Investigating the seasonal migration of Cobia (*Rachycentron canadum*) and the influence of temperature on movement ecology

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SEDAR95-RD-07

March 2024

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Honors Thesis
Presented to the College of Arts and Sciences
Cornell University
in Partial Fulfillment of the Requirements for the
Biological Sciences Honors Program

by

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May 2020

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Abstract

The pelagic Cobia (*Rachycentron canadum*) is the target of a popular recreational fishery from the Gulf of Mexico to the mid-Atlantic that shifts seasonally as these fish migrate along the east coast of the United States. Variation in migratory behaviors, when consistent through time, drives the formation of genetic substructure within a population. Movement ecology research works in combination with other stock delineation techniques, like genetic analyses, to indicate such population structure. Intrapopulation variability in spatio-temporal distributions has significant consequences for fishery encounter rates. Temperature is a proposed driver of this seasonal movement in Cobia. In this study, we used passive acoustic telemetry to investigate the migration of Atlantic Cobia. Our results corroborated the timing and spatial distribution of the described north-south Cobia spawning migration in which North Carolina waters serve as a migration corridor and Chesapeake Bay in Virginia is a major spawning site. We characterized seasonal differences in space use — longitudinal variation in path, with Cobia travelling nearshore in the spring and dispersing offshore in the fall — and other intrapopulation variation in migratory behavior (i.e., distinct subsets of Cobia overwintering offshore in North Carolina waters and spending the spawning period in marine habitat south of Chesapeake Bay) that will inform management of the fishery and future interpretation of genetic studies. Following our preliminary analysis, the influence of temperature (i.e., warm, thermally stable continental shelf habitat facilitating offshore overwintering in North Carolina) on the migration of this highly migratory species — and thus on a lucrative fishery — is better understood.

Introduction

The pelagic Cobia (*Rachycentron canadum*) is the target of a popular recreational fishery from the Gulf of Mexico to the mid-Atlantic that shifts seasonally as these fish migrate along the east coast of the United States (Shaffer and Nakamura 1989). For animals with such extensive seasonal movements, the temporal location of important life history events has substantial influence on the resilience and underlying structure of populations. Seasonal migration defines the ecological context and the spatio-temporal distribution of key life history events associated with growth, reproduction, and survival (e.g., feeding, spawning, wintering) and the level of human exploitation (e.g., fishing pressure) experienced over the life cycle of an individual (Lowerre-Barbieri et al. 2019). As a result, the spatial pathways between these events — the movement ecology — are as consequential for the resilience and structure of populations as the life history events themselves.

Variation between the migratory behaviors exhibited by a population, when consistent through time, indicates probable substructure within the population and may drive the formation of such substructure (Metcalfe 2006). Specifically, spatial or temporal isolation of spawning events, in which only a subset of a larger population contributes genetic material, drive the accumulation of distinct population structure (Lowerre-Barbieri et al. 2017; Lowerre-Barbieri et al. 2019). Distinct movement ecology of this kind is a key driver of differentiation even in migratory species that exhibit long distance dispersal and encounter no clear physical barriers to mixing (*Kajikia audax*, Mamoozadeh et al. 2019). Finer details of Cobia movement ecology, despite the species' heavily-fished status, are not yet understood. Cohorts with distinct migratory patterns (*Morone saxatilis*, Secor 1999) and genetic sub-groups intermingled with the larger stock (*Sebastes mystinus*, Burford et al. 2011; Darden et al. 2013) may exist undetected. In this study, we use the movement of Cobia between life history events mapped over time and space to expose distinct migratory patterns, identify probable units of population substructure, and link these to temperature as a physical driver of behavior.

Atlantic Cobia complete an annual northward spawning migration in the spring and early summer, progressing from the Southeast U.S. to Chesapeake Bay (Shaffer and Nakamura 1989), an important spawning estuary (Joseph et al. 1964). Euryhaline Cobia are batch spawners (Shaffer and Nakamura 1989) and use estuarine and marine habitat from as early as April into September (Shaffer and Nakamura 1989; Brown-Peterson et al. 2001; Lefebvre and Denson 2012; Resley et al. 2005), with peak spawning during May in South Carolina, June in North Carolina, and July in Virginia (Brown-Peterson et al. 2001; Smith 1995). For Cobia inhabiting Chesapeake Bay and the waters of the mid-Atlantic during spawning, site fidelity and philopatry — with distinct portions of the population either occupying the Bay (i.e., Chesapeake group) or the continental shelf region (the ocean group) (R. Gallagher, personal communication) — have been hypothesized as a plausible characterization of distinct migration patterns observed over consecutive spawning periods (Darden et al. 2013; Richards 1977).

The full path of Cobia migration along the southeast United States is not well understood. Though the timing and overall latitudinal pattern have been described and important spawning sites identified, overwintering sites and the routes used between distinct life history events remain to be investigated (SEDAR 28 2013). In the fall, a majority of the Atlantic Cobia stock migrates south towards Florida overwintering grounds (Shaffer and Nakamura 1989). Off South Carolina's coast, a shift offshore during colder months has been described with Cobia returning inshore during the spring (Perkinson et al. 2018; Shaffer and Nakamura 1989). Smith (1995) proposed that Cobia overwinter between Cape Fear in North Carolina and Cape Canaveral in

Florida at depths between 30 and 75 meters. More recently, limited records from pop-off satellite tags have shown that Cobia appear along the continental shelf break along the coast of North Carolina during the winter, indicating that these fish overwinter in deeper offshore habitat (Hammond 2008; Crear et al. 2020b).

Temperature is a proposed driver of Cobia movement ecology and migratory behavior — specifically during colder months in which it is suggested that Cobia seek out warmer waters and may shift offshore (Shaffer and Nakamura 1989) — although the relationship of temperature and Cobia behavior is not yet well studied in wild populations. Temperature is often a key physical factor guiding the spatio-temporal distributions of fish populations (*Acipenser oxyrinchus oxyrinchus*, Breece et al. 2017; *Cynoscion nebulosus*, Song et al. 2019; Lowerre-Barbieri 2019). A eurythermal species, Cobia occur in a wide temperature range from 16.8 to 32°C (Shaffer and Nakamura 1989) and have been found capable in laboratory studies of tolerating temperatures in or above the predicted end-of-century range (28 to 32°C) for the rapidly warming Chesapeake Bay (Crear et al. 2020a; Sun and Chen 2014; Sun et al. 2006).

In their migration along the United States east coast, Cobia encounter a marine environment characterized by significant temperature variation. During the northward spawning migration to Chesapeake Bay, Cobia pass Cape Hatteras, the site of a notable thermal boundary where the warm, saline Gulf Stream moves away from the continental shelf and water masses of dramatically different temperatures are in contact (McCartney 2013; Rasmussen et al. 2005). Below Cape Hatteras, the Gulf Stream follows the continental shelf break north. Due to this current, surface temperatures offshore in proximity to the shelf break are warmer and exhibit less variability than those from nearshore waters (Stéfansson et al. 1970).

Cobia are the target of a productive recreational fishery in the western Atlantic (Smith 1995; Shaffer and Nakamura 1989). Although Cobia are caught as a non-target species by commercial hook-and-line and net fisheries, recreational catch accounts for the majority of Cobia landings (Shaffer and Nakamura 1989). Cobia are also caught frequently as bycatch by commercial shrimp trawls and longlines (SEDAR 28 2013). In 2016, the estimated recreational Cobia catch exceeded the annual catch limit (ACL) resulting in a closure of the recreational fishery and prompting calls for improved understanding of the population structure and movement ecology of this species (NOAA 2017).

Under the management authority of the South Atlantic Fishery Management Council (SAFMC), the Cobia population of the U.S. east coast is divided in two: an Atlantic stock and Gulf stock (SEDAR 2013). The boundary between these stocks was first delineated as the Dade-Monroe county line in Florida (SAFMC 2011). These genetically distinct stocks (McDowell et al. 2018) were later divided at the Georgia-Florida line (SEDAR 2013) with a contentious mixing zone extending south of this boundary to Cape Canaveral, Florida (Perkinson and Denson 2012; Perkinson et al. 2019; Darden et al. 2013).

The substructure of these distinct stocks is not well understood; however, work by Darden et al. indicated distinct population structure from Cobia sampled inshore during spawning in Virginia and South Carolina and proposed the presence of local subpopulations, dispelling the notion of stock homogeneity despite the highly migratory nature of Cobia. A homogeneous group composed of Cobia sampled inshore in Virginia and offshore in North Carolina during this period was identified, although this may be the result of intermingling of subgroups during the spawning migration (Darden et al. 2013). The dispersal capabilities of planktonic larvae and migratory adults facilitate mixing (Shaffer and Nakamura 1989), but unseen physiology or behavioral drivers could precipitate genetic isolation and differentiation (Metcalfe 2006). Within the Atlantic stock, recent studies yield conflicting conclusions about the validity of this purported subpopulation structure. While evidence of genetic differentiation has been cited as an indicator of isolated offshore groups (Perkinson et al. 2018; Perkinson et al. 2019), recent genetic analyses renew support for a homogeneous Atlantic stock (R. Gallagher, personal communication). The presence of genetically and perhaps spatially distinct subpopulations would necessitate changes in management to account for differences in exploitation and resilience between these groups (Lowerre-Barbieri 2017). By utilizing observed Cobia movement ecology to inform analyses of these genetics results, a better picture of Cobia stock structure can be obtained.

Although North Carolina and Virginia account for the largest proportion of annual recreational Cobia landings, Cobia stock assessments are limited north of South Carolina (SEDAR 2013). This reflects a mismatch between research on the ecology of Cobia in this region and the distribution of fishing pressure. The waters off the coast of North Carolina and Virginia are thus an area of need for research into Cobia migration and stock structure. We studied the movement of Cobia within North Carolina State University's (NCSU) acoustic array and arrays in Virginia, to: 1) characterize the timing of the Cobia spawning migration; 2) identify distinct migratory groups within the larger Atlantic population; 3) compare the magnitude and spatial distribution of seasonal movement between these regions in order to discern migratory pathways; 4) describe the seasonal spatio-temporal distributions of Cobia on a finer scale during key life history events (i.e., spawning, wintering) and 5) begin to explore the influence of temperature (sea surface temperature (SST) and bottom temperature) on Cobia movement ecology and migration timing.

Material and Methods

Study Region and Duration — This study was conducted as part of ongoing research investigating the migration of Atlantic Cobia using passive acoustic telemetry out of the Applied Ecology Laboratory at the NCSU Center for Marine Sciences and Technology led by Dr. Jeffrey Buckel. A portion of my movement analysis is presented in my graduate mentor Riley Gallagher's M.S. thesis. This study spans late spring 2018 to late summer 2019, including two peak spawning seasons, defined as the summer months, June through August, and one winter period from December 2018 through February 2019. Each telemetered Cobia has an implanted tag which emits a sonic signal that is detected and logged by nearby acoustic receivers, each of which is equipped with an omnidirectional hydrophone with a range of approximately 500 meters. These stationary receivers are deployed in arrays managed by single organizations and, in combination, are part of larger coast-wide acoustic telemetry networks (i.e., the FACT, ACT, and iTAG networks). For this study, we analyzed detections of Cobia tagged by North Carolina State University collected directly from the NCSU acoustic array, part of the Florida Atlantic Coast Telemetry (FACT) network (Young et al. 2018; Young et al. 2019), and those provided by member institutions of the Atlantic Cooperativity Telemetry (ACT) network (Figure 1).

Telemetry Tagging — Beginning in 2018, we tagged Cobia through the spring and summer in North Carolina, both offshore and in the Pamlico Sound, and in Chesapeake Bay. We caught Cobia with hook-and-line using natural bait or artificial jigs and relied on the assistance and expertise of local charter captains. Fight times averaged five minutes and 10 seconds but ranged from less than a minute to 29 minutes and 15 seconds. Once at the boat, hooked Cobia were held submerged in a landing net prior to being brought on board in order to assess the qualitative condition of the fish. Each captured Cobia in good condition (i.e., no gut hooking, no bleeding gills, active during capture) was transferred to a cradle on board for tagging. In total, seven Cobia sustained severe fishing injury and were sacrificed for use in ongoing investigation of diet and age and growth. We recorded fork length (FL, mm; Figure 2), capture location coordinates, fight time (from hooking until the fish is netted), tagging duration (the time in which the fish is out of the water), and release condition (Heupel and Simpfendorfer 2002) for all individuals. Cobia were designated for telemetry tagging (FL greater than 760 mm) or conventional tagging only (FL less than or equal to 760 mm). In 2019, this minimum FL was decreased to 690 mm to increase the number of tags deployed.

For tagging, Cobia were secured in the surgery cradle dorsal side down to expose the ventral implantation site, and we used a hose to irrigate the gills with seawater for the duration of the procedure. We followed surgical implantation protocols for telemetry tagged fish (Wagner et al. 2011), first injecting local anesthetic (1.5 mL sodium bicarbonate and 1.5 mL lidocaine) before using a sanitized scalpel to make a small incision through the skin and musculature. We then inserted a uniquely coded acoustic tag (Vemco V16-4H, 69 kHz, 30-90 s random delay) into the abdomen of the fish. Deviating from Wagner et al. with the guidance of NCSU College of Veterinary Medicine staff, we closed incisions with skin staples (Conmed Reflex One stapler, 35 mm wide) rather than sutures. Surgery times ranged from two minutes to 15 minutes and 27 seconds with an average of five minutes and 52 seconds. The implanted transmitters have a four-year battery life and emit a signal every 60 seconds. The sonic signals are detectable within approximately 500 meters of a receiver and are recorded as a detection of an individual fish and denoted with the unique tag identification number along with the date and time.

We also tagged all Cobia with two red nylon wire core tags, an internal anchor (FM-95W) and dart (FIM-65, Floy Inc). Anchor tags were inserted into an incision in the posterior abdomen and dart tags were inserted in the dorsal musculature. All Cobia were released within 100 meters of their catch location. Immediately after tagging, Cobia were released headfirst, typically swimming away rapidly. Cobia exhibiting low activity were held underwater with a lip-grip tool with the boat under power until capable of swimming.

Following the same telemetry tagging procedures as above, Virginia Institute of Marine Science (VIMS) researchers implanted Cobia captured in Virginia waters with NCSU telemetry tags in 2018 (n = 20) and 2019 (n = 10) as part of a collaborative effort. A total of 98 Cobia were tagged (Table 1).

North Carolina Receiver Sites — We used the North Carolina State University acoustic array to detect tagged Cobia in Pamlico and Bogue Sounds, along the barrier islands of North Carolina, and offshore on the continental shelf. North Carolina State University's acoustic array, spanning the state's coastline and extending from inshore waters onto the continental shelf, stretches across the north-south Cobia migration corridor. Originally this array consisted of 30 acoustic receivers deployed inshore from Emerald Isle to Barden's Inlet from 2015 to 2017. In the beginning of our study, the array was expanded offshore to include receivers suspended in the water column from the Aids to Navigation (ATON) buoys extending 9 miles offshore from Beaufort Inlet and off Cape Lookout. Receiver sites varied in depth from 3 to 66 meters. The receivers in estuarine habitat — inlets and Bogue and Pamlico Sounds — and deployed from ATON buoys are Vemco VR2W models. Receivers in the former group are secured at the base of channel markers and floated with a small buoy to remain near vertical in the water column. ATON receivers are weighted and suspended from the buoy with steel cable. Vemco VR2AR model receivers were used at artificial reefs and deployment sites far out on the shelf (Figure 1). These use a distinct deployment mechanism: the receiver and an attached buoy are sunk with sacrificial ballasts. When signaled with a mobile VR100 hydrophone, the acoustic release mechanism is triggered allowing the receiver to surface for retrieval and download of its datalogger record.

North Carolina State University manages the routine maintenance of this acoustic array. VR2W receivers are retrieved quarterly and VR2AR type receivers biannually to download recorded detection data and conduct routine maintenance. These receivers are then either redeployed, given enough battery life and good condition (i.e., minimal biofouling, antifouling tape and paint intact), or replaced with prepared receivers. This yields near continuous coverage at each site. In the laboratory, we removed biofouling from the exterior of retrieved receivers, downloaded the data, installed a new battery, and replaced the antifouling treatments in preparation for redeployment. Ahead of major hurricanes (Florence 2018, Dorian 2019), receivers attached to ATON buoys and channel markers were removed temporarily. Three receivers were lost over the course of the study.

Virginia Receiver Sites — The combined acoustic arrays of VIMS (Weng et al. 2018) and the United States Navy provide dense coverage of Chesapeake Bay, a vitally important spawning estuary, and the waters outside of it, with receivers extending 68 kilometers offshore. Acoustic receivers in this region reach a maximum depth of 32 meters, shallower than the North Carolina shelf sites. The receivers stationed in estuarine habitat are positioned in the York and James Rivers and in a concentrated array within the mouth of the Bay. A chain of receivers extends latitudinally from the mouth of the Bay forming a gate on the shelf.

Temperature Data — The receivers used in this study log hourly Celsius temperature measurements. Therefore, the seafloor acoustic release receivers deployed off North Carolina's coast provide a unique bottom temperature record due to their position. For analysis, we extracted the depth at the coordinates of each receiver and grouped them into nearshore (shallower than 30 m), offshore (between 30 and 50 m), and shelf (deeper than 50 m) groups. To obtain a time series of ocean surface temperature, we accessed NASA's OceanColorWeb database maintained by the Ocean Biology Processing Group. The MODIS (Moderate Resolution Imaging Spectroradiometer) aboard the Aqua satellite provides a publicly available record of ocean conditions. We extracted average monthly satellite-recorded surface temperature at a resolution of 4 kilometers between latitudes 34.02° and 35.14° North and longitudes 75.66° and 76.44° West, corresponding to the region occupied by NCSU acoustic release receivers, over the period from August 1, 2018 to June 1, 2019.

Analyses and Figures — We used R version 3.6.2 (R Core Team, 2020), specifically utilizing tidyverse packages 'dplyr' and 'ggplot2' (Wickham et al. 2020) to conduct data analysis and generate plots. We consolidated detection data provided by FACT and ACT network members with our downloaded detections, exported using Vemco VUE software, into a combined database. We standardized detection timestamps into Coordinated Universal Time (UTC) and defined the release location of each tagged Cobia as the first detection. To map receiver locations, we used ArcGIS (ESRI 2020). We manually removed detections for two tagged fish from all analyses. Each of these Cobia was detected at numerous consecutive 60 second intervals at a single receiver, a pattern characteristic of a dead fish. To obtain bathymetry data, we queried the NOAA ETOPO database using the 'getNOAA.bathy' function from the 'marmap' package in R (Pante, Simon-Bouhet, and Irisson 2019). We extracted the mapped data from 33° to 38° North and 74° to 78° West at a cell resolution of 10 minutes.

Abacus Plot — We plotted detections of each unique transmitter identification number through time and coded them by state, to indicate latitudinal movements, and by depth category (i.e., inshore, nearshore, offshore, shelf) (Figure 3). Since the ranges of receivers used in this study have limited overlap except within Chesapeake Bay, we approximated the location of a fish at the time of detection by receiver location. We defined the spawning period as the summer, June through August. This centers on July, the peak spawning month in Virginia (Brown-Peterson et al. 2001; Smith 1995).

Network Analyses — We used network analyses to visualize the migration of Cobia by showing network use, seasonal movement patterns, and connectivity between North Carolina waters, Virginia waters, and Chesapeake Bay. This provides a detailed picture of movement and space use at multiple scales to inform the temporal patterns shown in the abacus plot. We used R packages ‘igraph’ (Csardi and Nepusz 2006) and ‘rgl’ (Adler and Murdoch 2020) to produce spatial networks of detections with weighted edges. We generated networks for Virginia receivers only (Figures 4-6), North Carolina receivers only (Figures 7-10), and the arrays of both states together (Figure 11) over the period from May 1, 2018 to May 1, 2019. At present, offshore detections recorded by the United States Navy in Virginia are absent for the 2019 spawning period and will be incorporated once received. We chose to restrict our network analyses to a one-year period excluding the second spawning period to avoid a skew towards inshore space use resulting from the missing data. For each of the three regions (i.e., North Carolina, Virginia, both states), we analyzed the detections occurring in three-month windows to yield a network for each season. For each network, we created an edge list by grouping consecutive detections of each unique transmitter (i.e., an individual Cobia) then removed multiple sequential detections of a fish at the same receiver, thereby retaining only movements to new locations, and tallied these detection pairs for each seasonal period. To display the relative importance of the network edges, we defined edge width (line thickness) of the links between receiver pairs by the magnitude of utilization (i.e., number of moves). More movements between two receivers will result in a thicker line between them in the network. We calculated global edge density — the fraction of available pathways utilized by tagged Cobia — to give a quantitative metric of the space use shown in each network (Jacoby et al. 2012, Lédée et al. 2015). A large edge density indicates a higher saturation of movement over space. In Virginia, the tight clustering of two groups of receivers, the southernmost receivers and those at the end of the Cape Charles peninsula, results in the reduced appearance (thinner edge width) of movements involving these receivers.

Temperature Plots — To display temperature regimes experienced by tagged Cobia and their spatial distribution during key periods of their annual movement, we mapped the locations of detections at acoustic release receivers in North Carolina during the A) spawning (June through August) and B) winter periods (December through February). At each acoustic release receiver site, the size of the plotted circles on these maps indicates the number of detections recorded at each receiver over that time. The average bottom temperature recorded by the receiver for the given time period (spawning or winter) at each site is denoted by the color of the circle (Figure 12).

To visualize the temperature ranges available to tagged Cobia, we plotted all seafloor-deployed acoustic release receiver and satellite temperature profiles together to compare the overall seasonal variation between surface and bottom temperatures over the entire study region (Figure 13). We then plotted the same satellite and receiver temperature data separately denoting nearshore, offshore, and shelf groupings defined by depth (less than 30 m, greater than 30 m, greater than 50 m respectively) (Figure 14). For the same time series, we generated an abacus plot with the detections at the acoustic release receivers grouped by depth (Figure 15). We plotted detections of all fish — different unique transmitter identification numbers — and overlaid shaded regions indicating spawning and winter periods. All detections recorded at each receiver are color coded to denote the depth grouping of that receiver. This plot was aligned with bottom and surface temperature profiles over the same time period.

Results

Movement Timing — The detections of tagged Cobia exhibit a clear migratory pattern corresponding to the peak spawning period (Figure 3). Cobia tagged in North Carolina were first detected in that state. Detections in Virginia waters and Chesapeake Bay start at the beginning of the peak spawning period in June in 2018, though slightly earlier in 2019. After these initial detections, Cobia remained in Virginia, resulting in repeated detections, until late August and early September at the end of the spawning period. These fish then return to North Carolina in the interim period between the spawn and winter. During the first spawning period, two Cobia (28153, 28110) exhibited behavior that was an exception to this pattern. These fish remained in North Carolina during the 2018 spawning period and were not detected in Virginia at any point. During the 2019 spawning period, a different small cohort of Cobia were only detected in North Carolina after being newly tagged. Ultimately, there will be more offshore detections in Virginia when data become available for receivers in that location. It is likely that the addition of these data will reduce the number of Cobia only detected in North Carolina during the second spawning period as some of these individuals might have registered detections offshore in Virginia that are masked at present. It is also of note that distinct vertical lines of detections in the abacus plot are generated by large groups of fish appearing on the array simultaneously and represent tagging events, one in North Carolina preceding the 2018 spawning period (light green shading), one in Virginia during that spawn, and one in North Carolina preceding 2019 spawning. Cobia tagged before the 2018 spawning period in North Carolina — excluding the two fish detected in North Carolina during the spawning period — were detected soon after in Virginia while those tagged in Chesapeake Bay during the 2018 spawn were detected later in North Carolina. This suggests that tagging did not interfere with migratory behavior.

In winter, a weak but persistent pattern of detections was observed in North Carolina waters (Figure 3) that consisted entirely of Cobia that were detected in Virginia during the spawning period, a mix of proposed Chesapeake Bay and ocean philopatric groups (Gallagher 2020, unpublished). During this time, Cobia were detected in North Carolina primarily in offshore and shelf regions moving in proximity to the deepest shelf-group receivers more often than in any other seasonal period. We recorded no winter detections in Virginia and presume that tagged fish that go undetected in the winter period progressed south of North Carolina to overwintering grounds.

Virginia Seasonal Movement Patterns

- In Virginia, no Cobia were detected over the winter.
- During the spring, tagged Cobia heavily trafficked the receivers at the mouth of Chesapeake Bay and those extending offshore. No movement occurred within the Bay and rivers (Figure 4).
- The summer network in Virginia showed the highest movement density out of the seasons within the Bay and the largest proportion of movement between available receiver pairs. Movements among the receivers outside the Bay and limited use of the York and James Rivers occurred during this period. The highest density of movement occurred just within the mouth of the Bay on the estuarine side of Cape Charles (Figure 5).

- In the fall, the limited movement within the Bay was generally concentrated on the inland side of Cape Charles and the mouth of the Bay. We observed no movement in the rivers. Movement within the array outside the estuary was comparable to that shown in the summer (Figure 6).

North Carolina Seasonal Movement Patterns

- During the winter, tagged Cobia were detected at fewer receivers than in other seasons and showed movement between nearshore, offshore, and shelf receivers. The most extensive movement was observed between a pair of nearshore and offshore receivers south of Ocracoke. The highest traffic at deep shelf receivers occurred in this period but indicates only limited movement (Figure 7).
- In the spring, the greatest amount of movement detected in all seasons was observed among nearshore receivers along the barrier islands of Pamlico Sound. The most movement was detected between the receivers off of Cape Lookout and south of Cape Hatteras. During this same period, limited detections were recorded by offshore, shelf, and nearshore receivers, including those stationed north of Cape Hatteras (Figure 8).
- During summer, Cobia moved between nearshore, offshore, and shelf receivers but none were observed north of Cape Hatteras. During this period, there was a low magnitude of movement, but a large relative proportion of receivers were involved in these movements (Figure 9).
- In fall, limited movement was observed at the nearshore, offshore, and shelf receivers, a large relative proportion of the array. We did not track any movements at receivers north of Cape Hatteras (Figure 10).

North-South Migration — The winter network including both Virginia and North Carolina detections is effectively identical to the network restricted to North Carolina as there were no detections in Virginia during this period (Figure 11A). The highest magnitude of movement between North Carolina and Virginia occurred during the spring with frequent detections along the barrier islands of Pamlico Sound and between nearshore receivers north of Cape Hatteras and receivers in the mouth of Chesapeake Bay (Figure 11B). During the summer, movement between North Carolina and Virginia continued at a lower density than in the spring (Figure 11C). In the fall, movement between North Carolina and Virginia increased as movement in the Bay decreased and a greater proportion of receivers registered consecutive detections throughout the array in North Carolina (Figure 11D). We detected the highest amount of latitudinal traffic in fall and spring — with spring exhibiting the greatest magnitude of any season — but the longitudinal distribution of movement differed between these seasons (Figure 11B, 11D). Movement primarily occurred nearshore in the spring with key nodes along the barrier islands of the Pamlico Sound, north of Hatteras, and at the mouth of Chesapeake Bay. In the fall, we observed increased offshore detections in Virginia and North Carolina and reduced traffic nearshore in North Carolina (Figure 11B, 11D).

Temperature Influence on Movement — Mapped Cobia detections (Figures 12) showed proximity to the bottom-deployed acoustic release receivers during both the 2018 spawning period (657 detections of eight fish) and the winter period (1939 detections of six fish). During spawning, the average bottom temperatures were warmer (21 to 25°C) and detections occurred at nearshore, offshore, and shelf receivers. In winter, average bottom temperatures were cooler (17 to 22°C) and Cobia were again detected in nearshore, offshore, and shelf regions. A shift offshore is apparent between these periods; Cobia were detected at the deep shelf group receivers with greater frequency in the winter, and a larger proportion of fish were detected offshore than nearshore. The bottom temperatures at which detections occurred over the duration of our record ranged from as low as 16.2°C and as high as 27.9°C.

Surface temperatures at all locations fluctuated dramatically between seasons, spanning a greater annual range than bottom temperatures (Figure 13). Bottom temperatures indicated less inter-seasonal variation compared to surface temperature with similar bottom and surface temperatures in the winter and cooler bottom temperatures in the summer (Figures 13). Nearshore temperatures, both at the surface and the bottom, showed the most inter-seasonal variability. Offshore and nearshore waters exhibited near identical patterns of seasonal variability in bottom temperature, but offshore winter surface temperatures were warmer than those in nearshore waters. The deepest receivers (the shelf group) had low variability between seasons and recorded the warmest winter temperatures, consistently above 15°C (Figure 14).

Overall, intermittent Cobia detections occurred in nearshore, offshore, and shelf regions with similar frequency at each NCSU acoustic release receiver during spawning and the transitional period between spawning and winter (Figure 15). Two nearshore receivers (546953, 546959) and one shelf receiver (546950) lacked detections during the 2018 spawning period. During the winter period, detections occurred with greatest frequency at shelf and offshore receivers, which tended to have surface and bottom temperatures that were warmer and more stable than at nearshore sites (Figure 15).

Discussion

Our work supports previous descriptions of the long-distance seasonal migration of Cobia along the southeastern United States as outlined by Shaffer and Nakamura (1989). This overall north-south migratory pattern is as follows: after passing through North Carolina waters in the spring, Cobia occupy Chesapeake Bay and nearshore waters off Virginia for the duration of the spawning period before shifting south into North Carolina in fall and continuing towards southern wintering grounds. We further refined this picture within the study region by contrasting the spring and fall movement linking the spawning grounds in Virginia and southern wintering grounds. As a result, we present a more nuanced picture of the destinations and pathways Cobia utilize in their seasonal migration. We also identified notable exceptions to this movement ecology scheme: 1) limited interannual variability in the timing of the spawning period exists between our years of study; 2) a subset of Cobia were detected only in North Carolina during the spawning period and were not recorded in Virginia at any point; and 3) a limited number of persistent detections occurred in North Carolina during the winter period, indicating a group of tagged Cobia overwintering farther northward than previously described.

During the northward spring migration, Cobia were heavily associated with nearshore receivers. We observed high traffic along the barrier islands of the Pamlico Sound before tagged fish arrived in Virginia. A large portion of this transitional movement between states occurred between nearshore receivers north of Cape Hatteras and receivers in the mouth of Chesapeake Bay indicating a continuation of the nearshore movement observed in North Carolina. In the fall as Cobia return southward, we observed an increase in offshore movement and decrease in nearshore movement relative to the spring migration. This longitudinal shift of the north-south Cobia migration clarifies the role of previously observed fall shifts into offshore waters (Crear et al. 2020b; Perkinson et al. 2018; Shaffer and Nakamura 1989) within the larger migratory cycle of these fish. Though limited receiver coverage in deeper waters restricts the resolution with which we can observe this shift, the difference in the spatial distribution of movements between spring and fall suggests two distinct seasonal migration patterns: a highly-trafficked nearshore migratory pathway along the coast of North Carolina in the spring and a dispersion of movement offshore and southward in the fall. This seasonal change in spatial distribution impacts the susceptibility of Cobia to fishing pressure over the course of their migration (Klibansky 2018; Lowerre-Barbieri 2019); Cobia are most catchable nearshore in spring and offshore in fall. During the spring northward migration, the movement of Cobia is concentrated nearshore, and this close proximity to land increases the ease with which they can be exploited (Crear et al. 2020a; Crear et al. 2020b).

Chesapeake Bay and the waters off Virginia both play a central role in the life history of Atlantic Cobia by serving as a primary spawning region. Activity of Cobia occurs throughout the Bay, even extending into the York and James Rivers, similar to spawning observed far inshore in South Carolina (Lefebvre and Denson 2012); however, activity during the spawn is most heavily concentrated within the Bay to the west of Cape Charles, a probable site of spawning aggregations (Richards 1967). Dense receiver coverage in this region likely contributes to the large number of detections recorded, but a high density of movement between multiple receiver pairs indicates that this is a main site of spawning activity. With a larger time scale, the persistence of this behavior will become clear. Furthermore, for the spawning periods analyzed in our study, the timing of the Cobia arrival into Virginia varied. Investigation is necessary to determine the magnitude of this interannual variation and consistency of spawn timing.

Transient seasonal spatial segregation during spawning and wintering isolates subsets of fish providing opportunity for genetic differentiation and different levels of human exploitation. Consistent isolation of spawning groups drives genetic differentiation between these groups and builds substructure within the larger stock (Darden et al. 2013; Lowerre-

Barbieri 2017; Metcalfe 2006). Prior genetic investigation of the Atlantic Cobia stock described spawning site fidelity and local subpopulations as a plausible driver of observed genetic differentiation and identified a possible homogeneous stock subunit inshore in Virginia's Chesapeake Bay and offshore in North Carolina during spawning (Darden et al. 2013). We detected Cobia year-round in North Carolina waters with persistent presence during both the winter and spawning periods but variation in their connection to Chesapeake Bay, a significant departure from the current described north-south migration with Cobia wintering south of North Carolina before leaving to spawn in Virginia.

Cobia included in the persistent winter group were detected in Virginia during spawning, joining the described spawning migration. Genetic sampling of these fish and those migrating from farther south into North Carolina waters as part of this northward migration could result in the apparent homogeneity between North Carolina and Virginia, while the sampled fish are in fact part of a cohort fidelitous to Virginia waters, specifically Chesapeake Bay. This could plausibly mask differentiation by Cobia spawning elsewhere but occupying North Carolina waters during the same period. Indeed, the small but distinct group of Cobia detected in North Carolina during spawning that were not observed in Virginia indicate the possibility of fish spawning in North Carolina separate from the genetically identified cohort. Because of these mutually exclusive groups — the winter and spawning period fish detected in North Carolina — our results call the Virginia-North Carolina spawning subpopulation into question. They do, however, indicate movement patterns capable of driving shifts in population structure.

Cobia wintering in North Carolina join the spawning activity in Virginia and, as a result, are unlikely to differentiate genetically from this portion of the larger stock. On a regional scale, this subset of fish is composed of tagged individuals that use either Chesapeake Bay or strictly ocean habitat off Virginia during the spawning period, so this wintering behavior appears unlinked to proposed spawning site philopatry (Gallagher 2020, unpublished).

Cobia that spend the spawning period in North Carolina waters, on the other hand, account for a small proportion of tagged fish but are indicative of spatially isolated spawning. Given consistent annual separation from other spawners by this subset of fish and successful spawning by these individuals, genetic differentiation and the development of substructure within the larger Atlantic stock is possible (Lowerre-Barbieri et al. 2017; Lowerre-Barbieri et al. 2019). It is worth noting that the zone between North Carolina and Virginia, in which receivers are absent, could be a site of mixing for fish outside of Chesapeake Bay. Further investigation into the interannual persistence of individual Cobia in North Carolina during the spawning period, the relative magnitude of spawning activity in this region, and the genotype of these fish will clarify the temporal scope and genetic impact of this spatial segregation. Conversely, spawning activity may go undetected elsewhere (i.e., in the region between the arrays deployed in North Carolina and Virginia) masking overlap between Cobia spawning on the shelf. Those fish characterized as potential North Carolina spawners might belong to a larger contingent of ocean spawners.

Spatial segregation of behavioral subgroups within the Atlantic Cobia stock results in different levels of experienced fishing pressure for each of these groups (Klibanksy 2018). If differentiated North Carolina and Virginia spawning groups exist, the size of each group and the magnitude of fishing pressure experienced in each region during the spawning period must be better understood to ensure that neither group is overexploited (Lowerre-Barbieri et al. 2017). The distinct wintering groups — Cobia that remain in North Carolina waters versus those that continue south toward Florida — are consequential for the fishery even with little to no winter harvest in either region. As these Cobia shift north to spawn, those already in North Carolina are less susceptible to fishery in their progress up the coast to Virginia spawning grounds given their shorter path.

Until recently, Cobia wintering behavior has been poorly understood and utilization of waters north of Cape Fear has gone virtually undescribed (Smith 1995). Beyond the latitudinal spatial separation of the North Carolina overwintering cohort from the rest of the stock migrating further south, we identified a longitudinal, inshore-offshore shift in the movement of the North Carolina wintering fish. Movement of these fish offshore on the continental shelf increased, indicating a transition into deeper waters during the fall and winter. From this, we draw that the continental shelf habitat off the coast of North Carolina is suitable for wintering, making it the northernmost known region of the winter range of Atlantic Cobia. Our observations support described seasonal offshore movement (Crear et al. 2020b; Shaffer and Nakamura 1989; Young et al. 2018) and strengthen the conclusion that movement into offshore waters during colder months is a significant component of Atlantic Cobia movement ecology. Limited receiver coverage offshore gives an incomplete picture of this wintering behavior; however, with a longer time scale, an increased number of tagged fish, and greater receiver coverage offshore, the relative magnitude and significance of this behavior can be better understood.

Our investigation demonstrates the link of temperature to Cobia movement and seasonal spatial distributions. The receiver temperatures at which tagged Cobia were detected in this study ranged from 16.2 to 27.9°C supporting the wide range of temperatures from 16.8 to 32.2°C described by Shaffer and Nakamura (1989). During the spring and summer, including the spawning period from June through August, Cobia were detected in all regions but exhibited a notable increase in their presence and movement in nearshore waters off North Carolina coinciding with a warmer range of available temperatures in this region. In the fall, Cobia moved southward and offshore, registering detections near the continental shelf break. In this region, temperature conditions are dominated by the warm, saline Gulf Stream (Stefánsson et al. 1971), and temperature logs indicated that winter temperatures — both at the surface and at the bottom — near the shelf break stayed warmer, often exceeding 20°C, and varied little relative to nearshore waters. During this period, we recorded markedly stable bottom and surface temperatures near the continental shelf break, suggesting that these deep waters provide suitable overwintering habitat.

Linking Cobia movement ecology and temperature refines our understanding of their migratory behavior and has utility for management (Lowerre-Barbieri et al. 2019; Metcalfe 2006). By identifying the range of temperatures used by wild stocks and thresholds at which spatial shifts occur, we gain increased predictive capacity for the short-term monitoring of seasonal migration timing (Breece et al. 2017) and for the long term as we seek to understand the response of Cobia to changing ocean conditions (Crear et al. 2020a). The movement ecology of this species defines the spatial and temporal context of life history events, thus driving the formation of possible population structure, and governs fishery encounter rates (Lowerre-Barbieri et al. 2019; Metcalfe 2006). Temperature is a key physical driver of seasonal movement (Breece et al. 2017; Song et al. 2019; Lowerre-Barbieri 2019), and further investigation will support effective stock management by connecting the complex migratory behaviors of Cobia to their physical environment.

Figures and Tables

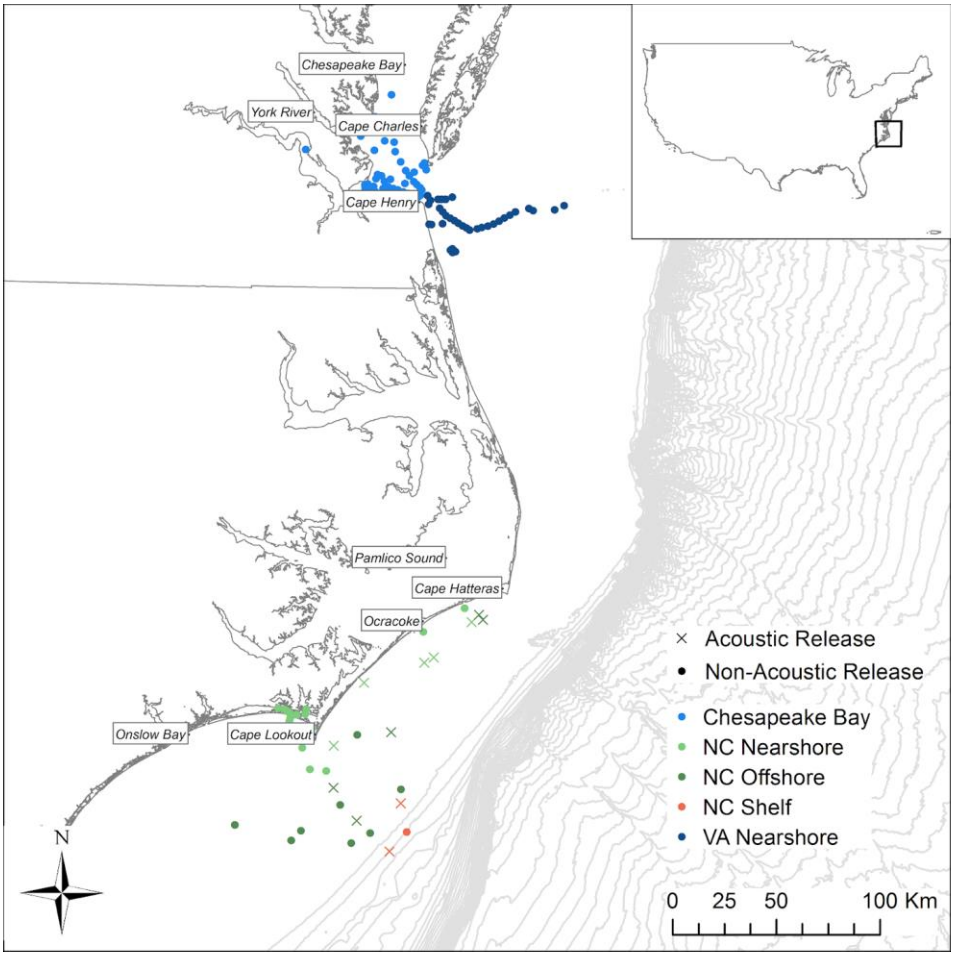


Figure 1. Passive acoustic receiver arrays in North Carolina and Virginia. Crosses differentiate bottom-deployed NCSU acoustic release receivers (Vemco VR2AR). Dark blue dots show receivers stationed nearshore (less than 30 meters in depth) in Virginia waters. Light blue dots indicate estuarine receivers within Chesapeake Bay. In North Carolina, light green receivers (dots and crosses) are nearshore, dark green are offshore (greater than 30 meters in depth), and orange are on the shelf (greater than 50 meters in depth).

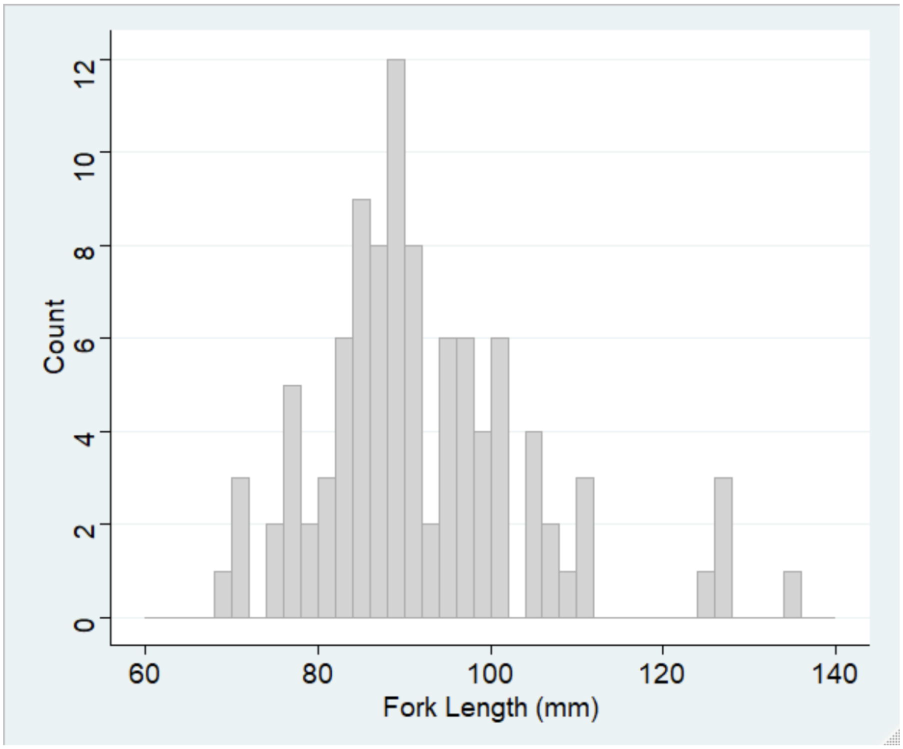


Figure 2. Length distribution of all telemetry-tagged Cobia (n = 98, mean = 923 ∓ 127 mm FL). This figure was prepared by NCSU M.S. student Riley Gallagher.

Table 1. Annual tagging effort, NCSU acoustic telemetry tags deployed by year and state. NCSU tagging in Virginia with assistance of VIMS collaborators.

Year	North Carolina tags	Virginia tags	Combined tags
2018	34	20	54
2019	34	10	44
Total	68	30	98

Figure 3. Individual detections (56843 detections, n = 77) of acoustically tagged Cobia (98 total) listed by unique transmitter identification number. Detections in North Carolina waters occurred at nearshore (light green dots), offshore (dark green dots), and shelf (orange dots) receivers. In Virginia, detections occurred inshore within Chesapeake Bay (light blue dots) or nearshore (dark blue dots) on the continental shelf. The summer spawning periods (June through August) are indicated by light green sections and the winter period (December through February) by the purple section. Nearshore detections in Virginia provided by the United States Navy are absent for the second spawning period; only detections within Chesapeake Bay are plotted for that period.

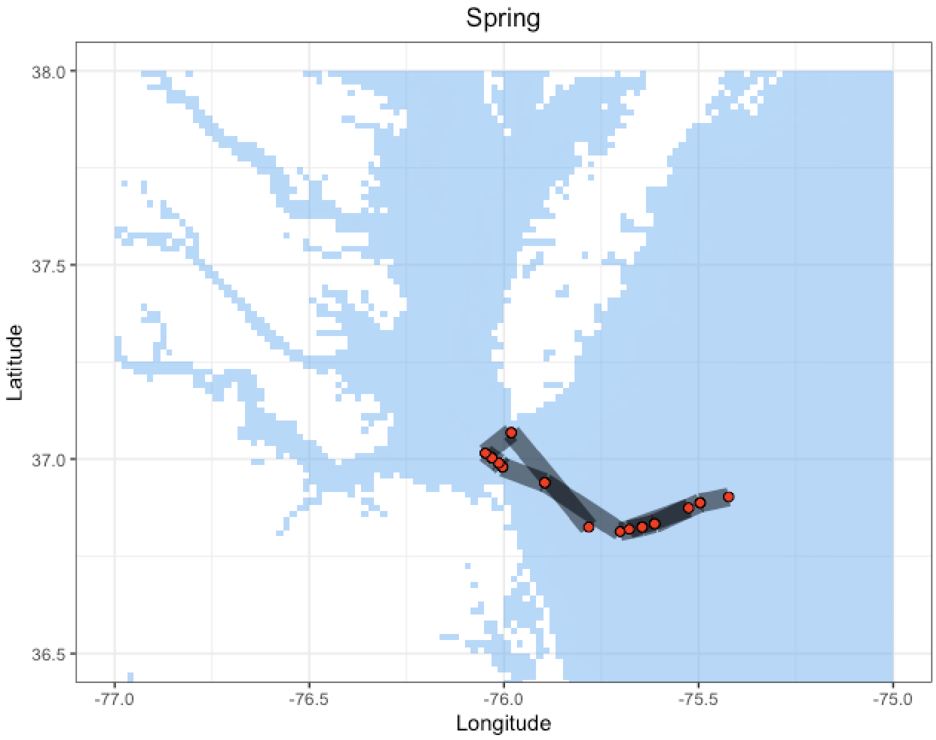


Figure 4. Spring network analysis in Virginia and Chesapeake Bay. This network was generated from detections recorded from May 1, 2018 through May 1, 2019 for the three-month seasonal period (March through May). Receivers that mark the beginning and end of a single movement by an individual fish are indicated by red nodes. Edge weight (thickness of black lines) is proportional to the number of movements between a receiver pair recorded within one seasonal period. Edge density — the proportion of receiver pairs used over the total available pairs — was 0.0029 for spring (n = 2). Relatively larger edge density indicates greater saturation of the array (i.e., greater space use).

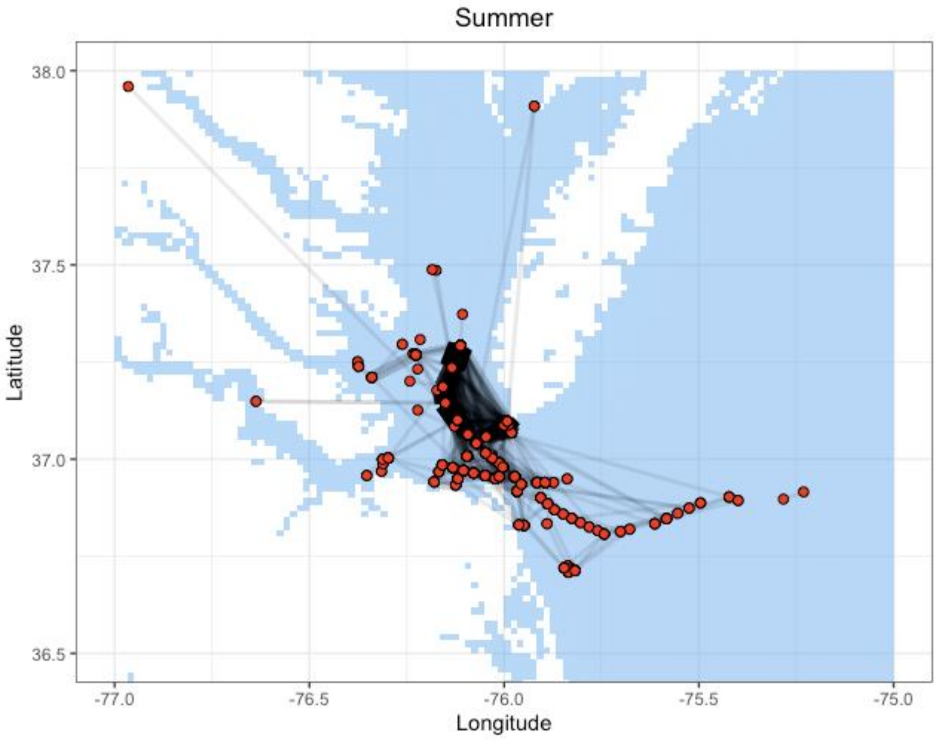
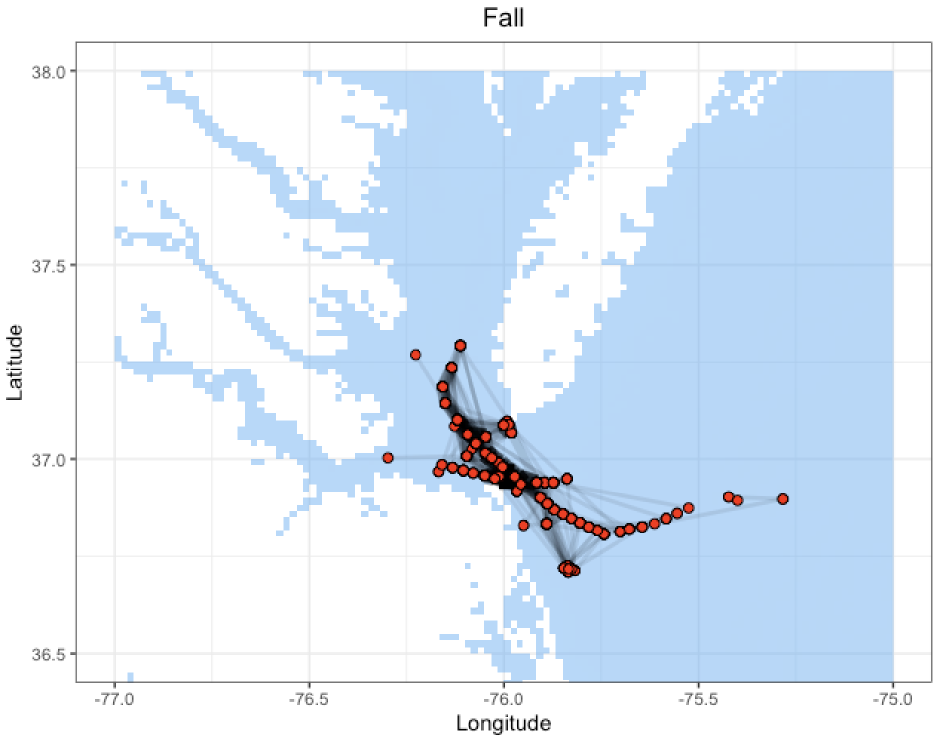


Figure 5. Summer network analysis in Virginia and Chesapeake Bay. This network was generated from detections recorded from May 1, 2018 through May 1, 2019 for the three-month seasonal period (June through August). Receivers that mark the beginning and end of a single movement by an individual fish are indicated by red nodes. Edge weight (thickness of black lines) is proportional to the number of movements between a receiver pair recorded within one seasonal period. Edge density — the proportion of receiver pairs used over the total available pairs — was 0.0779 for summer (n = 40).



Figures 6. Fall network analysis in Virginia and Chesapeake Bay. This network was generated from detections recorded from May 1, 2018 through May 1, 2019 for the three-month seasonal period (September through November). Receivers that mark the beginning and end of a single movement by an individual fish are indicated by red nodes. Edge weight (thickness of black lines) is proportional to the number of movements between a receiver pair recorded within one seasonal period. Edge density — the proportion of receiver pairs used over the total available pairs — was 0.0628 for fall (n = 32).

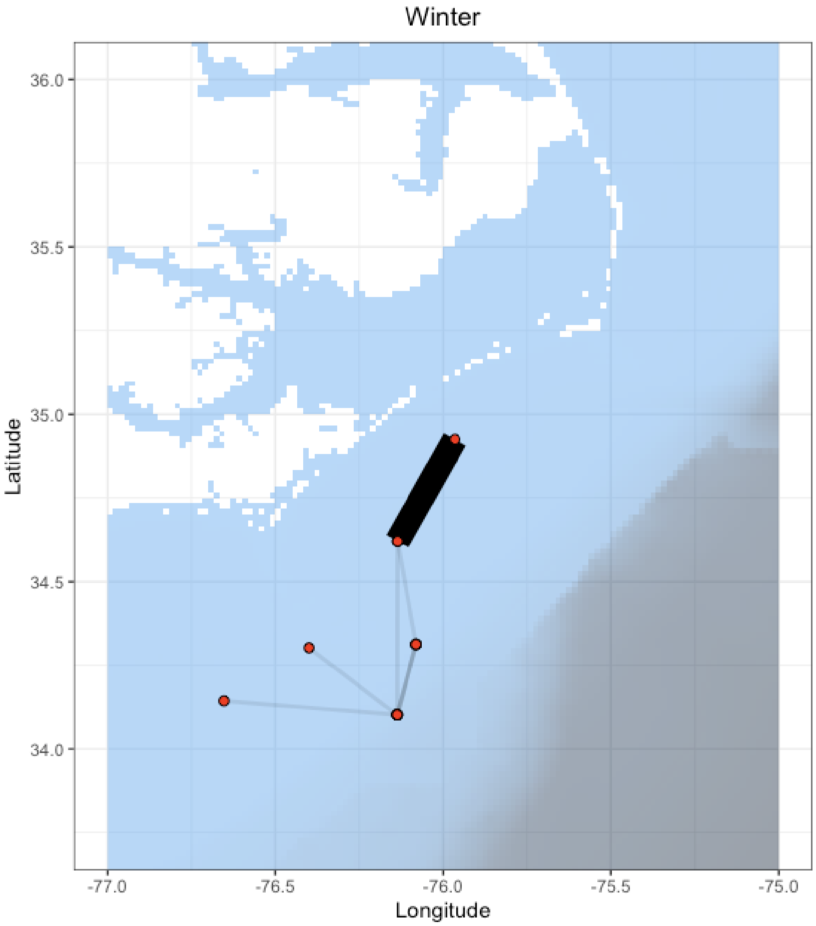


Figure 7. Winter network analysis in North Carolina. This network was generated from detections recorded from May 1, 2018 through May 1, 2019 for the three-month seasonal period (December through February) for receivers on the continental shelf off the coast of North Carolina. Receivers that mark the beginning and end of a single movement by an individual fish are indicated by red nodes. Edge weight (thickness of black lines) is proportional to the number of movements between a receiver pair recorded within one seasonal period. Edge density was 0.0085 for winter (n = 8).

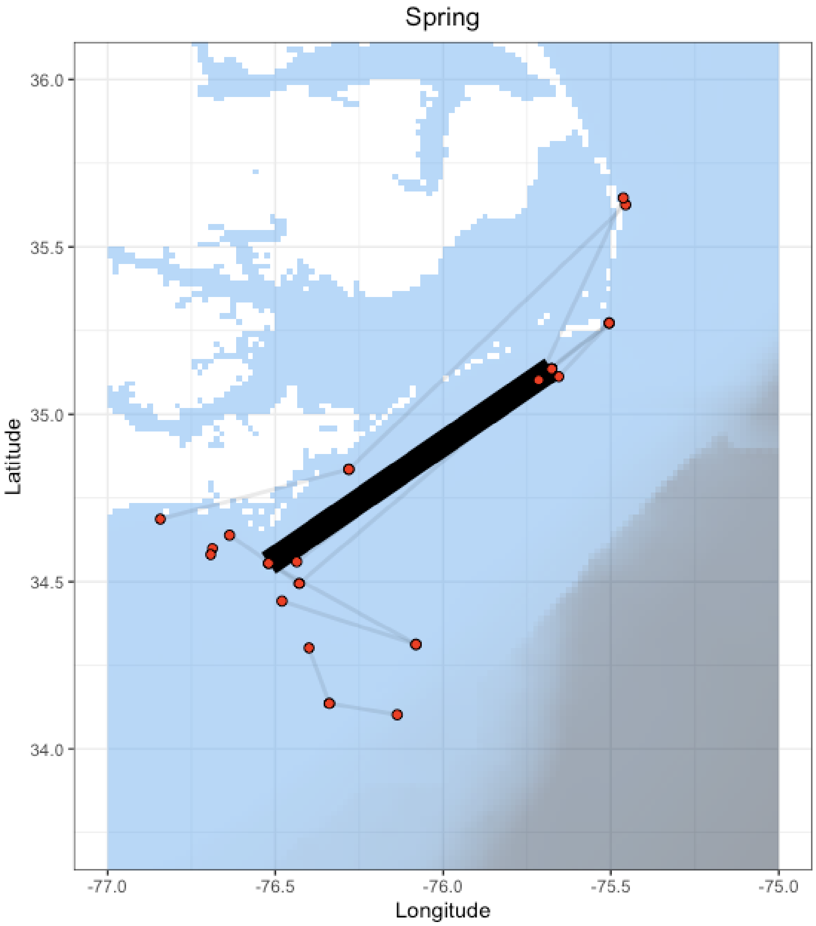


Figure 8. Spring network analysis in North Carolina. This network was generated from detections recorded from May 1, 2018 through May 1, 2019 for the three-month seasonal period (March through May) for receivers on the continental shelf off the coast of North Carolina. Receivers that mark the beginning and end of a single movement by an individual fish are indicated by red nodes. Edge weight (thickness of black lines) is proportional to the number of movements between a receiver pair recorded within one seasonal period. Edge density was 0.0213 for spring (n = 36).

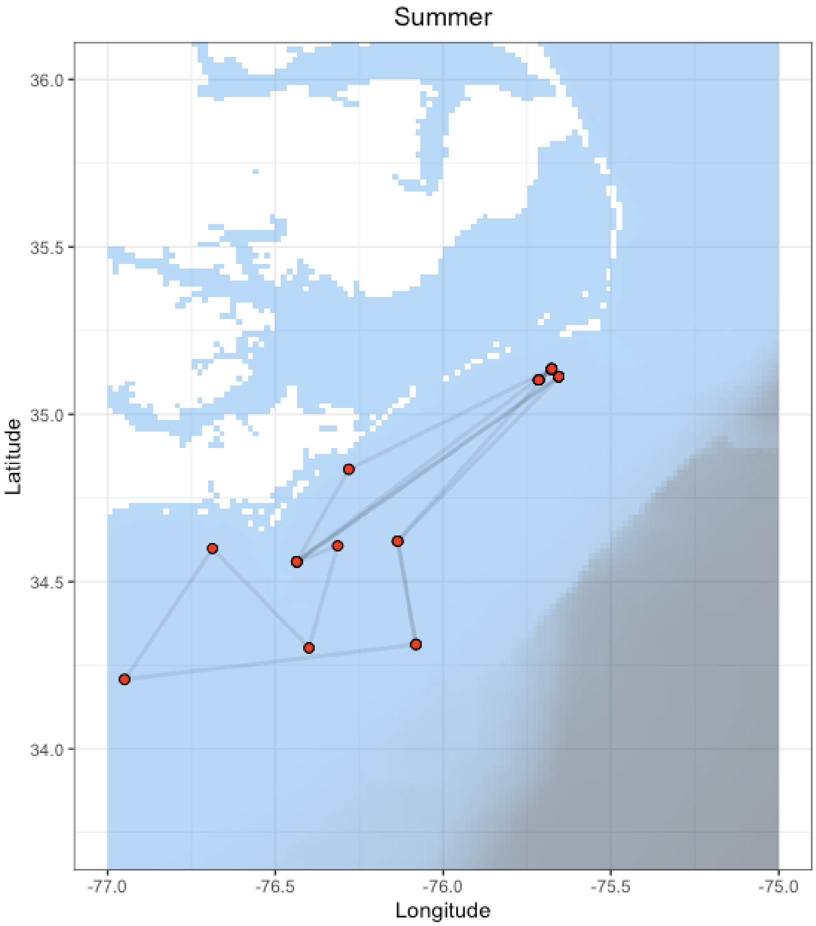


Figure 9. Summer network analysis in North Carolina. This network was generated from detections recorded from May 1, 2018 through May 1, 2019 for the three-month seasonal period (June through August) for receivers on the continental shelf off the coast of North Carolina. Receivers that mark the beginning and end of a single movement by an individual fish are indicated by red nodes. Edge weight (thickness of black lines) is proportional to the number of movements between a receiver pair recorded within one seasonal period. Edge density was 0.0256 for summer (n = 8).

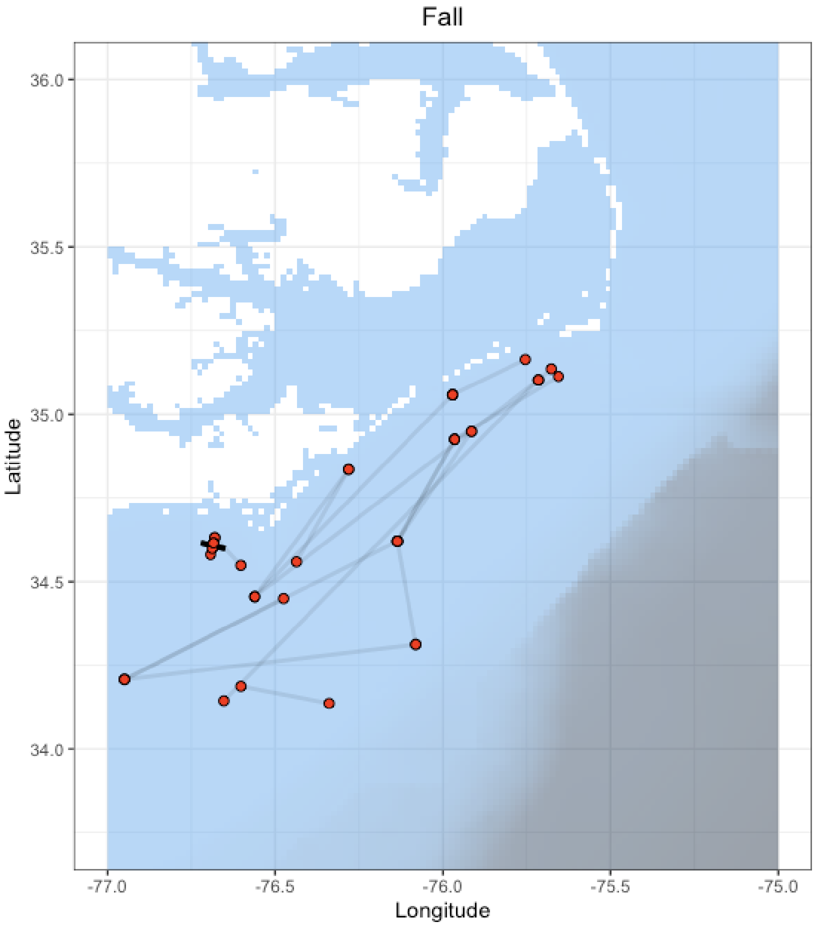


Figure 10. Fall network analysis in North Carolina. This network was generated from detections recorded from May 1, 2018 through May 1, 2019 for the three-month seasonal period (September through November) for receivers on the continental shelf off the coast of North Carolina. Receivers that mark the beginning and end of a single movement by an individual fish are indicated by red nodes. Edge weight (thickness of black lines) is proportional to the number of movements between a receiver pair recorded within one seasonal period. Edge density was 0.0299 for fall (n = 30).

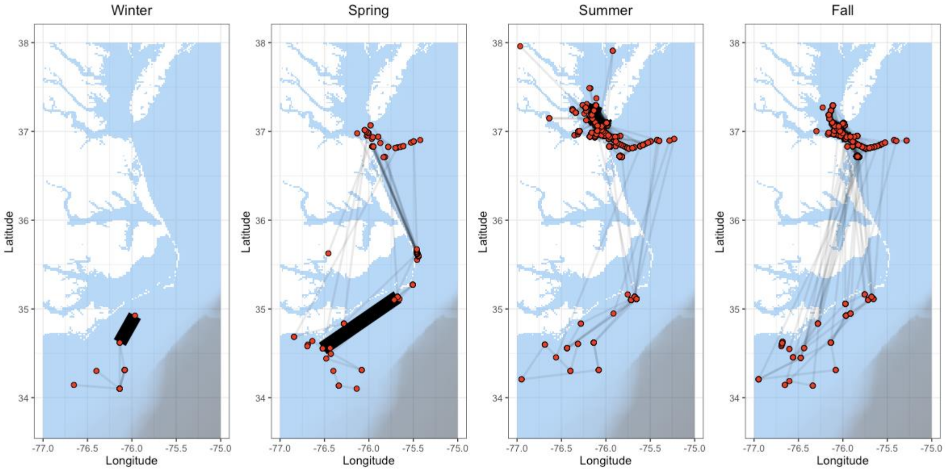
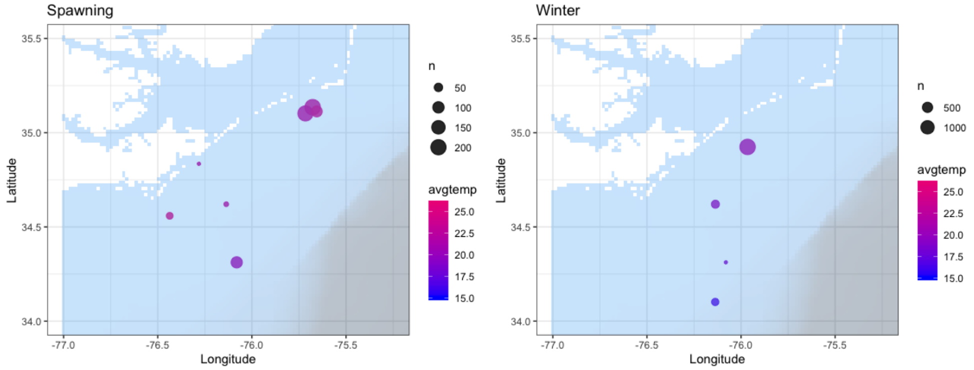


Figure 11. Seasonal network analysis for Virginia and North Carolina arrays. Networks were generated for May 1, 2018 to May 1, 2018 in three-month seasonal periods for receivers on the continental shelf off the coastlines of both North Carolina and Virginia and in the Chesapeake Bay. Receivers that mark the beginning and end of a single movement by an individual fish are indicated by red nodes. Edge weight (thickness of black lines) is proportional to the number of movements between a receiver pair recorded within one seasonal period. Edge density was 0.0006 for winter (11A, n = 8), 0.0045 for spring (11B, n = 36), 0.0352 for summer (11C, n = 44), and 0.0306 for fall (11D, n = 39).



Figures 12. Average bottom temperature of detections at NCSU acoustic release receivers. For the 2018 spawning period (June through August; 1314 detections; n = 8) and 2018-2019 winter (December through February; 3878 detections; n = 6) receivers at which detections were recorded are indicated with points. Point size is proportional to the number of detections registered at each receiver. Point color is assigned by the average bottom temperature recorded by each receiver for every detection recorded over the given period.

Figure 13. All North Carolina surface and bottom temperatures. Hourly temperature records from NCSU acoustic release receivers (light blue) are shown with a GAM fit line for a year-long period from April 2018 to April 2019. Monthly average satellite surface temperature (light green) are plotted as points with a range of one standard deviation. Receivers and satellite samples in nearshore, offshore, and shelf regions are included.

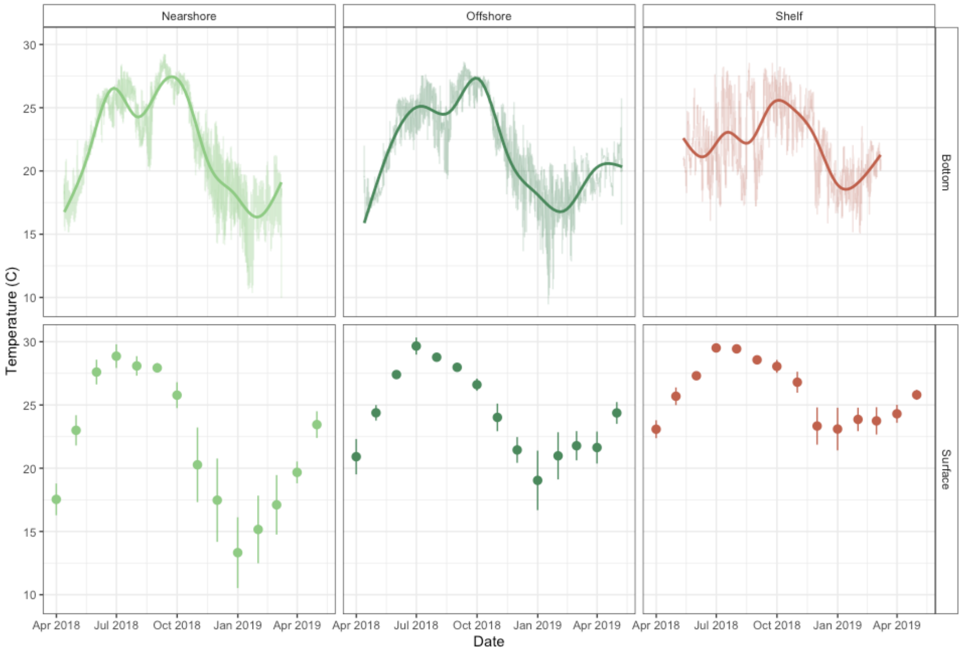


Figure 14. Surface and bottom temperature records by depth region. Average monthly satellite-recorded surface temperatures in nearshore (light green), offshore (dark green), and deep shelf (orange) regions are plotted as points with a range of one standard deviation denoted. Acoustic release receiver hourly bottom temperature records are plotted by depth group (light green: nearshore; dark green: offshore; orange: shelf) with a GAM fit line.

Figure 15. Bottom and surface temperatures and detections at NCSU acoustic release receivers by depth group. The top panel shows hourly temperatures recorded by the bottom-deployed acoustic release receivers with GAM fit lines. These profiles are divided by depth (light green: nearshore; dark green: offshore; orange: shelf). The middle panel shows average monthly satellite-recorded surface temperatures divided by depth (light green: nearshore; dark green: offshore; orange: shelf) with points and one standard deviation ranges. In the bottom panel, all detections (9381 detections, n = 34) recorded at each NCSU VR2AR receiver are plotted. Depth regions are denoted by dot color (light green: nearshore (N); dark green: offshore (O); orange: shelf (Sh)). The light green section indicates the 2018 spawning period (June through August) and the purple section denotes the winter (December through February).

Acknowledgements

I am extremely grateful to the faculty, students, and staff of Cornell University and North Carolina State University who assisted me for the duration of this project. It was a joy and privilege to work with my thesis advisor, Dr. Cliff Kraft. His thoughtful advice and unwavering support were enormously helpful, and I found our weekly meetings — even those over Zoom — to be both enjoyable and supremely thought-provoking. I would also like to express my deepest appreciation for Dr. Kraft's (now former) doctoral student, Ben Marcy-Quay, who provided technical assistance critical to the success of my thesis and volunteered his time to be a sounding board for my ideas. I also extend my most sincere thanks to Dr. Jeff Buckel, my mentor at North Carolina State's Center for Marine Sciences and Technology (CMAST). I have benefitted enormously from Dr. Buckel's mentorship and am grateful that he enabled me to pursue this challenge. My experiences serving as a CMAST summer fellow and working on this project, both under Dr. Buckel's guidance, have been instrumental in my growth as a scientist. I am also extremely grateful to NCSU M.S. student Riley Gallagher for taking me on as a summer fellow and teaching me about all things Cobia. Without his guidance, expertise, and hard work, this thesis would not be possible. Throughout my collaboration on Cobia research with Riley, I have appreciated how much he has challenged me to gain research skills and consider new ideas. Portions of this movement analysis are also presented in his thesis. In addition, I would like to thank the entire Buckel lab and the larger CMAST community for creating an engaging research environment that facilitated my development as a researcher. I was lucky to be surrounded by such an excellent group of people. I am also grateful to Dr. Eugene Won, my faculty advisor, for his guidance throughout my time at Cornell and his support of my application for the CMAST Summer Fellowship. His advice has been invaluable in these early stages of my career. I would also like to express my great appreciation for Drs. Willy Bemis, Irby Lovette, and Laura Schoenle for managing a successful Honors Program amid unprecedented challenges and prioritizing student wellbeing. In a time when the ceremony of senior year is absent, it is all the more meaningful to complete this capstone achievement and feel supported along the way. I would also like to thank Dr. Bruce Monger for his guidance in the world of physical oceanography and remote sensing. And lastly, to my close friends and loved ones who supported me along the way, thank you.

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