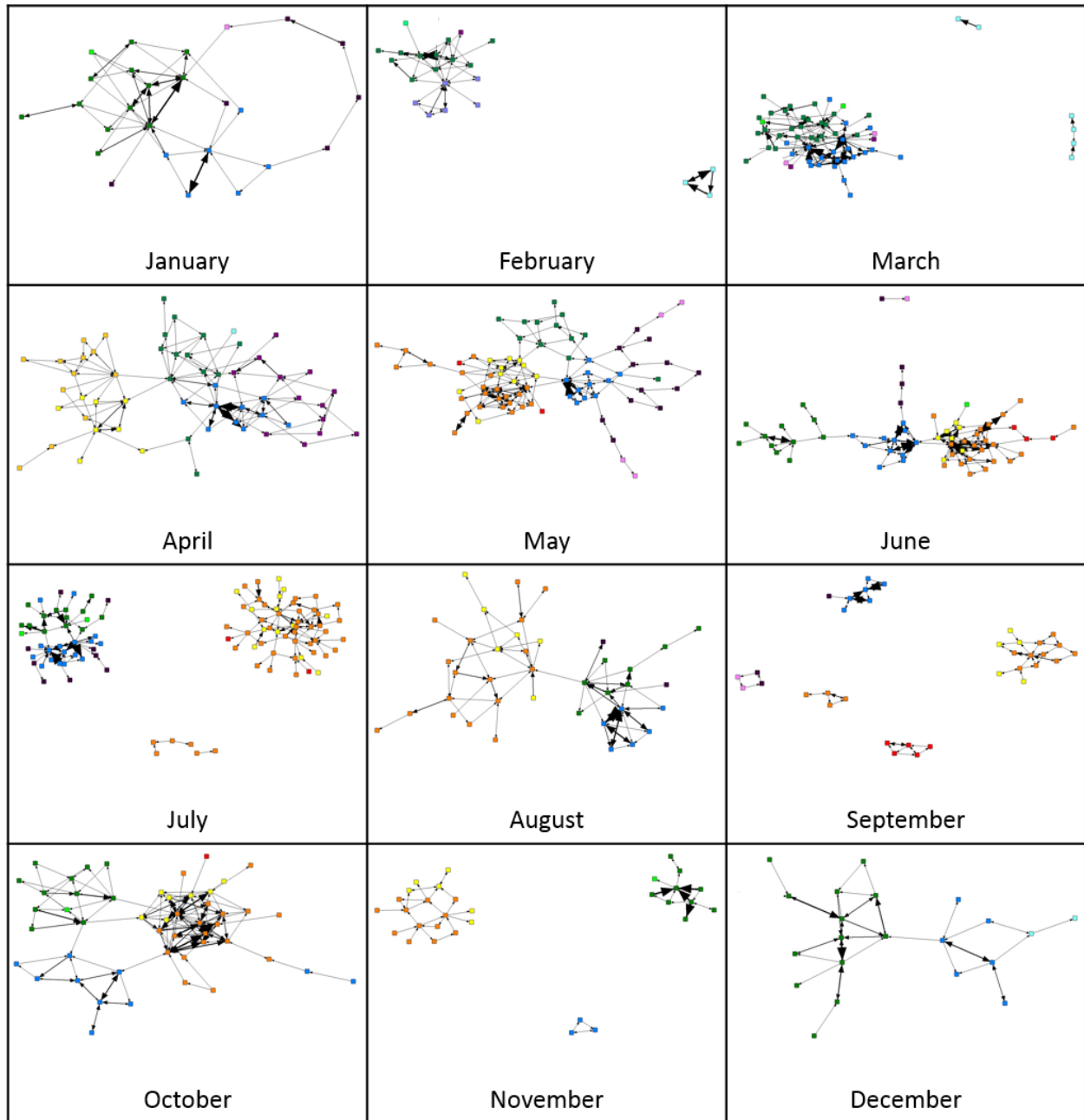


Figure 34. Networks of cobia movement by month. Layout is based on theoretical layouts, where locations that are more closely associated are pulled together and dissimilar areas are pushed apart.

Genetic Analysis

Including our prior dataset, genotypes for 2,355 cobia samples ranging from the panhandle of Florida to South Carolina were available to evaluate genetic population structure around the current stock boundary. Samples were only included if they were successfully genotyped at 8 or more loci, had known collection locations, and were collected during spawning seasons defined for each state: South Carolina and Georgia – April to July, and Florida – March to August. Only a single duplicate sample and 39 cultured fish occurred within the original dataset. No large family groups (>3) were present within the dataset and only 12 fullsib pairs were identified

($p=1.0$); therefore, no confounding effects from family structure are expected in further analyses. For the initial analyses, the dataset was partitioned into 10 geographic sections based on natural latitudinal breaks in the collection data. Collection locations included the following:

FLW – West coast of FL from Pensacola to Panama City ($n=45$)

FLS – Florida Keys ($n=8$)

FLE1 – East coast of FL from Boynton to Jupiter ($n=36$)

FLE2 – East coast of FL from St. Lucie to Ft. Pierce ($n=238$)

FLE3 – East coast of FL from the Cape Canaveral area ($n=77$)

FLGA – Ranging from Jacksonville, FL to Brunswick, GA ($n=16$)

GA – Offshore Savannah ($n=34$)

SCO1 – Offshore Port Royal Sound, SC ($n=430$)

SCO – Offshore, SC but not specific collection location ($n=615$)

SCI – Inshore the Port Royal Sound, SC estuary ($n=834$)

The initial STRUCTURE and pairwise F_{ST} analyses with all data included supported a genetically distinct South Carolina Inshore population (Figure 35; F_{ST} s ranged from 0.009 to 0.013, $P=0.001$). As such, the South Carolina Inshore samples were removed from the iterative AMOVA analyses which suggested that the strongest significant break ($F_{ST}= 0.0067$, $p=0.003$) among the groupings occurred when all the Florida locations were grouped together and the FLGA, Georgia, and South Carolina offshore populations were grouped, explaining 0.68% of the variation in the dataset. A second grouping scenario was also significant ($F_{ST}= 0.0062$, $p=0.016$), occurring when the FLGA samples were grouped with the rest of the Florida samples and Georgia was grouped with the South Carolina offshore samples, explaining 0.62% of the variation. Based on these results, three additional AMOVA analyses evaluated if a three genetic group scenario better explained the partitioning of genetic variation. The analyses included the FLGA location as a third group separate from the northern Georgia/South Carolina group as well as the southern Florida group, a combined FLGA and Georgia third group, and a combined FLGA and Cape Canaveral (FLE3) group. The last scenario (FLGA with FLE3) did not partition a significant amount of variation among groups, and the scenario with the FLGA location alone being the strongest by explaining a similar proportion of variation as the two group model (0.68%, $F_{ST}= 0.0068$, $p=0.003$). Initial pairwise F_{ST} comparisons also supported homogenous groupings in Florida ($p>0.173$) and offshore South Carolina ($p=0.552$) with the FLGA and Georgia samples not different from locations in either group ($p>0.470$). Additionally, the second level STRUCTURE analyses resulted in $K=2$ with a gradation occurring between the Florida and Georgia/South Carolina offshore samples (Figure 36). Final combined pairwise comparisons confirmed significant differences between a grouping of all Florida samples and a grouping of Georgia and South Carolina Offshore samples ($F_{ST}= 0.005$, $p=0.001$) as well as distinctness of the South Carolina Inshore samples from both ($F_{ST}= 0.002$, 0.007 , $p=0.001$). Due to the lower samples sizes from some of the Florida collection locations, deviations from Hardy Weinburg equilibrium (HWE) was evaluated (GenAlEx) to verify no substructure was being masked within this region. Only a single locus was out of HWE ($p<0.001$) in the combined Florida dataset supporting the grouping. Therefore, the results suggest the stock boundary, recognizing that biologically this represents a mixing zone with limited reproductive exchange, is occurring somewhere within a range north of Cape Canaveral, FL to south of northern Georgia, which is consistent with the current stock boundary along the Atlantic coast.

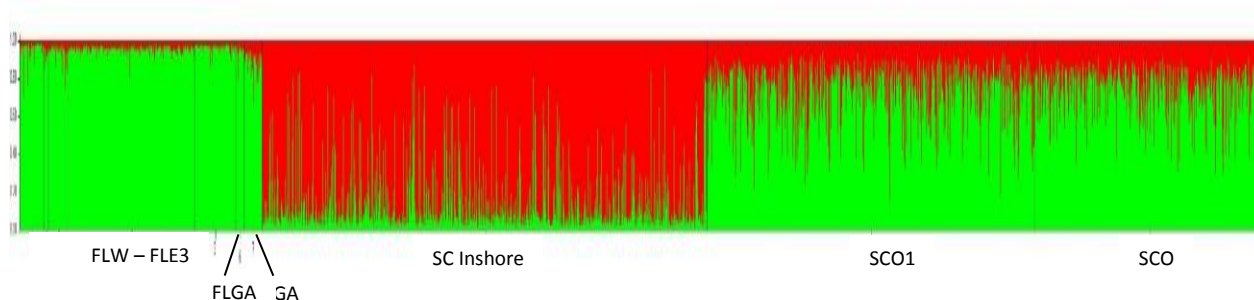


Figure 35. Results of initial STRUCTURE analyses indicating genetic distinctness of the South Carolina Inshore population ($K=2$). Collection location from left are FLW, FLS, FLE1, FLE2, FLE3, FLGA, GA, SCI, SCO1, SCO. Each vertical bar on the graph represents an individual with colors representing proportion of ancestry assigned to each genetic group.

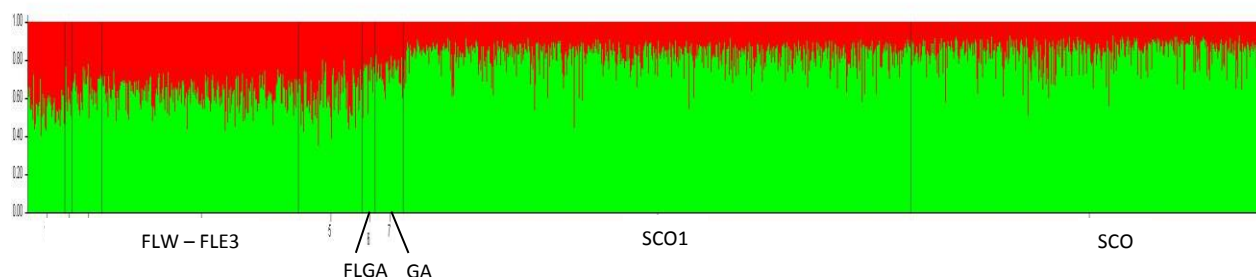


Figure 36. Results of second level (SC Inshore samples excluded) STRUCTURE analyses indicating $K=2$ populations in the dataset. Collection location from left are FLW, FLS, FLE1, FLE2, FLE3, FLGA, GA, SCO1, SCO. Each vertical bar on the graph represents an individual with colors representing proportion of ancestry assigned to each genetic group.

Products and Outreach

Throughout the project, we have engaged with our partner stakeholders throughout the southeastern US coast during the implementation as well as afterwards to communicate project results. Four presentations have been given at scientific meetings during the project period; the first by Joy Young at the Florida Atlantic Coast Telemetry Network annual meeting (2016). The second was Matt Perkinson at the SCDNR Marine Resources Division's Annual Conference (2017) which shared project goal, design, and preliminary results with both local scientists and resources managers, followed by Karl Brenkert at the national meeting of the American Fisheries Society in Tampa, FL (2017) which also conveyed preliminary project results with a larger audience of scientists and resource managers. Finally, Jim Whittington provided a recap of the project at the Florida Atlantic Coast Telemetry Network meeting in 2017. Most influentially, both the acoustic tagging and genetic data from this project will be provided for use in the upcoming SEDAR Stock Identification workshop later this spring (April 2018). Finally, two manuscripts are in preparation for publication from the project results; planned for submission later this spring.

Discussion

The origins of this project were rooted in the data workshop analysis during SEDAR 28, the last stock assessment for South Atlantic and Gulf migratory group cobia. During those proceedings, all available data relating to cobia migratory patterns and stock structure were reviewed to determine the boundary between the two major US stocks using the best available data. The major sources of data used were combined long-term external tagging datasets of cobia tagged throughout the southeastern US (Perkinson and Denson, 2012) along with a multistate analysis of genetic structure (Darden, 2012). Both data sources refuted the management boundary between migratory groups in the Florida Keys. The external tagging datasets suggested that a mixing area occurs along the east coast of Florida with Cape Canaveral likely included within this zone. Cobia tagged in the Cape Canaveral region were recaptured to the north (i.e., NC and VA) as well as to the south and in the Gulf of Mexico (Figure 37). The genetic data suggested that the mixing zone between stocks occurs somewhere between St. Lucie Inlet on the southeast coast of FL and Hilton Head, SC (due to a lack of samples between these locations). During the data workshop, the boundary was established at the FL/GA line. Research recommendations from the Review Workshop included increased tagging efforts, specifically electronic tagging, to refine our understanding of the stock boundary and migratory patterns in general. With the increased receiver coverage in the southeast, we looked to acoustic telemetry as a method that could yield more spatial and temporal data points for each individual fish than traditional tagging. The resulting telemetry data along with an expanded evaluation of genetic structure could be used with the available tagging data to provide a more comprehensive account of cobia stock structure.

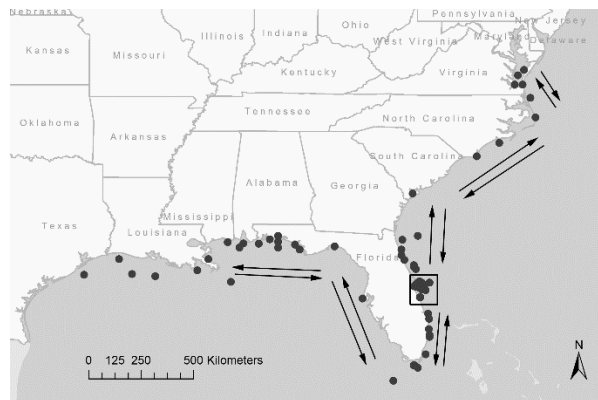


Figure 37. Recapture location of cobia externally-tagged off Brevard County, FL (Cape Canaveral) compiled for Perkinson and Denson, 2012. Arrows indicate general movement from the tagging area.

To our knowledge, the acoustic telemetry methods we utilized had not been applied to cobia to date. While receiver arrays have drastically improved in recent years, they still cover a very small percentage of the open ocean and the pelagic nature of cobia means that we could not guarantee that we would be able to detect our tagged animals. Furthermore, while previous experience with handling adult cobia suggested that they are a hardy species with ample room in the body cavity to carry the acoustic transmitter, there was also no guarantee that they would handle the surgical process and make a quick recovery. Despite these concerns, we were able to tag and release a few cobia to provide pilot data before the official start of this project. The

surgical methods proved to provide for a robust condition at release and these first fish began providing detection data as soon as the next receiver download cycle occurred. Overall, the 91% rate of detection of tagged cobia suggested that cobia cover large amounts of open ocean and that many receiver arrays are sited in ideal locations that are regularly utilized by cobia (i.e., artificial reefs, navigational buoys, etc.). Improvements in receiver infrastructure along with the long-term nature of the acoustic tags used in our project mean that we will continue to reap the benefits of these tagging efforts over the next 2-3 years and increase our understanding of seasonal migratory patterns.

As we began to compile detection data from cobia tagged during this project, a pattern began to emerge: there was very little exchange of cobia between South Carolina/Georgia and Florida. In fact, no cobia tagged in South Carolina or Georgia have been detected by a receiver in Florida to date, with one recaptured by an angler offshore of Jacksonville in December 2017. However, during most of the study period, no receivers were positioned in northern Florida waters between Brunswick, GA (31.1 N latitude) and New Smyrna Beach, FL (29.1 N latitude). A series of five receivers was established off St. Augustine, GA in 2017 and additional receiver deployments are planned for 2018, but no detections are available at this time. Therefore, tagged cobia could have potentially moved into northeast Florida and avoided detection. However, the receiver arrays around Cape Canaveral and the St. Lucie/Jupiter areas are quite robust and it is unlikely that tagged cobia would have moved into central or south Florida within 30 km of the coast without detection. Cobia tagged in this region utilized much of South Carolina/Georgia nearshore waters from April-November and had generally overlapping distributions (Figure 38). During December-March, they were completely undetected; had cobia initiated a southern migration along the coast of Florida as waters cooled, they surely would have been detected in Cape Canaveral, the northernmost area in Florida where nearshore water temperatures remain within cobia's biological tolerances (20°C+) throughout the winter. Detection patterns suggest that South Carolina and Georgia tagged cobia either moved offshore or offshore and south into deeper waters where receiver coverage is not available. Anecdotal evidence of cobia overwintering along the continental shelf of South Carolina and Georgia, and the recapture well offshore of Jacksonville, FL support this idea.

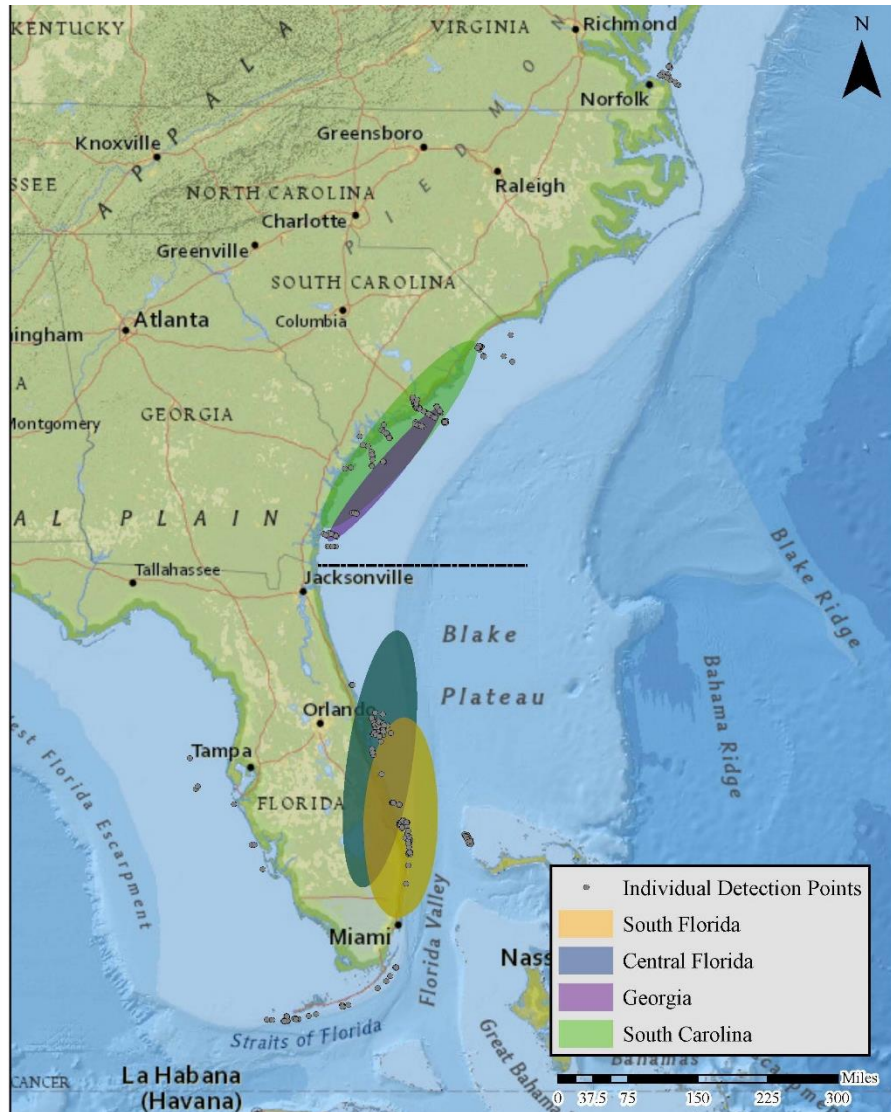


Figure 38. Directional distribution of cobia tagged in each of four regions at one standard deviation.

Cobia tagged in central and south Florida also had very little interaction with South Carolina and Georgia. Only four cobia tagged in south Florida and one in central Florida were briefly detected in South Carolina and Georgia with the vast majority (93%) of cobia tagged in Florida only being detected in Florida. In general, cobia tagged in central and south Florida had overlapping distributions with two apparent groups displaying different migratory behaviors. The majority (72%) of detected cobia that were tagged in this area appeared to be largely resident fish and were only detected along the central and southern coasts of Florida. This group was detected throughout the year, but were most present near the coasts from January-July and least detected during the fall and early winter, when some fish may have moved into deeper waters where receiver arrays are not present. Unlike in South Carolina and Georgia, coastal water temperatures in central and south Florida typically remain within the biological tolerances of cobia throughout the year, making resident behavior possible. A smaller group (21%) of detected cobia tagged in central and south Florida were detected moving out of these areas and into the Florida Keys,

mostly during April and May with isolated instances of cobia moving into the Gulf of Mexico as far north as Tampa, FL. While receiver coverage in the Florida Keys is fairly robust, coverage along the west coast of Florida is more porous, meaning that additional tagged cobia could have potentially migrated into the Gulf of Mexico without detection.

The behaviors we observed through our telemetry work largely agree with those observed in the comprehensive evaluation of available external tag data with some differences. As seen in Figure 37, a small portion of cobia that were externally tagged around Cape Canaveral were recaptured as far north as the Chesapeake Bay ($n=5$, 6.5%) with additional recaptures occurring off North Carolina ($n=4$, 5.2%). Our acoustically-tagged fish did not mirror this trend, with only one fish recaptured as far as South Carolina and no detections into North Carolina or Virginia. While there is currently minimal receiver coverage off the coast of North Carolina, the US Navy maintains a robust array in the Chesapeake area and it is unlikely that tagged cobia could elude detection (Figure 39). However, the externally-tagged cobia that were recaptured to the north were exclusively tagged in Jan-March. The majority of central Florida tagging in our study occurred during July-August (78%) during coastal upwelling events that saw cobia following Manta Rays on the surface. It is possible that tagging cobia during midsummer could effectively limit the odds of selecting fish that were apt to undertake a seasonal migration to the north. The shift in the central Florida cobia fishery to target these midsummer aggregations appears to be a recent one (Eric Reyier, personal communication). Both the acoustic tagging and external tagging datasets showed strong evidence of residency among a majority of cobia tagged in central and south Florida. Additionally, cobia tagged in central and south Florida that were detected moving into the Florida Keys (the previous management boundary) were never detected north of Cape Canaveral. Similarly, of the 182 recaptures of cobia externally-tagged in the Florida Keys, no recaptures occurred north of Cape Canaveral. Acoustic and external tagging datasets for South Carolina largely agree as well, with most externally-tagged cobia being recaptured back in South Carolina. However, 8.8% of cobia externally tagged off South Carolina were recaptured off north or central Florida, as opposed to none of our acoustically-tagged fish. Recapture descriptions for central Florida are not specific, so it is not possible to tell if these recaptures occurred in nearshore or deep offshore waters. No external tag data is available for Georgia for comparison.

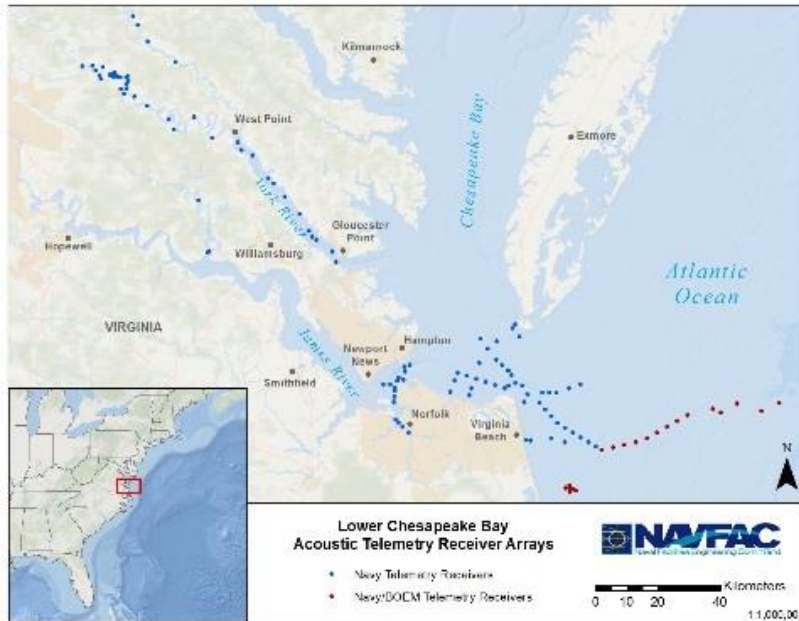


Figure 39. US Navy and Navy/BOEM acoustic receiver arrays in Chesapeake Bay.

The predominant modeling and network analysis findings were that 1) movement subgroups of cobia were found in Georgia/South Carolina and all of Florida, 2) exchange across the Florida/Georgia border was minimal and only occurred in April-June and October, and 3) connectivity of cobia along the Atlantic Coast is highest in the spring and summer, from April to June and August. Overall, these findings alone do not refute the current stock boundary at the Florida/Georgia border and strongly suggests the mixing zone is north of Cape Canaveral.

The predicted southerly movement of cobia, lowest from December to April, may be a result of a dominance of detections in south and central Florida during the same period. Cobia were not detected in Georgia/South Carolina from December-March and no movements were documented to suggest that fish in these regions migrated south. Thus, while the predicted average position is more southerly, detections from cobia north of the Georgia border are needed to confirm this movement pattern. Movement was more likely to occur within subgroups of Georgia/South Carolina and Florida than between subgroups. There were no significant differences in movements of fish between South Carolina and Georgia, suggesting this acts as a subgroup of cobia. In Florida, cobia moved from central to south Florida,

The additional genetic samples obtained during this project substantially increased the spatial context of analysis for cobia along the east Florida and Georgia coasts. With prior genetic analyses limited by a single sample collection location along the Florida east coast (St. Lucie) and none in southern or central Georgia, conclusions included a mixing zone occurring somewhere in the area north of St. Lucie, FL and southern South Carolina (i.e., SC/GA border). The results of the current analyses are consistent with both prior genetic analyses with a refined conclusion that a mixing zone occurs along the Atlantic coast somewhere north of Cape Canaveral and south of central Georgia. These results are also consistent with the acoustic tagging data in that a biological boundary exists within the range of the northern Florida/southcentral Georgia along the Atlantic coast and the occasional ‘straying’ observed in

the tagging data support the observed lower genetic differentiation statistics in cobia. Continued data collection from the acoustically tagged fish will provide a wealth of future data on the movement patterns of Atlantic coast cobia that may help better define the geographical bounds of the mixing zone. Additional genetic samples from the northern Florida and southern Georgia areas would be informative as well for inclusion in our dataset, although large samples will likely be necessary to tease apart patterns within the mixing zone. These data represent a highly valuable data resource that will be important and immediately relevant in the upcoming SEDAR Stock Identification Workshop this spring. The continued incorporation of additional data tools into the evaluation of cobia life history is a positive and powerful direction for successfully management of this species.

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