

5-15-2022

Winter use of Winyah Bay, SC by the Spiny Dogfish (*Squalus acanthias*), and their movements south of Cape Hatteras, NC

Meredith L. Langford
Coastal Carolina University

Follow this and additional works at: <https://digitalcommons.coastal.edu/etd>



Part of the [Aquaculture and Fisheries Commons](#), and the [Biology Commons](#)

Recommended Citation

Langford, Meredith L., "Winter use of Winyah Bay, SC by the Spiny Dogfish (*Squalus acanthias*), and their movements south of Cape Hatteras, NC" (2022). *Electronic Theses and Dissertations*. 140.
<https://digitalcommons.coastal.edu/etd/140>

This Thesis is brought to you for free and open access by the College of Graduate and Continuing Studies at CCU Digital Commons. It has been accepted for inclusion in Electronic Theses and Dissertations by an authorized administrator of CCU Digital Commons. For more information, please contact commons@coastal.edu.

Winter use of Winyah Bay, SC by the Spiny Dogfish
(*Squalus acanthias*), and their movements south of Cape
Hatteras, NC

By

Meredith L. Langford

Submitted in Partial Fulfillment of
the Requirements for the Degree of
Master of Science in Coastal Marine
and Wetland Studies in the School of
the Coastal Environment Coastal

Carolina University

2022

Major Advisor

Daniel Abel

Committee Member

Derek Crane

Committee Member

Gregory Skomal

Committee Member

Bryan Frazier

Dean, Gupta College of Science

Michael Roberts

CMWS Graduate Programs Director

Erin Hackett

© 2022 by Meredith Langford (Coastal Carolina University)
All rights reserved. No part of this document may be reproduced or transmitted in any form or by any means, electronic, mechanical, photocopying, recording, or otherwise, without prior written permission of Meredith Langford (Coastal Carolina University).

Dedication:

First, I would like to dedicate this thesis to my late grandfather, Judge John S. Langford Jr. Throughout my life he was a stalwart teacher and a monument to preparedness, thoughtfulness, and dedication. There was not a moment when he wasn't teaching us a useful skill or a meaningful lesson. He always rewarded his grandchildren for their achievements and always pushed us to be better than we were the day before.

I would like to also dedicate this thesis to my family, including my mother and father Leslie and David Langford, whose constant support and belief helped see me through the toughest parts of my project. I also want to thank my brother and sister, Jason and Margaret Langford, who cheered me on from the sidelines and supported me when "Mom and Dad had heard enough". Of course, no thank you would be complete without a nod to the wiener dog trio Tootsie, Ruby, and Marley. Carry on my long little dogs!

I would also like to dedicate this thesis to my Grandmother, Margaret Ellis Langford, the matriarch of the Langford family and the late Jack Langford's wife. You have always supported your grandchildren and showered us with love all of our lives. I am grateful to always have you in my corner.

I would like to also mention my dear friends whose support and camaraderie saw me through some of the hardest parts of my thesis, those who were "in the trenches" with me. Thank you to my colleges Caroline, Matt, Elise, and Jessie. I would also like to thank my friends Mike, Allison, Angie, Becca, and Yaakov for supporting me so tirelessly from Atlanta.

This thesis is also dedicated to my supportive therapist the talented Dr. Deborah Lathrop. Your tireless support and sound-boarding has helped me succeed. Thank you.

No dedication would be complete without acknowledging my dear four-legged friend Zuko. You were always there with wagging tail and supportive huff when I needed it. When I needed a break, you were always ready for a walk and a snack.

Acknowledgements:

I would like to first and foremost thank, Dr. Daniel Abel for taking me on as a graduate student and giving me the opportunity to pursue a Masters in shark science. Your tireless guidance, patience, and support have helped me grow as a scientist. Thank you so much.

A special thank you to my committee as well. Derek Crane you were my dedicated statistician and fisheries support throughout the project. Your substantial reviews helped me produce a more succinct and clear research project. Bryan Frazier, you supported me with strong feedback from your years of experience studying wild sharks with the South Carolina Department of Natural Resources. Your critical advice helped me build a stronger project. Finally, a special thank you to Greg Skomal with the Massachusetts Division of Marine Fisheries. Thank you for taking me on as a fisheries technician in 2019 as well as agreeing to join my committee.

I would finally like to give a very special thank you to Captain Edwin Jayroe who took me out sampling in cold weather to sample in Winyah Bay. To all my volunteers who took time out of their busy lives to come spend some time on cold mornings to try and catch sharks thank you so much. You all made this research possible.

Abstract:

South of Cape Hatteras, NC, little is known about the coastal distribution and movement of the Spiny Dogfish, *Squalus acanthias*. Between January 2018 and March 2020 this study conducted winter demersal longline sampling in Winyah Bay, SC to investigate habitat use by Spiny Dogfish. In addition to monitoring Winyah Bay use through catch-and-release, 13 individuals were outfitted with implanted Vemco™ acoustic transmitters to monitor large scale movements along the U.S. East Coast. Across three sampling seasons 84 female Spiny Dogfish were captured within lower Winyah Bay. No males were observed over the course of the study. The mean fork length of captured females was 79.6 cm (SD = 4.6 cm). Over 90% of captured females had fork lengths consistent with length-at-maturity data (FL = 72.5 cm) published by the American Fisheries Society (Campana *et al.* 2009). Spiny Dogfish were observed only for a short temporal window inside Winyah Bay. Raw abundance (n = 81) and CPUE (2.02 ± 4.12 ; mean \pm SD) were highest in the month of February with most individuals being caught in the first half of the month. The average capture temperature was $12^{\circ}\text{C} \pm 1.1$. Acoustic monitoring revealed northern movement from Winyah Bay, with all tagged sharks spending time in sheltered waters near Beaufort, NC in the months of March and April. Three tagged individuals were detected as far north as New Jersey, New York and Massachusetts. One tagged individual was detected again in Winyah Bay, logging detections in the bay nearly a year after its initial tagging. The brief but recurring nature of Spiny Dogfish in Winyah Bay suggest that coastal, and estuarine, waters off South Carolina function as overwintering grounds for mature females south of Cape Hatteras, NC.

Table of Contents

Title Page	i
Copyright	ii
Dedication:	iii
Acknowledgements:	v
Abstract:	vi
Table of Contents	vii
List of Tables	viii
List of Figures	ix
Introduction.....	1
Materials and Methods.....	6
Results.....	12
Discussion.....	18
Conclusions.....	27
References.....	41
Figures & Tables:.....	28

List of Tables

Table 1	General catch results
Table 2	Pooled abundance per month and pooled longline sets per month across all sample years
Table 3	Abiotic conditions for all longlines and for longlines yielding Spiny Dogfish captures
Table 4	Size of dissected females and gestational stage results
Table 5	General acoustic results for Spiny Dogfish tagged in Winyah Bay
Table 6	Use of North Carolina waters by tagged Spiny Dogfish as represented by number of detections per receiver and the number of visiting sharks per receiver

List of Figures

- Figure 1 Winyah Bay regions and Mother Norton Shoals
- Figure 2 Coastal Carolina University, and South Carolina Department of Natural Resources, Vemco™ receiver arrays
- Figure 3 Embryonic stages in Spiny Dogfish, (a) vitellogenic ova (b) candled embryo (c) free embryo with yolk sac attached
- Figure 4 Sample effort, and catch, in Winyah Bay from sample seasons in 2018, 2019, and 2020
- Figure 5 Mean monthly CPUE for Spiny Dogfish with mean monthly bottom water temperature and mean bottom water temperature for Spiny Dogfish captures
- Figure 6 Gantt chart of Spiny Dogfish residency in lower Winyah Bay
- Figure 7 Fork length frequency distribution of female *S. acanthias* (n = 78) in Winyah Bay, SC
- Figure 8 Linear regression of abundance per longline versus bottom water temperature ($R = 0.48$)
- Figure 9 Movement of tagged sharks in Winyah Bay, including distribution of tag deployment sites and the location of four acoustic receivers around the bay entrance
- Figure 10 Migratory routes of tagged sharks with inset map showing North Carolina movements

Figure 11 Movement of acoustically tagged sharks off Beaufort, NC

Introduction

Since 2002, the CCU Shark Project has been studying shark populations in Winyah Bay, SC (Fig 1). To date, the program has identified a distinct warm-weather shark season (April – November) based on catch rate and species composition (Abel *et al.* 2007; Gary 2009, Collatos 2018, Pullen 2019, Wingar 2019). These species include the Sandbar Shark, *Carcharhinus plumbeus*, Atlantic Sharpnose Shark, *Rhizoprionodon terraenovae*, Finetooth Shark, *Carcharhinus isodon*, Bull Shark, *Carcharhinus leucas*, Blacknose Shark, *Carcharhinus acronotus*, Lemon Shark, *Negaprion brevirostris*, Blacktip Shark, *Carcharhinus limbatus*, Spinner Shark, *Carcharhinus brevipinna*, Bonnethead, *Sphyrna tiburo*, and Scalloped Hammerhead, *Sphyrna lewini* (Abel *et al.* 2007; Gary 2009; Collatos 2018, Pullen 2018, Wingar 2019). However, little is known about elasmobranch use of Winyah Bay during winter months with the exception of sporadic winter catches of the Spiny Dogfish, *Squalus acanthias* (Gary 2009; Fordham *et al.* 2016). In the western North Atlantic Ocean, Spiny Dogfish summer along the coasts of Northeastern U.S. coast and Canada before migrating to the Southeastern U.S. coast for the winter (Castro 1993; Ulrich *et al.* 2007; Sagarese *et al.* 2014). Research has largely focused on exposed, nearshore habitat use, rather than utilization of sheltered coastal waters, like bays and estuaries. For the purpose of this research the term “inshore” shall refer to enclosed bodies of water such as sheltered bays, estuaries, and sounds. The term “nearshore” shall refer to unsheltered waters exposed the open ocean.

Spiny Dogfish, (*Squalus acanthias*)

Spiny Dogfish are known to utilize shallow inshore waters in the western North Atlantic Ocean (McMillan and Morse 1999; Gamble *et al.* 2002; Stehlik 2007, Dell'Apa *et al.* 2014a; Sagarese *et al.* 2014). Mature Spiny Dogfish generally prefer water temperatures ranging from 5°C to 15°C (McMillan and Morse 1999; Gamble *et al.* 2002; Sagarese *et al.* 2014). In the western North Atlantic Ocean, schools can be found up to hundreds of meters deep (Gamble *et al.* 2002; Sagarese *et al.* 2014). These sharks are generally found in salinities averaging 30 - 32 ppt (McMillan and Morse 1999). Spiny Dogfish are known to segregate by sex (Dell'Apa *et al.* 2014a). Females generally occupy shallower, inshore, waters while males tend to utilize more exposed, nearshore, areas (Sagarese *et al.* 2014; Dell'Apa *et al.* 2014b; Haugen *et al.* 2017). Spiny Dogfish of both sexes appear more abundant in exposed coastal waters as opposed to sheltered inshore waters such as enclosed bays and estuaries. (McMillan and Moore 1999; Gamble *et al.* 2002; Stehlik 2007).

In their northern range, Spiny Dogfish have been documented in sheltered inshore areas such as Chesapeake Bay, Long Island Sound, the Hudson-Raritan Estuary, and Buzzards Bay (McMillan and More 1999; Stehlik 2007). In Chesapeake Bay, Spiny Dogfish tended to occupy cooler, more saline, waters near the bay entrance, as opposed to waters further inland (Stehlik 2007). A similar, seaward distribution was observed in the Hudson-Raritan Estuary (Stehlik 2007).

Occurrence off the Carolinas

In the Southeastern U.S., Spiny Dogfish have been observed along the South Carolina and North Carolina coasts (Ulrich *et al.* 2007; Bangle *et al.* 2018). Spiny Dogfish were found in the Bulls Bay region of South Carolina between December and

April (Ulrich *et al.* 2007). Spiny Dogfish comprised only 1.3% of the study's total elasmobranch catch across all years of study. It must be noted that between 1998 and 2003, sampling in Bull's Bay occurred between the months of April and September, thus excluding most winter catch like Spiny Dogfish. Spiny Dogfish only arrived in the Bull's Bay region after water temperatures dropped to around 13°C (Ulrich *et al.* 2007). Both species emigrated when water temperatures reached 19°C (Ulrich *et al.* 2007). Further north from Bulls Bay, Gary (2009) observed Spiny Dogfish in the lower portions of Winyah Bay, SC. In sporadic winter sampling, Gary (2009) documented 11 female Spiny Dogfish between 2002 and 2006, and only in March 2003 and January 2006. Other than these observations, no further data exist on Spiny Dogfish in the Winyah Bay region. Furthermore, other than the work of Ulrich *et al.* (2007) and Gary (2009), there are few data on Spiny Dogfish south of Cape Hatteras, NC, resulting in a significant gap in our understanding of the species in its southern range.

Spiny Dogfish have also been observed further north in Pamlico Sound, NC (Bangley *et al.* 2018). These sharks were present in Pamlico Sound only during the winter months (Bangley *et al.* 2018). Temperature was the most significant factor affecting Spiny Dogfish distribution, as they showed a preference for waters averaging 13°C (Bangley *et al.* 2018). Nearly all of the 499 captured individuals were sexually mature. Spatially, Spiny Dogfish utilized only the most seaward portions of Pamlico Sound (Bangley *et al.* 2018). Bangley proposed the species could be making short trips into the estuary to avoid competition in nearshore waters.

Tagging Research and Habitat Use

Sulikowski *et al.* (2010) attached Pop-up satellite archival tags (PSATs) to three Spiny Dogfish in the Gulf of Maine to study vertical migration. In 2014, another project used PSATs to analyze the migratory behavior of 40 Spiny Dogfish along the U.S. East Coast (Carlson *et al.* 2014). Half the tags were deployed in the Gulf of Maine, while the rest were deployed off the coast of North Carolina, north of Cape Hatteras. Based on movement data, the study identified two subpopulations of Spiny Dogfish (Carlson *et al.* 2014). Of sharks tagged in the Gulf of Maine, 67% remained in waters between Cape Cod, MA and Rockland, ME (Carlson *et al.* 2014). Of sharks tagged off North Carolina, 73% limited their range to waters between Albemarle Sound, VA, and New Smyrna Beach, FL (Carlson *et al.* 2014).

By using PSATs, Carlson *et al.* assessed how abiotic conditions affected distribution in each subpopulation. Sharks tagged in the Gulf of Maine utilized deeper waters ($92.6 \text{ m} \pm 0.1$; mean \pm SE) than their counterparts ($26.9 \text{ m} \pm 0.2$; mean \pm SE) in the south (Carlson *et al.* 2014). Northern subpopulation Spiny Dogfish also utilized cooler waters ($9.2^\circ\text{C} \pm 0.1$; mean \pm SE) relative to southern subpopulation individuals ($12.7^\circ\text{C} \pm 0.1$; mean \pm SE) off the Carolinas and Virginia (Carlson *et al.* 2014). Preferred water temperature varied by season for both subpopulations (Carlson *et al.* 2014).

Growth and Reproduction

Spiny Dogfish have growth and reproductive characteristics that make it particularly susceptible to fishing pressure. Females have one of the longest known gestation periods among vertebrates, at 22 to 24 months (Campana *et al.* 2008; Campana *et al.* 2009; Natanson *et al.* 2017). Additionally, females reach sexual maturity as late as 12 to 16 years old (Nammack *et al.* 1985; Campana *et al.* 2009; Dutton and Gioia 2018).

They also produce very small litters, with an average of 4.5 to 4.7 pups (Campana *et al.* 2009; Natanson *et al.* 2017). Males reach sexual maturity earlier, between 6 and 10 years old (Nammack *et al.* 1985; Campana *et al.* 2009).

Fisheries

Despite their low reproductive potential, Spiny Dogfish have been the target of a thriving commercial fishery in the U.S. (Gamble *et al.* 2002; TRAC 2010; Dell’Apa *et al.* 2014a). Large U.S. commercial fisheries for the species continue to operate off of North Carolina, Virginia, Massachusetts, and New Jersey (Gamble *et al.* 2002; Rootes-Murdy *et al.* 2019). The species is mostly harvested for consumption in Europe (Gamble *et al.* 2002). The fishery was heavily targeted between the late 1970s and mid 1990s until estimated commercial landings peaked in 1996, at 27,241 mt (Gamble *et al.* 2002; Campana *et al.* 2008). During this time, large females were removed from the population at an unsustainable rate (Gamble *et al.* 2002). As a result, spawning stock biomass decreased below sustainable levels from 1998 to 2005 (Rootes-Murdy *et al.* 2019). In 1998, the National Marine Fisheries Service (NMFS) declared the Atlantic stock was overfished (Gamble *et al.* 2002). In 2002, the NMFS and the Atlantic States Marine Fisheries Commission (ASMFC) developed a Fisheries Management Plan, (FMP) to rebuild U.S. stocks (Gamble *et al.* 2002). Currently, the NMFS considers stocks not overfished, with no overfishing occurring (Rootes-Murdy *et al.* 2019). In 2018, U.S. commercial catch was estimated at 7,596.7 mt while the recreational catch was only about 35 mt (Rootes-Murdy *et al.* 2019).

Study Goals & Objectives

Given that prior research has indicated the winter elasmobranch assemblage of Winyah Bay consists primarily of Spiny Dogfish (Gary 2009), this study focused on Spiny Dogfish use of the bay and its use of nearshore and estuarine habitat across its southern range. This was assessed through in situ catch data analysis in Winyah Bay and by using acoustic telemetry to monitor large scale movements across its southern range. These tag data will be useful to future fishery management in understanding Spiny Dogfish regional distribution and habitat utilization. Furthermore, data acquired through this study will assist management and conservation efforts by providing baseline data on estuarine habitat use and activity of Spiny Dogfish south of Cape Hatteras. Such baseline data will be helpful in putting future analysis in context, as human development and climate change affect coastal ecosystems. To achieve these goals this study investigated (1) abundance, size, maturity, and sex of Spiny Dogfish in Winyah Bay, (2) temporal and spatial distribution of Spiny Dogfish in Winyah Bay, (3) abiotic factors affecting Spiny Dogfish distribution and presence in Winyah Bay, and (4), migratory patterns and distribution of acoustically tagged individuals in estuarine waters along the U.S. East Coast.

Materials and Methods

Sample Site and Period

Winyah Bay is a 65 km² mixed/salt wedge estuary located just south of Georgetown, SC. This estuary is the site of long-term elasmobranch monitoring programs by the Coastal Carolina University Shark Project. Over the course of various research initiatives, the CCU Shark Project has divided the estuary into 3 regions (Fig 1) based on

salinity profiles (Abel *et al.* 2007). In this winter-based project, sampling was focused on the most seaward of the three regions, designated Lower Bay. The decision to focus efforts here was made to maximize sample collection based on the areas historically high catch rates, and high salinity (Abel *et al.* 2007; Gary 2009; Collatos 2018). Sample collection occurred during high tides when salinity was highest, four to seven times a month, weather and logistics permitting. Field sampling was conducted during the winter months (January – April), when waters were coldest, starting in January of 2018 and ending in March of 2020.

Longline procedure

Animals were captured using demersal longline fishing methods as practiced by CCU Shark Program summer research (Abel *et al.* 2007; Gary 2009; Collatos 2018). Each demersal longline was approximately 122 m long. Twenty-five, 1.5 m long gangions, baited with Atlantic Mackerel, *Scomber scombrus*, were attached, at 4.5 m intervals, to each line. Due to the small size of Spiny Dogfish, 12/0 hooks were used to minimize animal stress. Before setting the longlines temperature and salinity measurements were taken from the surface and bottom of the water column with a YSI Model Pro2030. GPS and depth data were collected from the onboard GPS console. For each sample session, four longlines were deployed within Mother Norton Shoals, and left to soak for 45 to 60 minutes before recovery.

CPUE

To assess catch results, catch per unit effort (CPUE) was calculated for each sample season. Within each season, CPUE was calculated for each Julian month when

sampling occurred. CPUE was calculated using the formula $CPUE = n/l$, where n is the number of individuals captured, and l is the number of longlines.

Animal Processing and Acoustic Tagging

Animal handling and tagging procedures were conducted in accordance with SCDNR tagging permits SCI17-0137 #4295 and SCI18-0001 #4908, and SCDNR Scientific Permit No. 5471. All animals captured were brought on board and placed in a temporary holding tank for processing. The precaudal, fork, and total lengths (PCL, FL and TL) of each animal were measured to the nearest half centimeter. A one-way ANOVA was applied to see if the FL of individuals varied between and across sample years. Additionally, fork lengths were compared to known length-at-maturity data ($FL_{50} = 72.5$ cm) to assess maturity of individuals (Campana *et al.* 2009). The sex of all captured individuals was documented to establish a sex ratio for each season. Before release, each animal received a numbered dart tag, applied beneath the first dorsal fin.

To study movement and habitat use, fourteen individuals with $FL > 80$ cm had an acoustic transmitter (Model V16-4H, Innovasea Systems Inc., Nova Scotia) surgically implanted in the ventral body cavity. Before attempting each procedure, the health of each animal was assessed by observing the responsiveness of each animal. If an animal showed a lack of responsiveness or displayed signs of ventral blushing surgical implantation was not conducted and the animal was released. However, if the animal large enough and in good health, it was selected for surgery. To begin the procedure, each animal was held in a prone position to trigger tonic immobility. Each animal was held prone for the duration of the procedure. After the animal was fully in tonic, a 3.5 to 5 cm incision was made on the ventral side of the animal with a razor blade to break the skin.

After breaking the skin, a #11 scalpel was used to make an entry into the body cavity. If while entering the body cavity, a blood vessel was nicked and significant bleeding occurred, the surgery was aborted, the incision was sutured shut, and the animal was promptly released. Upon opening the body cavity, a V16-4H tag was activated and implanted through the incision. After the tag was inserted, the incision was sutured shut with UNIFY[®] PGA dissolvable sutures and the animal was released from its prone position. Once the animal showed signs of alertness and responsiveness to handling it was promptly released overboard. No surgeries took longer than 4 minutes.

Use of the Winyah Bay area was evaluated by utilizing existing arrays of VR2W Vemco acoustic receivers managed by CCU and the South Carolina Department of Natural Resources (SCDNR) as illustrated in Figure 2. Movement along the U.S. East Coast was analyzed using detections gathered by the Florida Atlantic Coast Telemetry Network (FACT) and Atlantic Cooperative Telemetry Network (ACT). Migratory patterns were mapped in QGIS (QGIS Development Team 2018) to assess Spiny Dogfish use of inshore and coastal habitat across their southern range.

Sex and Maturity of Spiny Dogfish in Winyah Bay

Evaluating gestational status involved dissection of sacrificed animals to examine the reproductive organs. Animals were sacrificed via pithing. Animal collection and processing procedures performed in the field were conducted under the Institutional Animal Care and Use Committee (IACUC) research permit #2015.05. Collection of animals for laboratory analysis was conducted in accordance American Veterinary Medical Association (AVMA) euthanasia guidelines and as allowed by SCDNR Scientific permit #5471.

Given that Spiny Dogfish are listed as vulnerable by the IUCN, no more than 10 animals were collected over the course of the study. As with released animals precaudal, fork, and total length, measurements were taken for each sacrificed female. To assess sexual maturity, the uteri and ovaries were removed and examined. A female was considered sexually mature if any of the following conditions are met, 1) the ovaries contain vitellogenic ova, 2) there are free, or candled, ova in the uteri, or 3) free embryos are present in the uteri (Fig 3). The number of vitellogenic ova present were totaled for each female. Intact candled embryos were measured to the nearest centimeter, and wet weights were recorded to the nearest gram. The fork and total lengths of present free embryos were measured to the nearest centimeter.

Abiotic Data Analysis

Temperature, salinity, and depth were recorded before deployment of each longline. Temperature and salinity measurements were taken from the surface and bottom of the water column. A linear regression and Pearson's Correlation were used to analyze the relationship between bottom water temperature and Spiny Dogfish abundance.

QGIS Mapping and Habitat Use Analysis

Raw detections gathered from the FACT and ACT networks were downloaded as Excel spreadsheets and filtered by tag ID number before processing the data for false detections. Even though false detections occur less than 0.05% of the time, detections gathered in this study were filtered for false data both manually, and with software programs, to remove false detections caused by signal collisions and interference (Pincock 2012, Simpfendorfer *et al.* 2015). Preliminary review of detections searched for

false detections by manually examining intervals between logged detections. Intervals that were shorter than the minimum 30 second interval issued by the VEMCO V16-4H tags used in this study were discarded. Anomalous single records of a tag number that occurred in extreme spatial and temporal isolation from further detections were deemed likely false, and removed from analysis. To specifically remove spatially isolated false data this study used QGIS and an understanding of swimming speeds (0.5 - 1.75 body length per second), to manually visualize each shark's movement and remove spatially isolated detections (Oeffner and Lauder 2012, Maia and Wilga 2015). For example, if a series of detections observed in Winyah Bay was followed a couple hours later by detections logged hundreds of miles away, and this distant detection was shortly followed by further detections back in Winyah Bay, the middle, and likely, erroneous, detections were removed as it was unlikely a Spiny Dogfish could swim that fast. After manually visualizing shark movement in QGIS, raw detections were filtered utilizing the Glatos R software package to remove remaining false detections.

After the removal of false detections, GPS coordinates for the receivers visited by each shark were mapped in QGIS to visualize migratory paths for each animal. Particular attention was given to any detections from CCU/SCDNR receivers within the Winyah Bay area as reported to FACT/ACT. To identify temporal movement within and beyond the bay, timestamps for visited receivers were analyzed and sorted by Julian date. For each shark, the total length of its migratory path was calculated by totaling the length in kilometers of the shortest straight paths between visited receiver sites. Distances calculated are given to provide minimum scale of movement up and down the U.S. eastern coastline.

For each shark, days at liberty, total number of detections, terminal migratory points, and number of receivers visited was noted. Any return trips to Winyah Bay were carefully logged and total migratory distance calculated for any returning animals. A receiver site was designated as the area within the receiver's effective range. Based on range testing in Winyah Bay, this effective range does not exceed 400 m, and in most cases is approximately 200 m based on tide cycle and water temperature (Collatos 2018). After an animal was first detected within a site, each subsequent detection was considered part of a receiver visit. A receiver visit was considered concluded when the time between detections was greater than 20 minutes. This 20 - minute qualifier was based on visit period protocol outlined in past acoustic research on Winyah Bay sharks (Collatos 2018). Any further detections outside of the 20 - minute gap were considered the beginning of a new receiver visit. The total number of such visits per shark was calculated for each visited receiver.

Results

Longline Survey

A total of 94 longlines were deployed in Lower Bay (Fig 4). Sites were ultimately selected in the field based on the severity of current, wave, and weather conditions at the time of sampling. All longlines were set between January and April of sample years 2018, 2019, and 2020, with the exception of four longlines that were set in December 2018. Out of 94 set longlines, only 18 yielded elasmobranch captures all of which were Spiny Dogfish. Eighty-four individuals were captured over the course of the study (Table 1). All captured individuals were female. Sharks were most commonly captured in

February of each sample year, and were also most abundant during this time, both in terms of raw abundance and in terms of catch per unit effort, CPUE. The highest raw abundance occurred on February 1, 2020, when 40 individuals were captured across four 25-hook longlines. Monthly abundance, pooled from all sample years and the number of longlines set each month, can be seen in Table 2. Sharks continued to be captured into early and mid-March in smaller numbers. No Spiny Dogfish were observed in Winyah Bay past mid-March.

CPUE was relatively low due to the high number of longlines with no catch ($n = 76$). Of the five sampled months, no sharks were captured in December or April (Table 2). January yielded only one capture in 2019, for a CPUE of 0.08. Likewise, March had a low CPUE of 0.06. February had the highest CPUE of all sample months at 2.02 (Fig 5).

Of the 84 individuals observed, 78 were landed and measured. The remaining six individuals fell off the hook before they could be brought on board and processed. All 84 individuals were captured on the western side of the dredged channel (Fig 4). Processed individuals were all female. Fourteen sexually mature females had an acoustic tag implanted in the body cavity and were released at their points of capture. Of 59 individuals tagged with numbered dart tags, no recaptures were reported. The size of processed Spiny Dogfish ranged from 67 to 91 cm FL (Fig 7). The mean FL was 79.6 cm with a standard deviation of 4.6 cm, and did not vary between sample seasons ($p = 0.6$, $DF = 2$, $F = 0.5$).

Spiny Dogfish were captured within a narrow temperature window within Winyah Bay. Ninety-eight percent of individuals were captured at bottom water temperatures between 10°C and 13°C (Fig 8). The mean capture temperature was 12°C \pm 1.1° (mean \pm

SD). Overall, there was a negative relationship between abundance and increasing temperature ($R^2 = 0.48$). The mean salinity at captures was $28.1 \text{ ppt} \pm 6.6$ (mean \pm SD). Mean capture depth was 8 m but ranged as deep as 10.4 m (Table 3).

Reproductive Demographics

Over the course of the study 10 females were dissected to assess reproductive stage (Table 4). Dissected females ranged in size from 67 to 83 cm FL (76.5 ± 5.0 ; mean \pm SD). All dissections yielded developing ova in the ovaries and oviduct, or in the uteri. Two out of the 10 dissected individuals, including the smallest dissected shark (FL = 67 cm), had candled embryos in the uteri. Due to rupturing of some candled embryos, only two were measured at 11 cm and 12 cm TL. The salvaged candled embryos had wet weights of 29.3 g and 29.0 g respectively.

Three dissections in 2019 yielded four free embryos in a single female with a fork length of 80 cm. The remaining two dissections yielded candled embryos. Further dissections, carried out in 2020, yielded a total of 22 free embryos from the uteri of six mature females. On average, each of the six females carried 3.7 pups with a standard deviation of 1.3. The largest observed litter was six pups carried by a female with a fork length of 83 cm. A seventh female, dissected in 2020, expelled an undetermined number of free embryos post mortem. This being the case, any expelled pups that could not be traced to a carrying female were removed from consideration and were not measured. For the 22 embryos found in the uteri of dissected females, total lengths ranged from 10.2 cm to 13.7 cm, (11.5 ± 1.0 ; mean \pm SD). Wet weights for embryos excluded the weight of attached yolks, as some yolk sacs were ruptured. Embryo weights ranged from 4.3 g to 9.6 g ($6.3 \text{ g} \pm 1.6 \text{ g}$; mean \pm SD).

Acoustic Data & Large-Scale Movements

Fourteen acoustic tags were deployed over the course of the study. All individuals were tagged in lower Winyah Bay (Fig 9). Return signals were acquired from twelve tagged individuals with a total of 14,901 detections logged. After filtering detections through the Glatos R package 14,846 were determined to be valid detections. Of the tagged sharks, seven were tagged in 2019 and the remaining seven were tagged in 2020 (Table 5). Only five of the individuals tagged in 2020 yielded returns. Only two tagged sharks did not yield any detections post release (Sharks ID7834 & ID7836). Days at liberty ranged from 0 (Sharks ID7834 & ID7836) up to 674 (Shark ID7840). The total number of receivers visited ranged from 0 (Sharks ID7834 & ID7836) up to 26 (Shark ID7840). The number of detections per shark ranged from 0 (Sharks ID7834 & ID7836) up to 2,940 (Shark ID7845). The minimum distance, calculated based on the shortest straight path between points, ranged from 0 km (Sharks ID7834 & ID7836) up to 2,403.5 km (Shark ID7841).

Detections were low within Winyah Bay, as only three individuals swam within range of Winyah Bay receivers. Most detections occurred at two receivers within the confines of the jetties (Fig 9). Two additional receivers, located outside the jetty entrance assisted in determining exit paths from the Bay (Fig 11). These receivers logged detections from two tagged sharks, ID7840 and ID7838. The former left Winyah Bay after tagging and did not return. This held true for all other tagged sharks, except for shark ID7838. After being tagged on February 1, 2020, this individual left for nearshore waters off Myrtle Beach, before returning to the mouth of Winyah Bay 21 days later. Five days after its return to Winyah Bay, the shark displayed similar migration patterns as

displayed by other tagged individuals, and embarked for North Carolina waters. With the exception of this individual, no sharks were re-detected within the confines of the jetty after being tagged.

From Winyah Bay, northward movement was detected by seven individuals off the coast of Myrtle Beach. (Fig 10). By mid to late March, and into April, all sharks were detected in North Carolina, near Beaufort and Morehead City (Fig 11). Three sharks (ID7835, ID7840 and ID7841) displayed significant migration north of Cape Hatteras (Fig 10). Two of the three logged detection outside Little Egg Harbor, NJ and the Jacques Cousteau National Estuarine Research Reserve in October and November. Shark ID7835 migrated directly from North Carolina waters to waters 76 km south of New Bedford, MA. This migration took place over the course of eight months (Feb 2020 – October 2020), during which no other detections were logged. Shark ID7840 also displayed a large temporal gap in detections. After being detected off Atlantic City, NJ in November 2019, the individual was not detected again until November 4, 2020 south of New Bedford, at the same receiver that detected shark ID7835. From Massachusetts, shark ID7840 logged detections south of Long Island on November 4, 2020 before quickly migrating south to Pamlico Sound by December 16, 2020.

All acoustically tagged sharks were detected off the Shackleford Banks near Beaufort, NC (Fig 11) with the exception of the two individuals who logged no detections at all. Here, this study observed use of inshore waters, particularly around Cape Lookout and near the Rachel Carson Estuarine Sanctuary. Within these areas, receivers picked up a total of 8,682 detections. In exposed waters outside of Shackleford Banks, only 1,320 detections were collected. Large scale movement patterns around the

Shackleford Banks identified North/South movement directly south of Beaufort, along an array of acoustic receivers (Fig 11). A second entry point is indicated by the presence of multiple East/West paths between the North/South receiver array and the narrow entrance to Lookout Bight (Fig 11). The indication of a second entry point is supported by the high number of detections logged at a receiver located at the entrance to Lookout Bight. From this narrow entry point, paths either moved inshore, deeper into Lookout Bight, or moved back West towards the North/South array.

The higher quantity of detections at inshore receivers, comparative to exposed nearshore receivers, indicates significant use of bay and estuarine waters around Beaufort, NC. For example, a receiver at the mouth of Lookout Bight saw 4,397 detections by a total of seven individual sharks. Further cases of visit overlap were observed in this study (Table 6). At another inshore receiver inside the Shackleford Banks, six individuals logged a total of 4,272 detections. Such overlap occurred throughout the Beaufort area array, as well as at the array off Myrtle Beach, suggesting a shared migration path. In fact, sharks tagged in 2019 visited some of the same receivers as sharks tagged in 2020. With the exception of Shark ID7840, all individuals were last detected around the Shackleford Banks. Terminal points occurred in both estuarine and bay water as well as in exposed nearshore waters.

The most significant migratory route was charted by Shark ID7841. This individual, tagged on February 12, 2019 in Winyah Bay, swam north to New Jersey waters and returned to South Carolina, where the individual's tag pinged on a Winyah Bay area receiver. The shark's return visit occurred on February 9, 2020, almost a year to

the day it was tagged. This is the only individual make a return trip to the vicinity where it was tagged.

Discussion

Spiny Dogfish in Winyah Bay, SC

Across all three sample seasons, only female Spiny Dogfish were identified as using the lower estuarine waters of Winyah Bay. Of measured individuals, 90.8% had fork lengths consistent with L_{50} measurements ($\geq 72.5\text{cm}$) from earlier research (Campana *et al.* 2009). Of interest, this study did identify through dissections a mature individual with an FL less than published length-at-maturity (FL = 67 cm). This suggests that female Spiny Dogfish could reach maturity earlier than previously thought.

Data indicating winter season use of Winyah Bay exclusively by mature female Spiny Dogfish is consistent with Gary (2009) who found similar results during his sporadic winter sampling. The skew in sex ratio found in Winyah Bay is reflected in further research along the U.S. eastern coastline (Ulrich *et al.* 2007; Dell'Apa *et al.* 2014b; Dell'Apa *et al.* 2017; Sagarese *et al.* 2014; Haugen *et al.* 2017). While there is little research exploring use of enclosed bays and estuaries, extant research has identified female individuals distributing closer to shore than their male counterparts (Dell'Apa *et al.* 2014a; Dell'Apa *et al.* 2014b; Sagarese *et al.* 2014; Dell'Apa *et al.* 2017; Haugen *et al.* 2017). Surveys along the U.S East Coast have identified a negative relationship between female distribution and bathometry (Dell'Apa *et al.* 2017; Haugen *et al.* 2017). Both Haugen *et al.* (2017) and Dell'Apa *et al.* (2017) found males in deeper and more saline waters in comparison to the shallower, less saline, waters occupied by females.

Based on these more expansive studies, if males are present off South Carolina, they could be occupying deeper, offshore, waters. If possible, further Winyah Bay area research should sample outside the jetty to investigate potential male Spiny Dogfish distribution.

The lack of male Spiny Dogfish in Winyah Bay could be a result of females exhibiting social avoidance to reduce aggressive mating encounters (Sims 2005). It is also possible that the mature females identified in this study could be further utilizing the sheltered waters of Winyah Bay for foraging or shelter. The implications for foraging come from stomach contents of two individuals, one who regurgitated fresh menhaden and another who was dissected with a whole fish found in the stomach. The whole fish could not be identified. As this study identified mature and even gravid females inside the bay, these warmer sheltered waters could function as a metabolic sanctuary (Sims 2005; Sagarese *et al.* 2014). However, this is not likely the case in Winyah Bay as acoustic data does not suggest these gravid females remain in the bay for long enough for their residency to have an impact on embryonic growth. Rather this study suggests male avoidance and foraging as potential drivers for mature female Spiny Dogfish presence in Winyah Bay.

Distribution within the bay was restricted to the lower western portions, which suggests limited spatial use of Winyah Bay. This spatial distribution was consistent across all sample years, suggesting that Spiny Dogfish distribute within the seaward portions of the bay. As water temperature is known to affect distribution of Spiny Dogfish (Stehlik 2007; Ulrich *et al.* 2007; Campana *et al.* 2008; Carlson *et al.* 2014; Sagarese *et al.* 2014; Banglely *et al.* 2018), this study compared sample site water

temperatures with data taken at an upriver monitoring station. Temperature values logged for successful longline sets were consistent with sampling efforts along the U.S. eastern coastline (Gamble *et al.* 2002; Stehlik 2007; Ulrich *et al.* 2007 Carlson *et al.* 2014; Dell’Apa *et al.* 2014a; Sagarese *et al.* 2014; Bangley *et al.* 2018). That Spiny Dogfish became less abundant in the bay as waters warmed is also consistent with extant migratory research that indicates temperature change affects movement patterns (Stehlik 2007; Ulrich *et al.* 2007; Sagarese *et al.* 2014; Bangley *et al.* 2018). Based on this, it is likely that warming waters in mid to late March could function as a trigger for Spiny Dogfish emigration from the Winyah Bay area.

In a post hoc comparison middle bay salinity was found to be significantly lower than lower bay values over the winter months. Higher salinity in lower Bay was consistent with previously established salinity profiles (Abel *et al.* 2007; Gary 2009; Wingar 2019). Physiologically there is little recent research on how the Spiny Dogfish osmoregulates, though like all elasmobranchs, it uses the rectal gland for osmoregulation (Abel and Grubbs 2020; Burger and Hess 1960). In the taxonomically related North Pacific Spiny Dogfish, *Squalus suckleyi*, fluctuating hypo- and hyper-saline environments in their estuarine habitat were found to trigger changes in urea and ammonia excretion (Deck *et al.* 2016). Production of both were observed to increase at low salinities (Deck *et al.* 2016).

In this study acoustic monitoring did not suggest any movement into lower salinity middle bay waters. When taken in conjunction with catch data it is unlikely that Spiny Dogfish venture far into Winyah Bay. Research in Pamlico Sound, Chesapeake Bay, and the Hudson Rarity Estuary also found distribution concentrated towards

seaward areas (Stehlik 2007; Banglely *et al.* 2014). In depth analysis of temperature and salinity has identified Spiny Dogfish distributing in shallow coastal areas that exhibit low temperatures and high salinities (Stehlik 2007). These conditions are only met within lower Winyah Bay. This could be a factor restricting Spiny Dogfish distribution to this area.

However, during this study, three longlines had captures ($n = 40$) at relatively low salinities (<20 ppt). While at first this seems a high number of captures, most of these captures ($n = 38$) occurred on a day when the salinity probe was malfunctioning and giving inaccurate readings. The other two captures occurred on days when lots of fresh water from recent rainfall was flooding the Winyah Bay watershed. Further inaccuracies could be caused by strong current suspending the lightweight probe in the water column preventing true at-depth readings. As Winyah Bay is a mixed estuary, it is also possible that water currents carried the probe into pockets of fresh water that do not accurately reflect the salinity at points of capture. Additionally, this study logged some highly variable, outlying salinity values, that were likely due to equipment error. With the exception of three longlines, and despite these caveats, this study's overall results corroborate the occurrence of Spiny Dogfish in estuarine waters that possess low temperatures and mid to high salinity.

Temporal distribution in Winyah Bay proved to be just as restricted as spatial distribution. While summer species displayed presence in Winyah Bay over a period of months (Gary 2009, Collatos 2018, Pullen 2019, Wingar 2019), Spiny Dogfish presence was mostly restricted to the month of February. It is worth noting that sample effort was low in January due to equipment availability and logistical complications. Therefore, this

study is unable to pinpoint a precise arrival time in the Winyah Bay region based on catch data alone. Despite being unable to pinpoint an exact arrival period, the decreasing abundance as waters warmed in March suggests that Spiny Dogfish emigrate from Winyah Bay during this time, and are absent by April.

Movements South of Cape Hatteras, NC

Emigration from the bay in late February to mid-March is supported by acoustic data from the 14 tagged individuals. After tagging, most sharks left the bay area and were not detected again within its confines. Only two sharks did not yield any further detections post-release. These sharks possibly died before logging any detections. Only two tagged individuals (ID7838 & ID7840) tagged logged detections at Winyah Bay receivers. It is possible more sharks utilized Winyah Bay but did not enter the 200 – 400 m detection range of receivers within the bay (Collatos 2018). Even so, acoustic results show these two individuals left the bay at the end of February and followed similar northward migratory routes to other tagged sharks. In particular, ID7838 showed that even though it remained near Myrtle Beach, SC for over a week after tagging, it left South Carolina waters by the beginning of March. The proposed emigration period in mid-March is further supported by the fact that by this time all tagged individuals were detected in North Carolina around the Shackleford Banks near Beaufort, NC.

Based on the finding of this study and the findings of Ulrich *et al.* (2007), coastal South Carolina waters may be functioning as overwintering grounds for mature females south of Cape Hatteras. While no individuals tagged during this study displayed movement south of Winyah Bay this study cannot claim that Winyah Bay is the southernmost extent of winter migratory routes. This conclusion is based on evidence of

Spiny Dogfish inhabiting the waters of Bulls Bay, SC approximately 45 km south of Winyah Bay (Ulrich *et al.* 2007). Sampling conducted in late January and in March, identified 136 female individuals in the shallow nearshore environment of Bulls Bay. These historical catches support this study's findings that Spiny Dogfish residency in South Carolina waters runs from late January into March. Furthermore, Ulrich *et al.* (2007) documented the species occupying waters with similar average temperatures (13°C) as that of the average capture temperature in Winyah Bay (12°C).

Lacking connective data between Winyah Bay, SC and the Shackleford Banks, NC, inferences on precise migratory paths between the two points are difficult to make. However, there are data pointing to aggregations of Spiny Dogfish inhabiting shallow coastal waters along the coast between Myrtle Beach, SC and Morehead City, NC (Rulifson and Moore 2009). Gillnet surveys set in February and March identified 6 aggregations in waters up to 16 m deep along the South Carolina coast (Rulifson and Moore 2009). Of interest both Ulrich *et al.* (2007) and Rulifson and Moore (2009) identified primarily or exclusively females using shallow coastal waters along South Carolina as observed in the Winyah Bay area. While study this suggests shallow coastal waters along the South Carolina coast are important overwintering grounds, this research cannot rule out that overwintering females venture into deeper water offshore as they migrate off South Carolina, as seen along other portions of the U.S. East Coast (Sulikowski *et al.* 2010; Carlson *et al.* 2014),

In particular, large aggregations were identified in Long Bay, along the South Carolina coast, and in Onslow Bay, along the North Carolina coast between Cape Fear and Cape Lookout (Rulifson and Moore 2009). Rulifson and Moore (2009) further found

that among these aggregations the majority (96.6%) were large females. The sexual composition agrees not only with this study but also with extant literature concerning female distribution in shallow waters (Dell'Apa *et al.* 2014a; Dell'Apa *et al.* 2014b; Sagarese *et al.* 2014; Dell'Apa *et al.* 2017; Haugen *et al.* 2017). The temporal distribution of acoustic detections in Winyah Bay in February, and later, off the Shackleford Banks in North Carolina during March, coincides with the temporal distribution of the aggregates detected by Rulifson and Moore (2009). These two data sets, taken together, suggest female Spiny Dogfish presence along the Carolina coasts between the beginning of February and the end of March. Given the lack of detections at receivers between Winyah Bay and Beaufort, NC, in addition to the knowledge that females have been known to, this study suggests that a corridor for female Spiny Dogfish migration could run along the South Carolina/North Carolina coastline and should be taken into account when managing the fishery. Satellite tags should be deployed to outline the exact pathways taken by female Spiny Dogfish as they overwinter in their southern range.

Use of estuarine habitat near Beaufort, NC

Within inshore and nearshore waters around the Shackleford Banks acoustic data suggest the presence of two overall movement patterns. The latitudinally oriented receiver array immediately south of Beaufort was traversed by multiple sharks traveling North and South. From this North/South array multiple sharks displayed East/West movement to the mouth of Lookout Bight. Movement along the North/South array and between this array and the mouth of Lookout Bight suggest shared movement patterns among multiple tagged sharks. These shared movements suggest that Lookout Bight and

the Beaufort Inlet function as shared entry points to estuarine waters by migrating Spiny Dogfish.

When comparing the number of raw detections inside the Shackleford Banks to those in the exposed nearshore environment, the higher quantity of inshore detections suggests a significant amount of time spent in sheltered waters. This is particularly true for the entry point to Lookout Bight for example. Detections also indicate regular and extended use of sheltered waters surrounding the Rachel Carson Estuarine Sanctuary and in the sheltered waters of Lighthouse Bay, just off the eastern point of the Shackleford Banks. Given that this study lacks in situ abiotic data for Lookout Bight and for waters surrounding the Shackleford Banks, few inferences can be made on why Spiny Dogfish distribution appears the way it does. Future research should examine how water temperature, salinity, tide, and abundance of prey around the Shackleford Banks could affect the distribution patterns observed through acoustic telemetry.

While this study found that female Spiny Dogfish make significant use of shallow waters surrounding the Shackleford Banks in March and into April, there is evidence that they could remain in the area into May. Gillnet and longline surveys near the Rachel Carson Estuarine Sanctuary captured four female Spiny Dogfish in May in waters over 22°C (Bangley and Rulifson 2014) One additional individual was observed further north at the mouth of Jarret Bay and Wade Creek. This study made particular note of the fact that these captures represented unique observations of Spiny Dogfish in warm water.

The low catch observed by Bangley and Rulifson (2014) taken in context with this study's research indicating use of the Shackleford Banks area in March/April could be indicative of Spiny Dogfish schools leaving the area in the spring as waters warm.

However, given that 13 out of 14 migratory paths terminated off the Shackelford Banks, it is also possible that predation or fishing pressure could be removing individuals in the area. It is also possible that individuals moving northwards could simply be moving into waters that lack receiver arrays. Existing PSAT data has indicated that north of Cape Hatteras, Spiny Dogfish schools do exhibit movement offshore, into deeper waters that lack acoustic receiver arrays (Carlson *et al.* 2014).

Movement North of Cape Hatteras, NC

The three sharks that travelled north of Cape Hatteras provide some insight into the range of Spiny Dogfish overwintering off South Carolina. Carlson *et al.* (2014) provided powerful insights into the movements of Spiny Dogfish along the U.S. eastern coastline. In their research, they found indications of two sub-populations based on distinct movement patterns. As their study only tagged sharks as far south as Cape Hatteras, the research from Winyah Bay provides data that supports prior evidence of Spiny Dogfish utilizing coastal waters south of Cape Hatteras (Gamble *et al.* 2002, Ulrich *et al.* 2007). When considering overlap between the two subpopulations proposed by Carlson *et al.*, the movement of three sharks from the Winyah Bay study suggests that overlap could occur in the New Jersey/New York region and as far North as Massachusetts. These northern detections by Winyah Bay sharks, support existing suggestions that waters off southern New England could function as genetic mixing grounds for subpopulations of Spiny Dogfish (Carlson *et al.* 2014). Worth noting in this Winyah Bay study, is the return of shark ID7841 to Winyah Bay nearly a year after its tagging. Not only did this shark exhibit potential overlap with northern Spiny Dogfish but this individual's movements also display a return to southern waters, suggesting a degree

a philopatry in regards to South Carolina waters. Further telemetry and satellite tags data should be gathered to visualize the movements of Spiny Dogfish in their southernmost range, in context with movements exhibited by other Northwest Atlantic populations along the coast.

Conclusions

The recurring nature of mature female Spiny Dogfish in Lower Winyah Bay suggests limited inter-annual use of the estuary in mid-winter. Dissections further suggest that the majority of the population in Winyah Bay may also be gravid, providing implication for management of the species in the area. Spatially, occupation within the Bay was restricted to the more saline, seaward, portions within Mother Norton Shoals, suggesting narrow use of Winyah Bay. The combination of a narrow catch window from the end of January to mid-March and a high catch in February suggests temporally brief occupation of the area before migrating northwards. From Winyah Bay northwards, migration paths suggest additional use of inshore waters off Beaufort, NC. These findings provide insights into the composition and occupation of Spiny Dogfish south of Cape Hatteras and should be considered when managing coastal aggregates of females off South Carolina.

Figures & Tables:

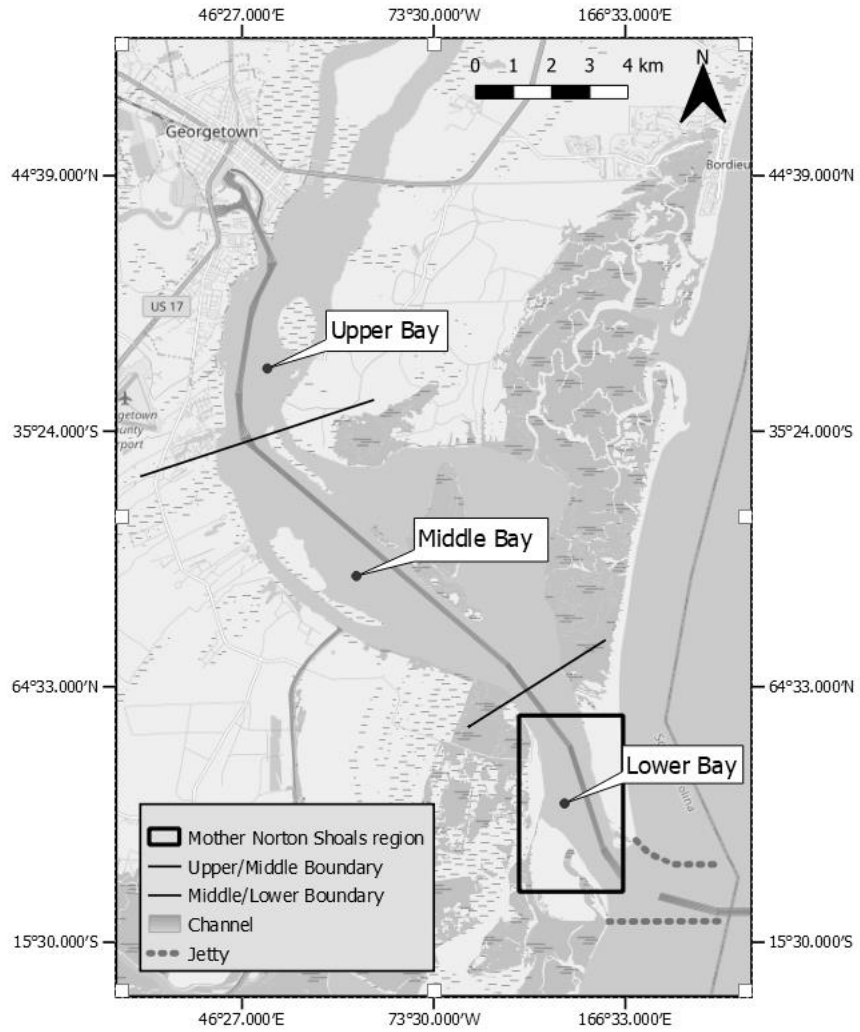


Fig 1: Winyah Bay regions and Mother Norton Shoals

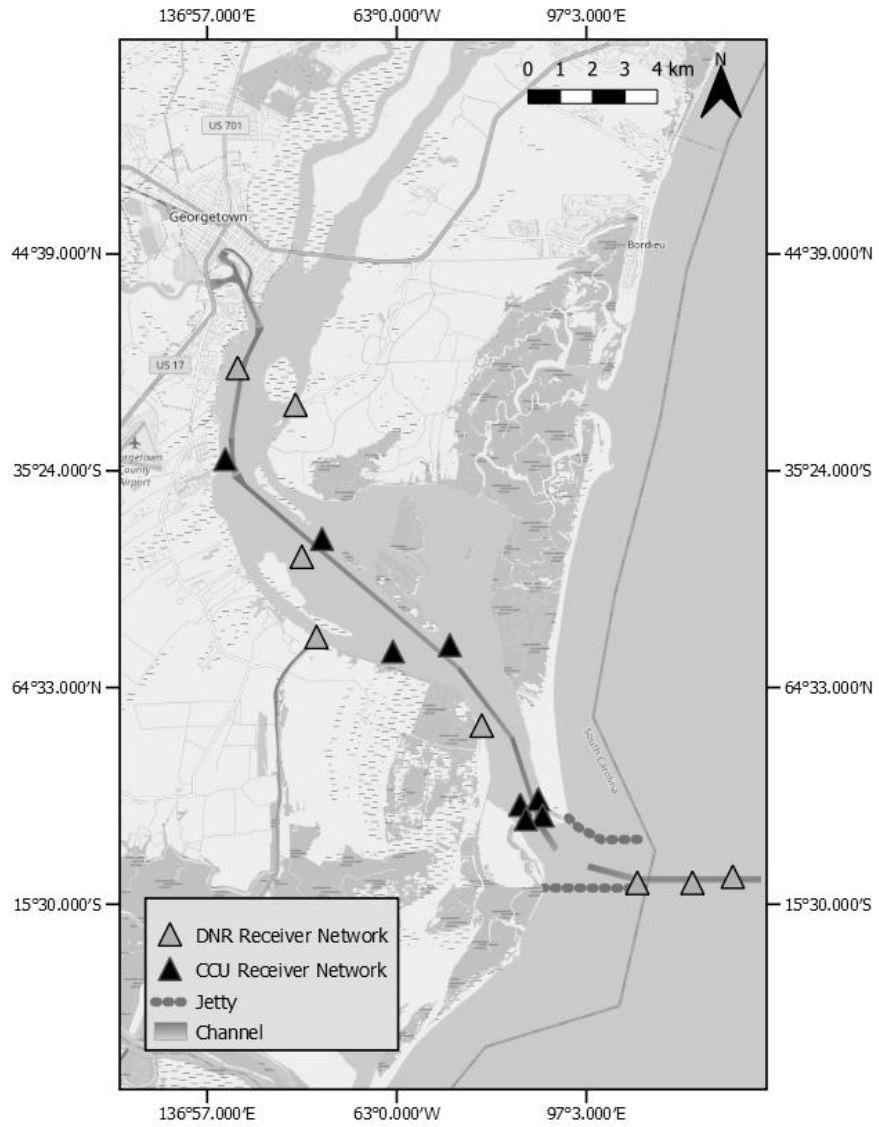


Fig 2: Coastal Carolina University, and South Carolina Department of Natural Resources, Vemco™ receiver arrays

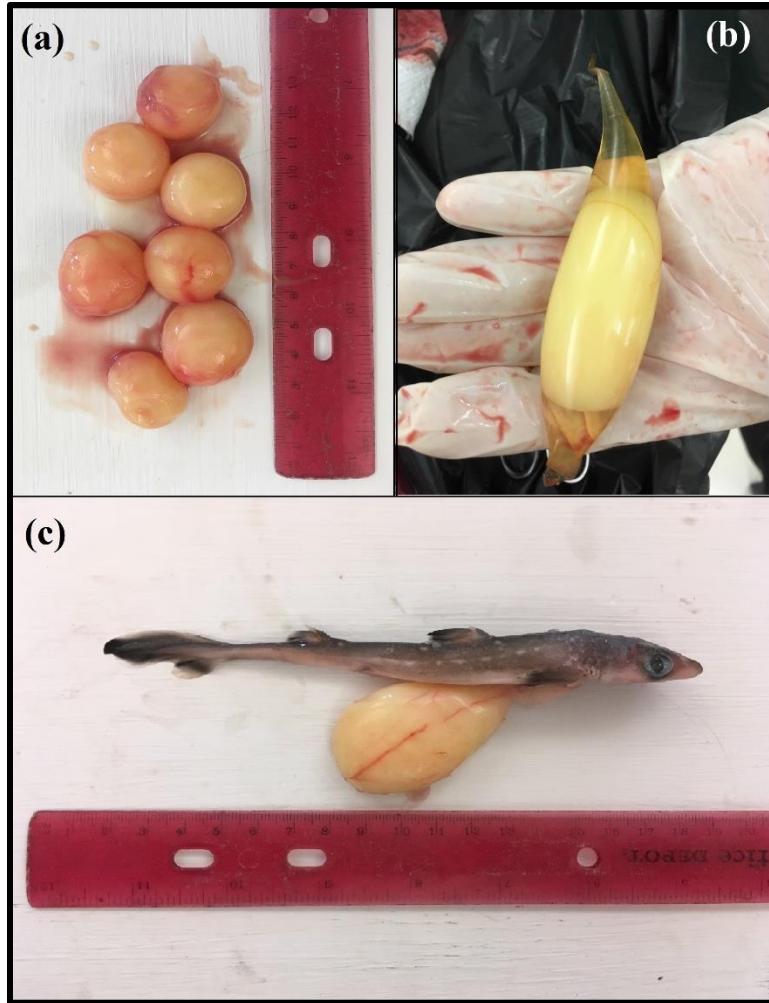


Fig 3: Embryonic stages in Spiny Dogfish, (a) vitellogenic ova (b) candled embryo (c) free embryo with yolk sac attached (Photo credit: Meredith Langford)

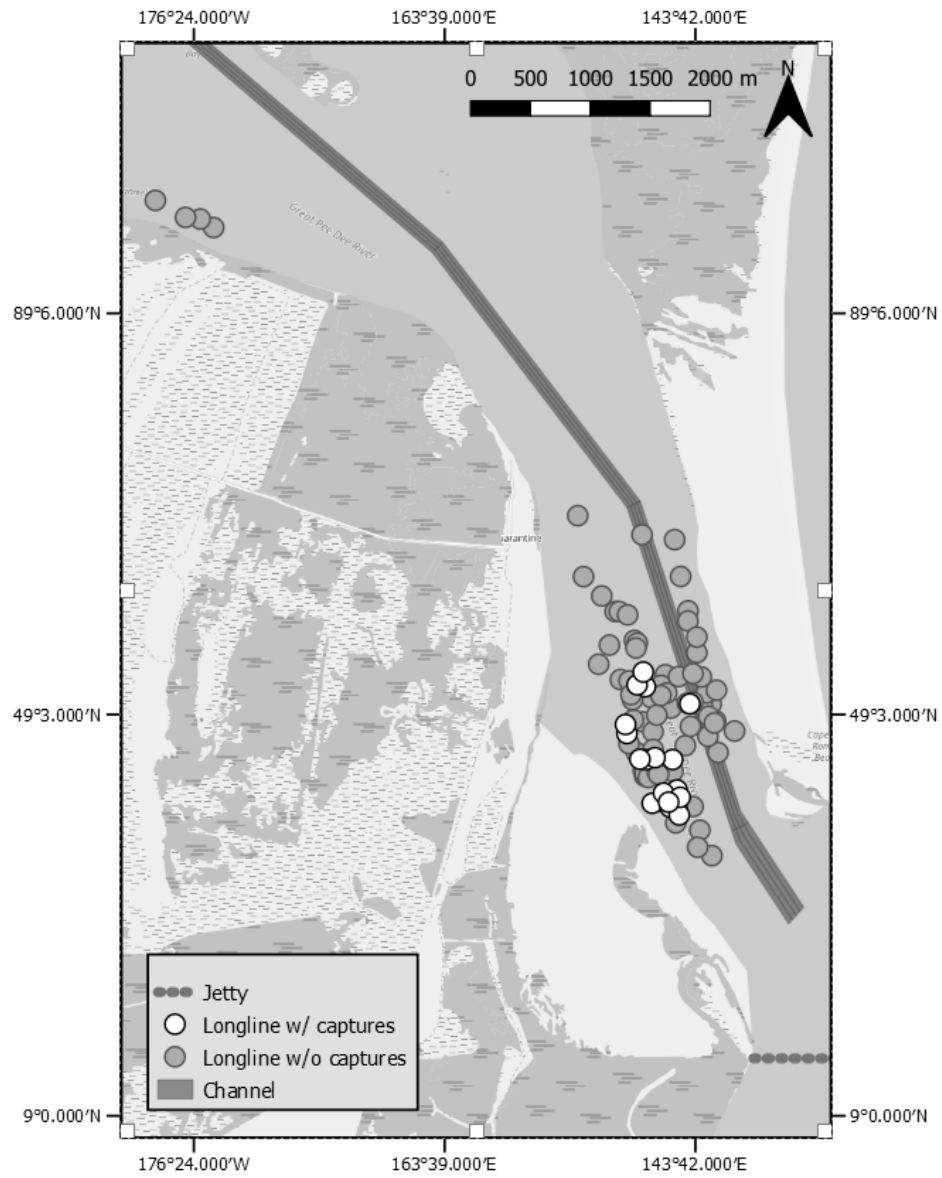


Fig 4: Sample effort and catch in Winyah Bay from sample seasons in 2018, 2019, and 2020. Longlines with no Spiny Dogfish captures are denoted by a grey marker. Longlines with Spiny Dogfish captures are denoted by white markers

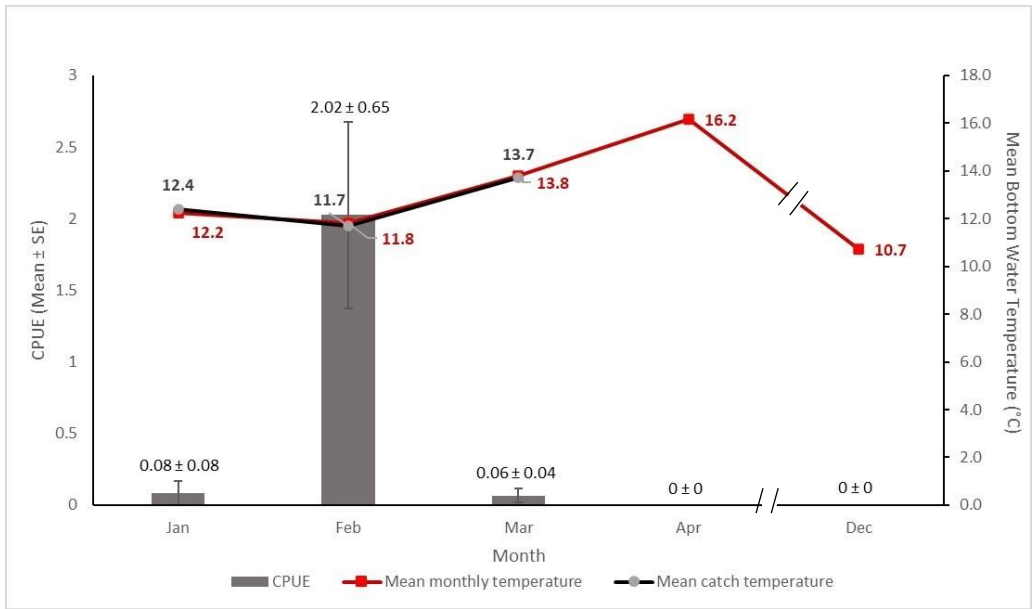


Fig 5: Mean monthly CPUE for Spiny Dogfish with mean monthly bottom water temperature (indicated by red line) and mean bottom water temperature for Spiny Dogfish captures (indicated by black line). No sampling or temperature monitoring occurred between mid-April and early December.

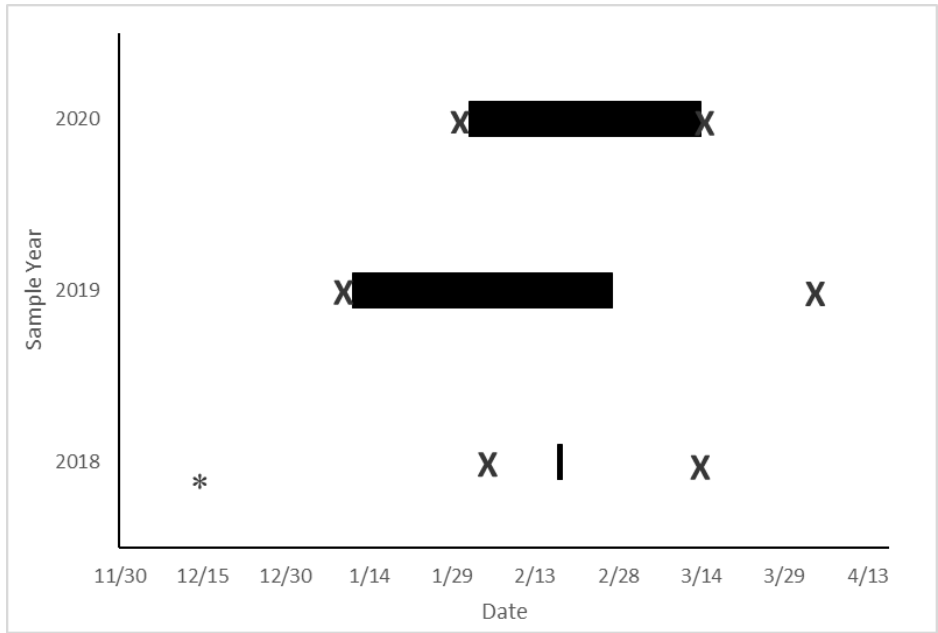


Fig 6: Gantt chart of Spiny Dogfish residency in lower Winyah Bay. Black bars indicate the dates between which Spiny Dogfish were captured in Lower Bay. “X”s indicate the beginning and end of each sample year. The asterisk indicates the four longline sets conducted in December 2018.

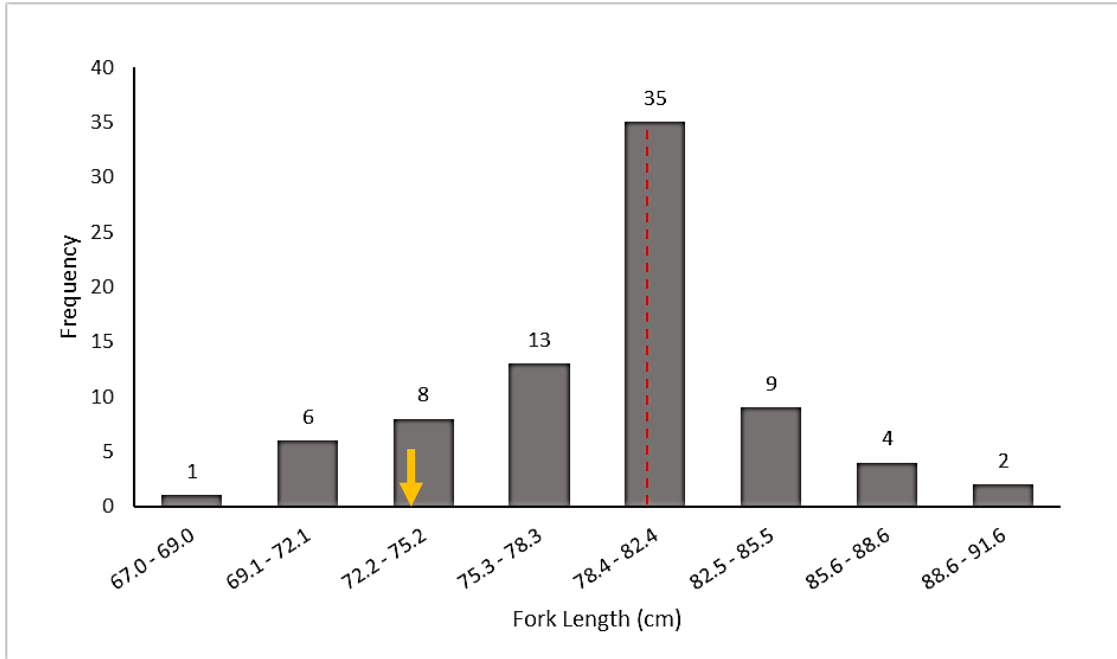


Fig 7: Fork length frequency distribution of female *S. acanthias* (n = 78) in Winyah Bay, SC. The red dashed line indicates the mean fork length of 79.6 cm. Published length at maturity ($L_{50} = 72.5$ cm FL) is denoted by a downward facing yellow arrow (Campana *et al.* 2009).

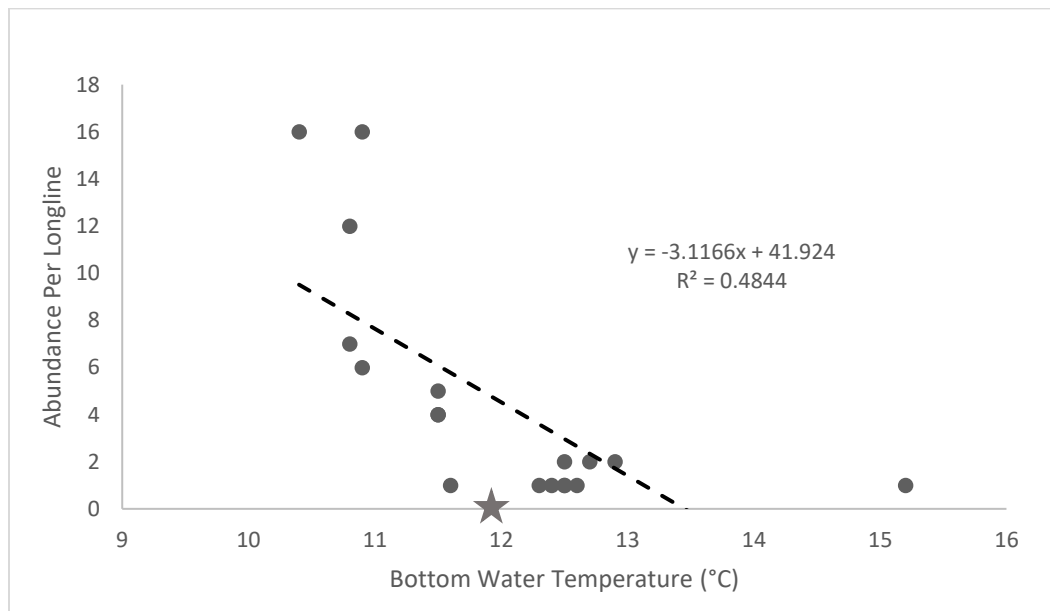


Figure 8: Linear regression of abundance per longline versus bottom water temperature ($R = 0.48$). Only longlines with successful captures are included in the graph. The star indicates the mean capture temperature of 12°C.

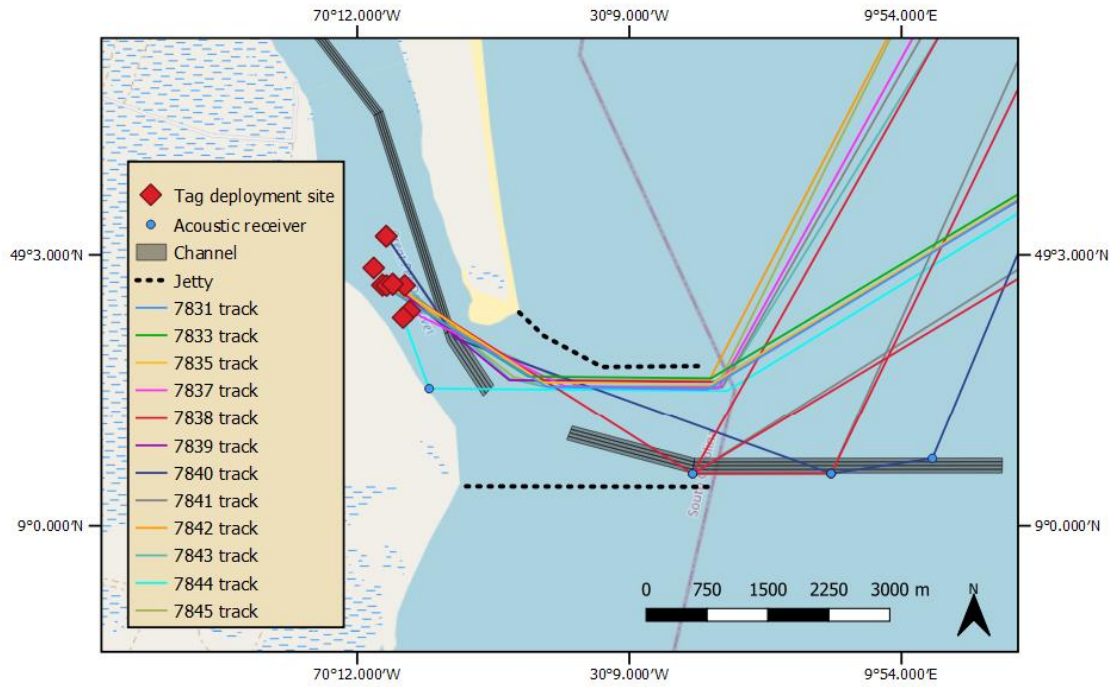


Fig 9: Movement of tagged sharks in Winyah Bay, including distribution of tag deployment sites and the location of four acoustic receivers around the bay entrance

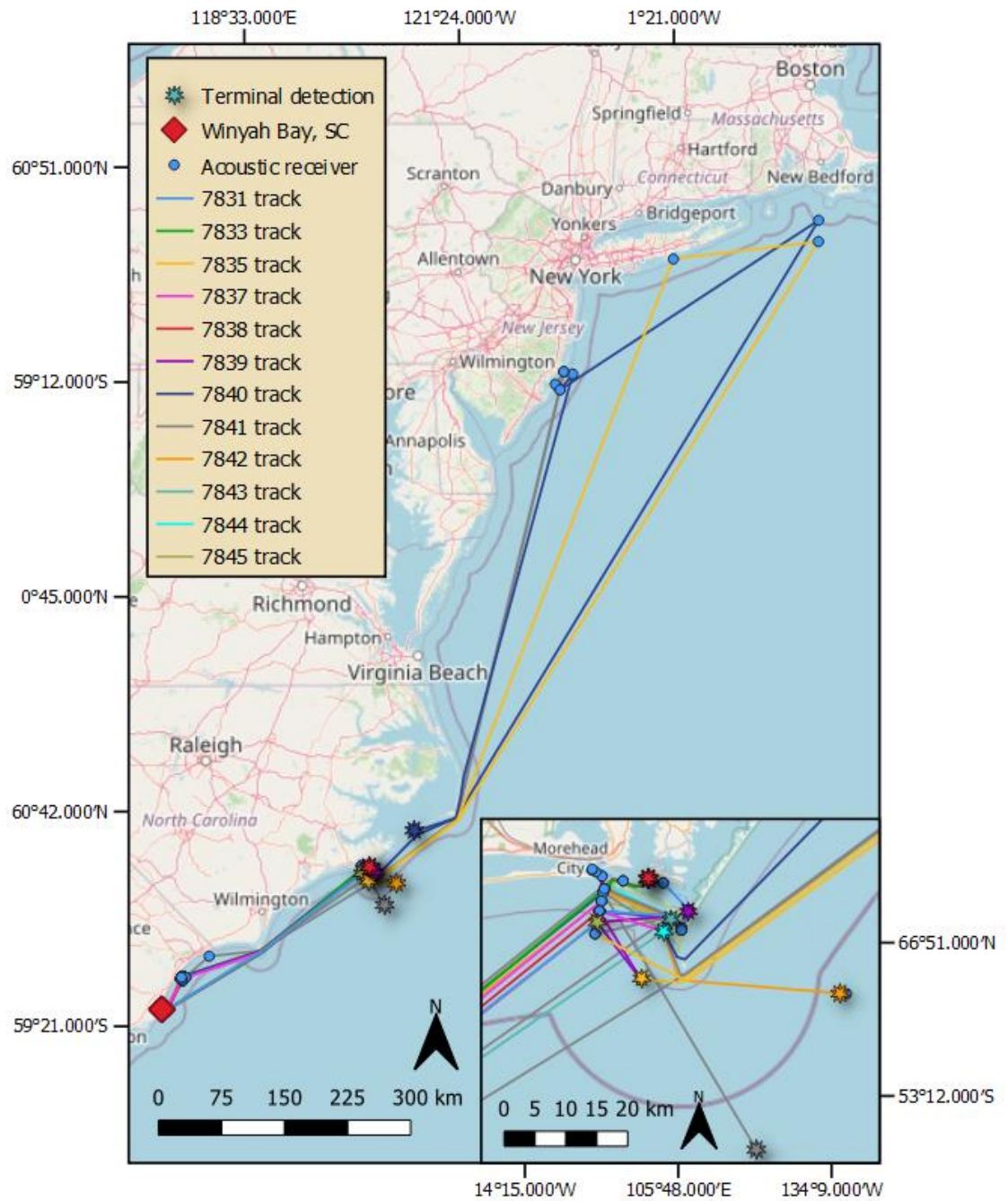


Fig 10: Migratory routes of tagged sharks with inset map showing North Carolina movements

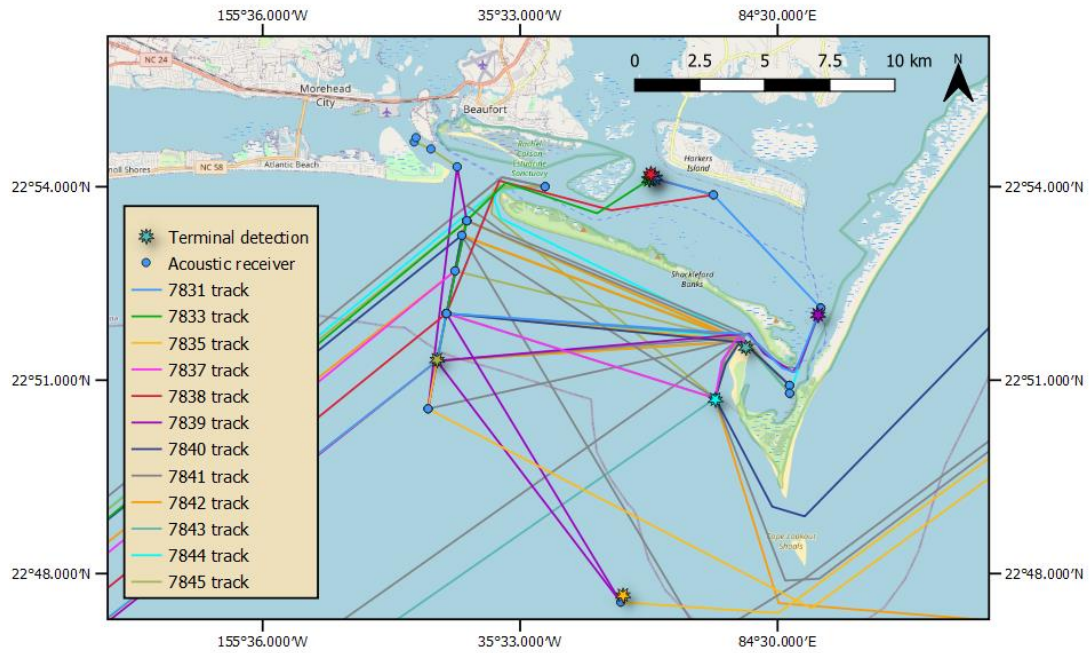


Fig 11: Movement of acoustically tagged sharks off Beaufort, NC

Table 1: General catch results

Longlines set in Winyah Bay, SC	94
Longlines with Spiny Dogfish captures	18
Total Spiny Dogfish captured	84
Total Spiny Dogfish dissected	10
Spiny Dogfish acoustically tagged	14
Mean Spiny Dogfish fork length (cm)	79.6
Fork length range (cm)	67 - 91

Table 2: Pooled abundance per month and pooled longline sets per month from across all sample years

SAMPLE MONTH	ABUNDANCE	LONGLINE SETS	CPUE ± SD
JANUARY	1	12	0.08 ± 0.29
FEBRUARY	81	40	2.02 ± 4.12
MARCH	2	28	0.07 ± 0.25
APRIL	0	8	0.00 ± 0.00
DECEMBER	0	4	0.00 ± 0.00

Table 3: Abiotic conditions for all longlines and for longlines yielding Spiny Dogfish captures

	LONGLINE ABIOTIC CONDITIONS		CONDITIONS FOR LINES WITH SPINY DOGFISH	
	Mean ± SD	Range (min - max)	Mean ± SD	Range (min - max)
BOTTOM WATER TEMPERATURE (°C)	13.2 ± 1.8	9.4 - 17.4	12.0 ± 1.1	10.4 - 15.2
BOTTOM SALINITY (PPT)	25.8 ± 7.7	1.6 – 33.9	28.1 ± 6.6	12.3 – 33.5
DEPTH (M)	8.0 ± 1.6	5.00 – 11.0	8.0 ± 1.7	5.4 – 10.4

Table 4: Size of dissected females and gestational stage results

Dissection #	Capture year	Fork Length (cm)	Total Length (cm)	# Developing Ova in uteri	# Free Embryos	# Canded Embryos	Notes
1	2020	77	85.5	5	4	0	
2	2020	73	93	6	2	0	
3	2020	72	91	4	3	0	
4	2020	74.5	83.5	4	4	0	
5	2020	76	83	5	3	0	
6	2020	83	94	6	6	0	
7	2020	81.5	90	4	0	0	expelled pups post mortem
8	2019	80	90	-	4	0	
9	2019	81	90.5	-	0		ruptured canded embryos present
10	2019	67	76	-	0	2	

Table 5: General acoustic results for Spiny Dogfish tagged in Winyah Bay

Shark ID	Date tagged	Last detection	Days at liberty	Receivers visited	# Detections	Starting latitude	Northernmost latitude	Terminal latitude	Min distance traveled (km)
7831	3/2/2020	3/30/2020	29	5	159	33.21297	34.69443	34.69443	314.2
7833	3/13/2020	3/27/2020	15	4	95	33.20975	34.69443	34.69443	314.3
7834	2/28/2020	N/A	0	0	0	33.2195	N/A	N/A	N/A
7835	2/1/2020	1/8/2021	343	6	121	33.21308	40.88958	34.54843	2117.0
7836	2/1/2020	N/A	0	0	0	33.21308	N/A	N/A	N/A
7837	2/26/2019	3/13/2019	16	11	1014	33.21011	34.66248	34.61865	348.7
7838	2/1/2020	4/23/2020	83	8	1545	33.21308	34.69443	34.69443	417.6
7839	2/1/2020	3/25/2020	54	7	132	33.21308	34.6983	34.64968	348.3
7840	2/12/2019	12/16/2020	674	26	1289	33.2184	39.62008	39.46838	2171.5
7841	2/12/2019	4/6/2020	420	23	2475	33.2184	39.64402	34.30183	2403.5
7842	2/25/2019	4/7/2019	42	19	2476	33.21293	34.67975	34.61865	489.7
7843	2/8/2019	3/9/2019	30	6	904	33.21294	34.64783	34.63595	355.1
7844	2/12/2019	4/2/2019	50	8	1719	33.20937	34.67975	34.61865	446
7845	2/12/2019	4/11/2019	59	19	2933	33.21489	34.70833	34.63149	621.8

Table 6: Use of North Carolina waters by tagged Spiny Dogfish as represented by number of detections per receiver and the number of visiting sharks per receiver

Longitude	Latitude	Inshore/estuarine vs. exposed waters	# Detections	# Visiting individuals
-76.39946	34.30183	Exposed	4	1
-76.60234	34.54843	Exposed	14	1
-76.68307	34.61503	Exposed	63	3
-76.56275	34.61865	Exposed	678	7
-76.53156	34.62038	Inshore/estuarine	4272	6
-76.67938	34.63149	Exposed	214	8
-76.54993	34.63595	Inshore/estuarine	4397	7
-76.67538	34.64783	Exposed	111	11
-76.51855	34.64968	Inshore/estuarine	115	4
-76.67177	34.66248	Exposed	40	4
-76.66893	34.67471	Exposed	105	4
-76.66686	34.67975	Exposed	197	6
-76.56351	34.68864	Inshore/estuarine	552	2
-76.63404	34.69146	Inshore/estuarine	243	3
-76.58935	34.69443	Inshore/estuarine	902	3
-76.6709	34.6983	Inshore/estuarine	13	2
-76.6819	34.70442	Inshore/estuarine	29	1
-76.68888	34.70684	Inshore/estuarine	11	1
-76.68812	34.70833	Inshore/estuarine	3	1
-76.02859	35.073373	Inshore/estuarine	19	1
-76.6023	34.54843	Exposed	26	1
-76.6013	34.55097	Exposed	12	1
-76.2418	34.52827	Exposed	157	1

References

- Abel, D. C. and Grubbs, R. D. 2020. Shark Biology and Conservation Essentials for Educators, Students, and Enthusiasts. Johns Hopkins University Press, Baltimore, Maryland.
- Abel, D. C., R. F. Young, J. A. Garwood, M. J. Travaline, and B. K. Yednock. 2007. Survey of the Shark fauna in two South Carolina estuaries and the impact of salinity structure. In: Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. American Fisheries Society Symposium 50, Maryland, pp 109–125.
- Bangley, C. W., L. Paramore, S. Dedman, and R. A. Rulifson. 2018. Delineation and mapping of coastal shark habitat within a shallow lagoonal estuary. PLOS ONE 13(4):e0195221.
- Bangley, C., and R. Rulifson. 2014. Observations on spiny dogfish (*Squalus acanthias*) captured in late spring in a North Carolina estuary. F1000Research 3(189).
- Bigelow, H. B. and W. C. Schroeder. 1948. Sharks. Pages 59 - 546 in Tee-Van, J., C. M. Breder, S. F. Hildebrand, A. E. Parr, and W. C. Schroeder. 1948. Fishers of the Western North Atlantic, Part 1, Lancelets, Cyclostomes, Sharks. Sears Foundation for Marine Research, Yale University, New Haven, CT.
- Burger, J. W., and W. N. Hess. 1960. Function of the Rectal Gland in the Spiny Dogfish. Science 131(3401):670–671.

- Campana, S. E., W. Joyce, and D. W. Kulka. 2009. Growth and reproduction of spiny dogfish off the eastern coast of Canada, including inferences on stock structure. *Biology and Management of Dogfish Sharks*. (Eds VF Gallucci, GA McFarlane, and GG Bargmann.) pp:195–208.
- Campana, S. E., J. F. Gibson, L. Marks, W. Joyce, R. Rulifson, and M. Dadswell. 2008. Stock Structure, life history, fishery and abundance indices for spiny dogfish (*Squalus acanthias*) in Atlantic Canada. Canadian Science Advisory Secretariat Research Document 2007/089.
- Carlson, A. E., E. R. Hoffmayer, C. A. Tribuzio, and J. A. Sulikowski. 2014. The Use of Satellite Tags to Redefine Movement Patterns of Spiny Dogfish (*Squalus acanthias*) along the U.S. East Coast: Implications for Fisheries Management. *PLoS ONE* 9(7): e103384. Doi:10.1371/journal.pone.0103384
- Collatos, C. 2018. Seasonal Occurrence, Relative Abundance, and Migratory Movements of Juvenile Sandbar Sharks, *Carcharhinus plumbeus*, in Winyah Bay, South Carolina. *Electronic Theses and Dissertations*.
- Dell’Apa, A., P. Maria Grazia, and C. Bonzek. 2017. Modeling the habitat distribution of spiny dogfish (*Squalus acanthias*), by sex, in coastal waters of the northeastern United States. *Fishery Bulletin* 115(1):89–100.
- Dell’Apa, A., C. W. Bangley, and R. A. Rulifson. 2014a. Who let the dogfish out? A review of management and socio-economic aspects of spiny dogfish fisheries. *Reviews in Fish Biology and Fisheries* 25:273-295.

- Dell'Apa, A., J. Cudney-Burch, D. G. Kimmel, and R. A. Rulifson. 2014b. Sexual Segregation of Spiny Dogfish in Fishery-Dependent Surveys in Cape Cod, Massachusetts: Potential Management Benefits. *Transactions of the American Fisheries Society* 143:833-844.
- Fordham, S., Fowler, S.L., Coelho, R.P., Goldman, K. & Francis, M.P. 2016, March 13. *Squalus acanthias*, Spiny Dogfish. International Union for Conservation of Nature.
- Gamble, M. E., B. Halgren, B. Kelly, T. Moore, and W. Outten. 2002. Interstate Fishery Management Plan for Spiny Dogfish. Atlantic States Marine Fisheries Commission. Fishery Management Report No. 40. Arlington, Virginia.
- Gary (Jr.), S. J. 2009. Shark Population Structure and Partitioning in Winyah Bay, SC. Coastal Carolina University.
- Haugen, J. B., T. H. Curtis, P. G. Fernandes, K. A. Sosebee, and P. J. Rago. 2017. Sexual segregation of spiny dogfish (*Squalus acanthias*) off the northeastern United States: Implications for a male-directed fishery. *Fisheries Research* 193:121-128.
- Maia, A., and Wilga, C. 2015. Dorsal fin function in spiny dogfish during steady swimming. *Journal of Zoology*. 28(2).
- McMillan, D.G., and Morse, W.W. 1999. Essential Fish Habitat Source Document: Spiny Dogfish, *Squalus acanthias*, Life History and Habitat Characteristics. NOAA Technical Memorandum NMFS-NE-150, Woods Hole, Massachusetts.

- Nammack, M. F., J. A. Musick, and J. A. Colvocoresses. 1985. Life History of Spiny Dogfish off the Northeastern United States. *American Fisheries Society* 114:367-376.
- Natanson, L. J., C. T. McCandless, K. James, and J. Hoey. 2017. Gestation period and pupping seasonality of female spiny dogfish (*Squalus acanthias*) off southern New England. *Fishery Bulletin - National Oceanic and Atmospheric Administration* 115:473-483.
- Oeffner, J., and Lauder, G. V. 2012. The Hydrodynamic Function of Shark Skin and Two Biometric Applications. *Journal of Experimental Biology*. 215(5):785-795.
- Pincock, D.G., 2012. False detections: what they are and how to remove them from detection data. VEMCO, DOC-004691 Available: www.vemco.com/pdf/false_detections.pdf.
- Pullen, E. V., 2019. Microplastics in the Digestive System of the Atlantic Sharpnose Shark (*Rhizoprionodon terraenovae*) in Winyah Bay, SC. Master's thesis. Coastal Carolina University, Conway, South Carolina.
- QGIS Development Team. 2018. QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>
- Rootes-Murdy, K., G. Skomal, T. Moore, P. Burns, and T. Scott. 2019. 2019 Review of the Atlantic States Marine Fisheries Commission fishery management plan for Spiny Dogfish (*Squalus acanthias*) 2018/2019 fishing year. Atlantic States Marine Fishery Commission. 2019 FMP Review Report, Arlington, Virginia.

- Rulifson, R. A., and T. M. Moore. 2009. Population Estimates of Spiny Dogfish Aggregation Overwintering South of Cape Hatteras, North Carolina, Using an Area Density Method. Pages 133–138 in V. F. Gallucci, G. A. McFarlane, and G. G. Bargmann, editors. *Biology and Management of Dogfish Sharks*. American Fisheries Society, Bethesda, Maryland.
- Sagarese, S. R., M. G. Frisk, T. J. Miller, K. A. Sosebee, J. A. Musick, and P. J. Rago. 2014. Influence of environmental, spatial, and ontogenetic variables on habitat selection and management of spiny dogfish in the Northeast (US) shelf large marine ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences* 71(4):567–580.
- Simpfendorfer, C. A., C. Huveneers, A. Steckenreuter, K. Tattersall, X. Hoenner, R. Harcourt, and M. R. Heupel. 2015. Ghosts in the data: false detections in VEMCO pulse position modulation acoustic telemetry monitoring equipment. *Animal Biotelemetry* 3(1):55.
- Sims, D. W. 2005. Differences in habitat selection and reproductive strategies of male and female sharks. Pages 127–147 in K. Ruckstuhl and P. Neuhaus, editors. *Sexual Segregation in Vertebrates Ecology of the Two Sexes*. Cambridge University Press, New York.
- Stehlik, L. L. 2007. Essential Fish Habitat Source Document: Spiny Dogfish, *Squalus acanthias*, Life History and Habitat Characteristics. NOAA Technical Memorandum NMFS-NE-203, Woods Hole, Massachusetts.

Sulikowski, J. A., B. Galuardi, W. Bubley, N. B. Furey, W. B. D. Iii, G. W. I. Jr, and P.

C. W. Tsang. 2010. Use of satellite tags to reveal the movements of spiny dogfish *Squalus acanthias* in the western North Atlantic Ocean. *Marine Ecology Progress Series* 418:249–254.

TRAC (Transboundary Resources Assessment Committee). 2010. Northwest Atlantic Spiny Dogfish. NOAA Fisheries, Fisheries and Oceans Canada, Status Report 2010/02.

Ulrich, G. F., C. M. Jones, W. B. Driggers, J. M. Drymon, D. Oakley, and C. Riley. 2007.

Habitat utilization, relative abundance, and seasonality of sharks in the estuarine and nearshore waters of South Carolina. Page 125 *American Fisheries Society Symposium*. American Fisheries Society.

Wingar, J., 2019. Osmoregulation and Salinity Preference in juvenile Sandbar Sharks (*Carcharhinus plumbeus*) in Winyah Bay, SC, USA. Master's thesis. Coastal Carolina University, Conway, South Carolina.

