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Broad-Scale Vertical and Horizontal Behavior of the White Shark (Carcharodon Carcharias) in the Western North Atlantic

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Thesis of
Taryn Szalay

Submitted in Partial Fulfillment of the Requirements for the Degree of

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Approved:
Thesis Committee

Committee Chair: David Kerstetter

Committee Member: Gregory Skomal

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NOVA SOUTHEASTERN UNIVERSITY
HALMOS COLLEGE OF ARTS AND SCIENCES

Broad-scale vertical and horizontal behavior of the white shark (*Carcharodon carcharias*) in the western North Atlantic

By

Taryn Elizabeth Szalay

Submitted to the Faculty of the
Halmos College of Arts and Sciences
in partial fulfillment of the requirements for
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Abstract

The ecology of white sharks *Carcharodon carcharias* in the western North Atlantic (WNA) is largely unknown. With a lack of essential fish habitat (EFH) identified by the National Oceanic and Atmospheric Administration (NOAA), understanding white shark behaviors is crucial to protect aggregation sites and other essential habitats (e.g., mating, parturition) for white sharks. To better understand the movements of these animals, data from 26 tagged white sharks are examined here. Data from the pop-up satellite archival transmitting (PSAT) tags from these sharks were analyzed using the HMMoce package for R (R Development and Core Team 2015) and tracks were generated for all 26 individuals. Additional environmental parameters from the PSAT data were used to generate improved tracks, which were cross referenced with oceanographic data from ocean observing system portals.

Vertical movements uncovered 3 main behavior clusters: ROD (rapid oscillatory dives), Travel, and Coastal. These behaviors occurred both on and off the continental shelf, but ROD did not occur in waters around Cape Cod. This behavior was also not present in juveniles (n = 3). There was no evidence of an offshore common foraging area, but Cape Cod was shown to be a large aggregation site, likely due to the increased seal population and warm waters in the summer months. Overall, this research provides a more comprehensive understanding of the temporal and spatial movements in white sharks in the WNA. It also helps establish the diving behaviors of this population. With large knowledge gaps regarding the white shark life history and ecology, these findings help pinpoint areas of importance for white sharks in the WNA, to better assist with management of this species and its habitat.

Keywords

White shark · Habitat utilization · Migration · *Carcharodon carcharias* · Diving behavior · HMMoce

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Introduction

White Shark

The white shark is a member of Family Lamnidae, the mackerel sharks, and is a highly migratory shark species with a cosmopolitan distribution (Castro, 2011). As defined by the National Oceanic and Atmospheric Administration (NOAA), highly migratory species (HMS) are fish species that carry out extensive migrations and can occur in both exclusive economic zones (EEZs) and high seas (NOAA, 2006). The white shark carries out long trans-oceanic movements and dives to depths up to 1200 m (Bonfil et al., 2005; Bonfil et al., 2010; Duffy et al., 2012; Skomal et al., 2017). The maximum size of the white shark is undefined, but it is the largest of the lamnid sharks and estimated to reach 600–640 cm total length (total length; TL) (Compagno 2001). This species, previously thought to have a maximum lifespan of ~30 years, has been reported to live to at least 70 years based on bomb radiocarbon validation of vertebral sections (Goldman & Cailliet, 2004; Hamady et al., 2014; Natanson & Skomal, 2015).

The white shark is generally considered a solitary species, although small feeding aggregations are occasionally seen, usually involving whale carcasses (Compagno, 1984). Historically, adult white sharks were once thought to feed on pinnipeds in the WNA (Wood et al., 2009), but the regional extirpation of seal populations occurred during the 20th century (Wood et al., 2009). In response to this decrease in seal abundance, it is hypothesized that there was a dietary shift in white sharks to other prey and the scavenging of whale carcasses (Carey et al., 1982; Curtis et al., 2014; Skomal et al., 2012). Since the implementation of the U.S. Marine Mammal Protection Act in 1972, seal populations in the WNA have rebounded (NMFS, 2009; Wood et al., 2009). Currently, subadult and adult white sharks in the WNA are thought to be increasingly incorporating seals into their diet due to improved gray seal, *Halichoerus grypus*, abundance (Skomal et al., 2012). In contrast to adults, juvenile white sharks have been reported to be piscivorous, primarily feeding on smaller sharks, a variety of bony fishes, and even some invertebrates (Casey & Pratt, 1985; Castro, 2011).

At present, there is limited information about white shark reproduction. However, it is estimated that male white sharks reach maturity at around 340 cm total length (TL) while females are thought to mature at 475 cm TL (Castro, 2011). Parturition is thought to occur in temperate regions in the spring and summer (Francis, 1996). Like other mackerel sharks, females exhibit ovoviviparity (aplacental viviparity) where embryos develop inside eggs that are held within the mother until after they hatch, and the pups are born live (Francis, 1996). Broods consist of 7-14 pups (Bruce, 1992; Castro, 2011; Francis, 1996; Uchida et al., 1996) ranging in length from 120-150 cm TL (Uchida et al., 1996; Francis, 1996).

White shark conservation is challenging for several reasons. The immense geographic scale of pelagic marine ecosystems inhibits the ability to monitor entire white shark populations (Bonfil, 1994; Baum et al., 2003). The broad horizontal movements of these animals also make them very difficult to monitor. White sharks are occasionally caught as fisheries bycatch and are susceptible to overfishing, like most sharks, due to their relatively slow growth rate, late maturity, and low fecundity (Bonfil, 1994). As fishing fleets have expanded further into the open ocean, large marine predators, occasionally including white sharks, have been exposed to bycatch mortality (Bowlby and Gibson, 2020). Many shark species have been increasingly caught as bycatch in recent decades in pelagic longline fisheries since the early 1960s (Baum et al., 2003; Bowlby and Gibson, 2020). Since the 1970s, there was a 63-73% decrease in white shark abundance in the WNA, making this species particularly vulnerable to bycatch. However, populations are now starting to rebound (Bowlby and Gibson, 2020; Curtis et al., 2014). Juveniles are especially sensitive, as shown by Weng et al. (2007b) in the United States and Mexico. Without the ability to properly monitor these populations, knowledge gaps regarding the ecology of this species such as population assessments, the identification of EFH, and diving behaviors hinder management and conservation efforts.

Aside from bycatch, white sharks have been genetically linked to part of the illegal fin trade (Shivji et al., 2005). As stated by Baum et al. (2003), the exploitation of sharks for their fins is of international concern. Even though the capture and trade of white sharks is prohibited in multiple countries, the illegal trade of this species' fins still occurs internationally. In Shivji et al. (2005), seized shark fin product purchased from commercial fishermen fishing in U.S. Atlantic waters that was intended for Asian markets was labelled as "porbeagle." This product was seized by agents of the U.S. National Oceanic and Atmospheric Administration's Office of Law Enforcement (OLE) from the warehouse of a seafood dealer in the U.S. East Coast (Shivji et al., 2005). Genetic analyses later revealed that these fin pairs originated from 21 different white sharks. This finding demonstrates that there is exploitation of a highly protected shark species in the WNA, with unknown consequences to their population status. Due to this uncertainty, increased monitoring of white shark populations would be beneficial.

Currently, the white shark in Atlantic waters is managed under the 2006 Consolidated Atlantic Highly Migratory Species Fishery Management Plan (CAHMS FMP), which is administered by the Highly Migratory Species Management Division of NOAA's National Marine Fisheries Service (NMFS). The CAHMS FMP also includes other highly migratory species such as tunas, sharks, swordfish (*Xiphias gladius*), and istiophorid billfishes in the U.S. fisheries of the Atlantic Ocean, Gulf of Mexico, and Caribbean waters. The white shark is listed as 'vulnerable' by IUCN, the International Union for Conservation of Nature and Natural Resources (Rigby et al., 2019), and is protected via trade agreements such as Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2005) and in Appendix I and II of the Convention on the Conservation of Migratory Species (CMS, 2002).

White sharks in the Western North Atlantic

In contrast to their Pacific counterparts, the ecology of white sharks in the WNA is poorly known . Historically, the white shark has been documented in the WNA from fishing logs and sighting reports, but information regarding their ecology is still lacking. White sharks in the WNA have been shown to exhibit the "north-south seasonal migration" seen in several other highly migratory species (Curtis et al., 2014; Itoh et al., 2003; Neilsen et al., 2009; Skomal et al., 2017). Along with this movement information, essential areas in the WNA have been identified. For example, Skomal et al. (2017) identified the continental shelf along the eastern coast of the United States as an important foraging habitat for white sharks of all age classes. Skomal et al. (2017) also hypothesized that adult white sharks may mate opportunistically while on the shelf for foraging, and more specifically during their time in the New York Bight (Figure 1) during the summer months previously documented by Pratt (1996). The New York Bight was also found to serve as an essential nursery habitat for juvenile white sharks (Casey & Pratt, 1985; Curtis et al., 2018). Even with these studies, more information is still needed to fully understand the scope of white shark ecology in the WNA.

Migration in White Sharks

Vertical Migrations

Diel vertical migration (DVM) is the behavior where fishes occur in deep layers during the day but occur in shallower waters during the night (Nelson et al., 1997; Sims et al., 2005; Weng & Block, 2004). These behaviors are connected by ascents and descents that are triggered by crepuscular period light level changes (Ringelberg & Van Gool, 2003) and occur in several large marine fishes, including swordfish (Dewar et al., 2011) and bigeye thresher sharks, *Alopias superciliosus* (Weng & Block, 2004). White sharks have also been shown to exhibit DVM (Jorgensen et al., 2012; Nasby-Lucas et al., 2009; Weng et al., 2007a). Both males and females in the Pacific were shown to make extensive vertical oscillatory movements throughout the day, but depths were shallower and near the boundary of the mixed layer at night while in offshore waters (Nasby-Lucas et al., 2009). In the Pacific, juvenile white sharks were also shown to occupy deeper depths during day, dawn, and dusk than at night (Weng et al., 2007b). Specifically, Dewar et al. (2004) suggested that white sharks might swim downwards and then slowly upwards while searching for prey silhouettes against down-welling light. However, other explanations have been given for vertical dives such as mating, orientation, and parturition, because the exact reason for these movements is still undetermined (Carey & Scharold, 1990; Weng et al., 2007a).

White sharks spend the predominant portion of their time in waters shallower than 25 m (Bonfil et al., 2010; Nasby-Lucas et al., 2009; Skomal et al., 2017; Weng et al., 2007b). Other than the DVM previously described, there are other vertical patterns white sharks have been known to exhibit. In particular, Weng et al. (2007a) described a repeated movement to depth as ‘rapid oscillatory dives’ (ROD); this pattern was also seen by Nasby-Lucas et al. (2009) and Jorgensen et al. (2012) in the “Shared Offshore Foraging Area” (SOFA; Domeier & Nasby-Lucas, 2008) of the eastern Pacific Ocean (Figure 2). These ROD movements were noted for an entire 24-hour cycle, where dives continued during both the day and night, with the night dives having a shallower maximum depth. DVM has been documented as a common pattern in shark species in the Pacific potentially reflecting behaviors such as mating in white sharks (Jorgensen et al., 2012; Weng et al., 2007a) and foraging in blue, *Prionace glauca*, and bigeye thresher sharks (Cary & Scharold, 1990; Stevens et al., 2010; Weng & Block, 2004). In the WNA, Winton et al. (2021) found that tagged sharks spent much of their time at shallow depths, but also made frequent excursions to deeper pelagic waters. Sharks in this study spent the majority (95%) of their tracked time at depths from 0–31 m. Unlike sharks in the Pacific, diving patterns in the WNA have not been studied on a large scale.

In Jorgensen et al. (2012), researchers described four distinct diving patterns for sharks in the Pacific: DVM, ROD, Coastal, and Travel. DVM consisted with a daytime peak centered between 350 and 500 m, a nighttime peak in the upper 200 m, and a clear dusk and dawn vertical migration between depths. ROD is characterized as even distribution between 30 and 200 m with shallower dives during nighttime hours. The Coastal mode was described as vertical distribution shallower than 50 m and mostly concentrated in the upper 30 m of water. Travel behavior is indicated by almost all the animal's time spent in the upper 5 m of water. WNA white sharks have currently not been documented exhibiting these diving behaviors on a large scale.

Regional Migrations

Large-scale regional migrations are common in many large pelagic fishes such as thunnid tunas, swordfish, and other shark species (Abascal et al., 2010; Gore et al., 2008; Itoh et al., 2003). Similarly, white sharks are known to make vast, even transoceanic, migrations (Bonfil et al., 2005; Bonfil et al., 2010; Bruce et al., 2006; Duffy et al., 2012; Weng et al., 2007a). There is documentation of white sharks in the WNA participating in large regional migrations that follow the common "north in the summer, south in the winter" trend seen in many other species (Curtis et al., 2014; Itoh et al., 2003; Neilsen et al., 2009; Skomal et al., 2017). This same general migration pattern has been seen in the WNA for white sharks that are primarily shelf-oriented (Skomal et al., 2017). While making these migrations, white sharks tend to spend much of their cruising (sustained speed to maintain place in water column) time in the upper 50 m (Bonfil et al., 2005; Duffy et al., 2012; Weng et al., 2007a).

As previously stated, white sharks in the Pacific migrate annually to a large mid-ocean foraging area known as the SOFA or "White Shark Café" (Figure 2) (Domeier & Nasby-Lucas, 2008; Nasby-Lucas et al., 2009; Weng et al., 2007a). This large-scale migration is thought to be motivated by foraging (Domeier & Nasby-Lucas, 2008; Weng et al., 2007a). However, white sharks in New Zealand did not show a large pelagic offshore aggregation site like the SOFA; sharks in these waters migrated to separate areas in the South Pacific (Duffy et al., 2012). While normally feeding on young pinnipeds, the New Zealand white shark diet could potentially shift to cetaceans when adult male pinnipeds establish mating territories, causing the young to abandon the rookery (La Boeuf & Laws, 1994). Large-scale cetacean migrations, which could draw white shark populations away from the seal rookeries, are present in that area and could be one reason for the lack of an aggregation site (Bonfil et al., 2010). This hypothesis remains plausible due to the ability of white sharks to shift their diet based on prey availability, as previously demonstrated during the decline in seal abundance (Skomal et al., 2012). Unlike sharks in the Pacific, white sharks in the WNA tagged during the Skomal et al. (2017) study did not exhibit homogenous use of the pelagic habitat. Aside from the summer months, which sharks spent their time on the shelf, pelagic behavior was observed throughout the year (Skomal et al. 2017). The differences in offshore migrations between populations could indicate region-specific behaviors that are related to foraging or even mating (Weng et al., 2007a). The reasons behind these large-scale migrations are largely unknown in the WNA, and such behaviors are considered important regarding conservation and minimizing anthropogenic threats.

Knowledge of essential fish habitat (EFH) for all size classes of white sharks in the WNA is also generally unknown. NOAA considers habitat data on neonate white sharks (≤166 cm TL) and adult white sharks (≥480 cm TL) to be insufficient to be able to identify EFH for these life stages (CAHMS FMP, 2006). Juveniles (167 to 479 cm TL) do have two specified EFHs: one which is offshore northern New Jersey and Long Island, NY in coastal waters from the 25 to 100 m isobath in the New York Bight. The second EFH for the juvenile size class is offshore of Cape Canaveral, FL between the 25 and 100 m isobaths (as designated by NOAA; CAHMS FMP, 2006). With a lack of specified EFH, understanding white shark behaviors is crucial and could potentially lead to management actions to protect aggregation sites and other essential habitats (mating, parturition, etc.) for white sharks.

Ultimately, this study aimed to identify swimming behavioral modes in white sharks in the WNA, which were distinguished using a hierarchical cluster analysis of tagging data to indicate differences in diving behavior. Two new shark (SC1802 and SC1803) tracks were also modeled to give more insight into movement patterns, one of which (SC1802) was a juvenile. These behaviors and tracks did not suggest evidence of an offshore aggregation site but highlighted the importance of the aggregation site in the waters surrounding Cape Cod.

FIGURE 1. New York Bight, outlined in red, is the continental shelf waters between Cape Cod, Massachusetts and Cape May, New Jersey and is a portion of the Mid-Atlantic Bight. Map created using R (R Development Core Team, 2015).

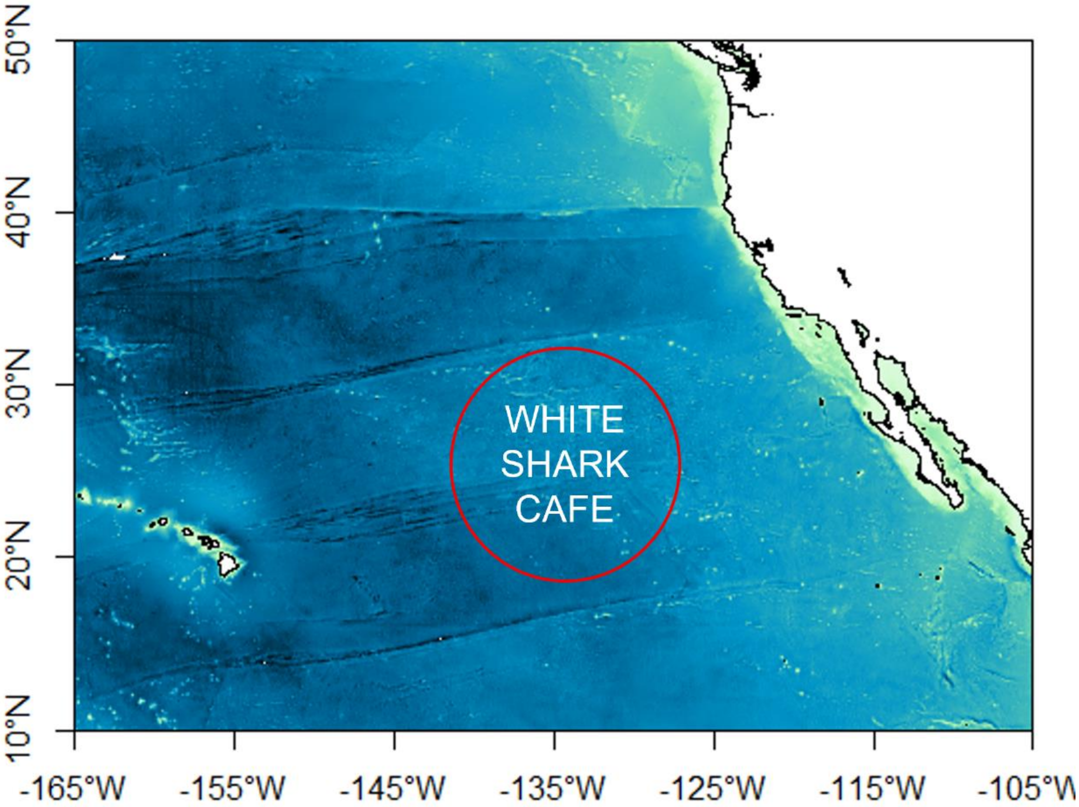

FIGURE 2. The "White Shark Café," a known white shark offshore aggregation site found in the Pacific Ocean found halfway between the Baja peninsula and the big island of Hawaii.

Materials and Methods

Data Collection – Tagging

As described in Skomal et al. (2017), white sharks were tagged (n = 31) off Cape Cod, Massachusetts from 2009 to 2014 during the summer months (July to October). However, for this study, only 24 individual tracks were used from Skomal et al. (2017) due to compatibility with the geolocation model. Some tag types did not record all the parameters (depth, light, temperature, location) needed for the HMMoce model. Two additional tags were deployed in 2018 and data from these are also included in this study for a total of 26 individual tracks. All tags were attached to free-swimming sharks using the modified harpoon technique as described by Chaprales et al. (1998) where the head of the harpoon was modified to hold an electronic tag, and sharks were spotted by plane.

Tag Descriptions

- Pop-up satellite archival transmitting (PSAT) tags:
    - Models MK10-PAT [MK10, n = 7], Wildlife Computers Inc. (Redmond, WA) –set to record depth (range = 0−1000 m, resolution = 0.5 m ± 1.0%), water temperature (−40 to +60°C; 0.05 ± 0.1°C), and light level (470 nm, logarithmic range = 5 × 10−12W cm−2 to 5 × 10−2 W cm−2) every 10 seconds. This tag type was set to detach after 122 to 308 days and transmit processed data through the Argos satellite system.
    - Model miniPAT [mP, n = 16], Wildlife Computers Inc. (Redmond, WA) – programmed to record depth (range = 0-1700 m, 0.5 m ± 1.0%), water temperature (−40 to +60°C; 0.05 ± 0.1°C), and light level (470 nm, logarithmic range = 5 × 10−12W cm−2 to 5 × 10−2 W cm−2) every 15 seconds. The miniPAT was set to detach after 122 to 308 days and transmit processed data through the Argos satellite system.
    - Model MK10AF [n = 7], Wildlife Computers Inc. (Redmond, WA) - The MK10AF is another type of PSAT tag that was set to record depth (range = 0−1000 m, resolution = 0.5 m ± 1.0%), water temperature (−40 to +60°C; 0.05 ± 0.1°C), and light level (470 nm, logarithmic range = 5 ×

10−12W cm−2 to 5 × 10−2 W cm−2) every 10 seconds. This tag type was set to detach after 122 to 308 days and transmit processed data through the Argos satellite system.

Shark length was estimated from aerial photos taken from spotter planes, although Skomal et al. (2017) stated that shark size was likely underestimated and should be therefore considered minimum estimates. Maturity classes were assigned as follows: juvenile (<3.0 m), subadult (male: 3.0-3.5 m, female: 3.0-4.8 m), and adult (male: ≥3.5 m, female ≥4.8 m). Size classes were based on length estimates published by Castro (2011), Francis (1996), and Pratt (1996). Seasons are based on the lunar calendar (mo/d: Spring, 3/20−6/19; Summer, 6/20−9/19; Fall, 9/20−12/19; Winter, 12/20−3/19).

Light-based Geolocation

Electronic tagging of marine fishes typically uses light levels and sea surface temperature to estimate movement patterns to be able to discern life history patterns in marine fishes (Braun et al., 2015; Block et al., 1998). Historically, however, only sea surface temperature and bathymetry were used (Hill & Braun, 2001). This was beneficial for determining geolocation, but a more robust method using light levels was then introduced. The light level geolocation theory uses quantified ambient light levels to determine an organism's geographic position from astronomical algorithms. While longitude was fairly simple to calculate, latitude in the spring/autumn months was harder to identify. This is due to the lack of variation in day length around the equinoxes (Hill & Braun, 2001). Common environmental factors such as weather, topography, and vegetation have also been shown to affect the accuracy and precision of geolocation (Lisovski et al., 2012). This method alone also does not account for organisms undergoing large-scale vertical movements, however. Extended diving behavior at crepuscular periods makes it extremely difficult to determine dawn/dusk times with just light. This makes tracks that only rely on light-level for geolocation purposes often less precise and often have large error issues with position estimates as noted by Braun et al. (2015).

Contemporary light-based geopositioning models are commonly cross-referenced with other data to narrow positions down further. Such data includes parameters like tidal patterns, which were used to determine Atlantic cod habitat use (Pedersen et al., 2008), or ocean heat content, which was used to assess fish migrations (Luo et al., 2015). Having data to cross reference with light-based geolocation ultimately improves individual location estimates. Hidden Markov Models (HMM) are now of particular interest and these models use animal movements and a model of the environment to estimate an animal's location as well as their behavior. Braun et al. (2018) recently developed a model that uses HMM but is specific to improving estimates of tagged marine organisms. This model, HMMoce, uses electronic tag data and oceanographic data from ocean observing system portals to estimate animal movements, behavior, and residency (time spent in a given space within an identified interval) (Braun et al., 2018a), and is the model this study incorporated to improve white shark geolocation estimates.

Data Analysis

The transmitted data from the tags deployed by Skomal et al (2017) were decoded using a cloud-based portal software and are shown in Table 1. Geolocation positions of the 26 sharks was re-estimated by the HMMoce package (Braun et al., 2018a) for R (R Development Core Team 2015) using depth, sea surface temperature (SST), and light information collected from PSAT tags, which was then cross referenced with oceanographic data from ocean observing system portals such as sea surface temperature (SST), bathymetry, and the Hybrid Coordinate Ocean Model (HYCOM). Likelihoods for the most probable daily position were then constructed for each individual. Likelihood combinations for each track were determined using Akaike Information Criterion (AIC). From this, probable tracks for each animal were identified. Individuals were also classified as 'coastal' or 'pelagic,' similar to Skomal et al. (2017), based on where an individual spent the majority of its time, either on or off the continental shelf. Aside from improving animal movement estimates from the Skomal et al. (2017) study, this model also allowed for the estimation of behavior state and residency. Track distances (km) were calculated using Great Circle distance between track locations that were averaged daily.

A dive data analysis was performed by aggregating depth bins to common bins among all individuals. Time-at-depth (TAD) bin limits were aggregated to <10, 10–25, 25−50, 50−100, 100−200, 200−400, 400−600, 600−800, and >800 m. Depth records <0 m were assumed to be zero. In addition to the 26 transmitted records, archival records from two of the tags (WS13-02 and SC1803) were used with their transmitted data. These tags were recovered and contain raw data records collected every 10 or 15 secs (depending on model), which far exceed those that are transmitted. Four sharks (WS 10-01, WS 10-02, WS 14-25, and WS 09-05) were removed from the depth analysis due to incompatible, non-overlapping bins or incomplete data. Equivalent binned data were recreated by compiling data into the same bins as the MK10 tags with R (R Development Core Team 2015) and were then compiled with the transmitted records for a total of 22 individual tag records with between 17 and 375 (mean = 196) days of histogram data and a total across all tags of 3276 days. Of the 22 individuals, six were male (n = 6), ten were female (n = 10), and six were of unknown sex (n = 6).

Using the methods described in Jorgensen et al. (2012), a distance matrix was calculated to determine the similarity among the 3276 “shark days” based on differences in vertical distribution. Distances (average distance along each dimension) were calculated using the “Manhattan” measure in R (‘dist’ function in R; R Development Core Team). From this, a hierarchical cluster tree was created using an un-weighted average distance (UPGMA) linkage algorithm (‘hclust’ function in R; R Development Core Team) and clusters were plotted with a dendrogram using the R ‘as.dendrogram’ function. For each shark day represented by the histogram data, estimated geolocations from the HMMoce model were incorporated into the depth data, which allowed the data to be grouped by their cluster and plotted to provide information on patterns based on geography, season, and sex (Braun et al., 2018a; Jorgensen et al., 2012). Shark behaviors were classified using Jorgensen et al. (2012) diving descriptions for comparison. Diel patterns were also identified using data from the cluster’s density of depth points over a 24-hour period. To visualize diel patterns, we compiled the two sets of archival data (WS 13-02 and SC1803) for each cluster that contained data in 60 second resolution. These data comprised 20% of the shark days and the density of depth readings was plotted over a single 24-hour cycle to visualize the diel patterns. Other patterns such as seasonality and sex were also examined in this study.

TABLE 1. Tagging information for 23 individual white sharks tagged near Cape Cod, Massachusetts (USA) and 3 tagged on the Florida Shelf between 2009 and 2018. Sex—F: female, M: Male, U: unknown. Track distance refers to absolute track distance (see 'Materials and Methods'). Observation likelihoods are those observations used in HMMoce to construct the most probable track for each tagged animal: L, light-based longitude; S, sea surface temperature; H, HYCOM depth-temperature profiles.

ID	**Tag type**	**PTT**	**Tag date**	**Tag location**		**Total Length (m)**	**Sex**	**End Date**	**Duration (d)**	**End location**		**Max depth (m)**	**Track distance (km)**	**Habitat**	**Observation Likelihoods**
				Lat (˚N)	**Long (˚W)**					**Lat (˚N)**	**Long (˚W)**				
WS09-01	MK10	78249	05.09.2009	41.60	69.98	3.0	U	24.01.2010	141	30.71	80.20	88	1855	Coastal	LS
WS09-02	MK10	95970	05.09.2009	41.60	69.96	3.7	U	15.01.2010	132	30.37	80.56	512	2442	Coastal	LSH
WS09-03	MK10	67822	08.09.2009	41.59	69.98	2.4	U	01.03.2010	174	29.02	80.57	272	3050	Coastal	SH
WS09-04	MK10	86228	08.09.2009	41.62	69.96	3.8	U	13.04.2010	217	36.06	73.73	96	3548	Coastal	SH
WS09-05	MK10	78248	08.09.2009	41.59	69.99	3.7	U	05.11.2009	58	41.11	70.01	48	3371	Coastal	LSH
WS10-01	mP	95985	27.07.2010	41.65	69.65	3.6	F	01.02.2011	189	30.50	80.97	700	4658	Coastal	LS
WS10-02	mP	95989	31.07.2010	41.63	69.95	2.8	U	15.08.2010	15	41.46	70.08	48	497	Coastal	LH
WS10-04	MK10AF	64282	21.08.2010	41.66	69.93	3.7	U	13.10.2010	53	35.15	75.67	400	2012	Coastal	LSH
WS10-05a	MK10AF	64318	27.08.2010	41.63	69.61	5.3	F	05.04.2011	221	31.15	78.40	832	11496	Pelagic	LSH
WS10-05b	mP	110494	13.09.2012	41.67	69.93	5.3	F	30.09.2012	17	41.24	68.11	176	450	NA	LH
WS10-06	MK10AF	64280	01.09.2010	41.59	69.98	3.4	U	01.01.2011	122	24.60	86.00	760	3385	Coastal	LH
WS12-01	MK10	67833	14.08.2012	41.60	69.99	3.7	M	10.07.2013	330	40.28	62.42	880	7344	Pelagic	LSH
WS12-13	mP	110489	30.08.2012	41.81	69.94	4.9	F	01.07.2013	305	35.56	74.75	1064	4331	Pelagic	SH
WS13-01	mP	121325	03.03.2013	30.39	81.38	4.4	F	31.08.2013	181	30.67	79.97	1080	9282	Pelagic	LSH
WS13-02	mP	110492	15.08.2013	41.61	69.96	3.8	F	01.05.2014	259	23.59	84.48	197	5507	Coastal	LSH
WS13-04	mP	121333	20.09.2013	41.68	69.93	4.0	F	10.04.2014	202	30.03	81.21	128	4360	Coastal	SH
WS13-05	mP	121329	03.10.2013	41.67	69.93	4.9	F	01.06.2014	241	36.00	73.22	1128	10242	Pelagic	SH
WS14-17	mP	95974	04.09.2014	41.64	69.94	3.7	M	14.04.2015	222	32.08	79.01	888	8265	Coastal	LH
WS14-18	MK10AF	100993	26.08.2014	41.58	69.99	4.0	M	15.03.2015	201	29.45	80.75	592	3585	Coastal	LS
WS14-23	MK10AF	100994	26.08.2014	41.64	69.95	3.4	M	15.03.2015	201	33.21	76.91	808	4097	Pelagic	LSH
WS14-25	mP	95977	04.09.2014	41.72	69.92	4	M	09.09.2014	5	41.49	68.82	84	124	NA	LSH
WS14-50	MK10AF	106796	29.09.2014	41.66	69.94	4.3	F	26.10.2014	27	41.24	69.91	64	611	Coastal	LS
WS14-56	mP	108188	06.10.2014	41.69	69.95	5.2	F	12.11.2014	37	41.18	69.92	48	208	Coastal	LH
WS14-57	MK10AF	106774	09.10.2014	41.68	69.93	4.3	F	01.06.2015	235	38.17	75.13	976	8599	Pelagic	SH
SC1802	mP	163724	15.03.2018	32.55	79.67	2.1	M	04.09.2018	174	41.29	69.51	321	3236	Coastal	LS
SC1803	mP	163722	04.12.2018	32.13	80.55	3.0	M	13.12.2019	375	29.77	81.25	464	7690	Pelagic	LH

Results

Horizontal Movements

Of the 27 shark tracks shown in Skomal et al. (2017), 24 of those reporting tags contained data compatible with the HMMoce model (n = 24). Two tags were deployed after the conclusion of the 2017 study (SC1803, SC1802), and both of those tags had data usable with the model as well for a total of 26 tracks (n = 26) (Table 1). Two tags from WS13-02 and SC1803 were recovered, thereby providing archival data. Estimated sizes of tagged sharks ranged from 2.1 to 5.3 m total length (TL) (mean ± SD, 3.9 ± 0.314 m). Tracks were reported for 11 females (5 adults, 6 sub-adults, 4.5 ± 0.343 m) and 7 males (4 adults, 2 sub-adults, 1 juvenile, 3.4 ±0.464 m), with a resulting sex ratio (M:F) of 0.64 (Figure 3). The sex of 9 individuals was undetermined (2 juveniles, 6 subadults/adults), but tracks were still given for these animals. Tag deployment (n = 26), ranged from 5 to 375 d (mean = 167 d) and totaled 4334 d. Over these 4334 days, individuals travelled up to 11496 km (mean = 4800 km; range 208-11496 km) (Table 1).

As shown in Skomal et al. (2017), these tracks may be indicating ontogenetic changes in habitat use. Juveniles (<3 m) remained close to or on the continental shelf while larger individuals (>3 m) seemed to move between the shelf and throughout pelagic habitats. Based on the Skomal et al. (2017) study, the shelf-oriented sharks (n = 15) comprised juvenile (n = 2), subadult (n = 6), adult (n = 3), and sub-adult/adult (n = 4) sharks of both sexes. Sharks that moved to pelagic habitats (n =7) were subadults (n = 4) and adults (n = 3) of both sexes. This habitat use pattern still holds true with the updated tracks. For the two new tags deployed after the original 2017 study, SC1803 (Figure 4) had wide-ranging movements off the continental shelf while SC1802 was mainly shelf-oriented (Figure 5). With the inclusion of this information, the shelf-oriented sharks (n = 16) comprised of juvenile (n = 3), subadult (n = 6), adult (n = 3), and sub-adult/adult (n = 4) sharks of both sexes. Sharks that moved to pelagic habitats (n = 8) were subadults (n = 5) and adults (n = 3) of both sexes.

Sharks that tended to remain on the continental shelf from the Skomal et al. (2017) study indicated seasonal migrations between their tagging locations and northern latitudes in the summer, throughout the mid-Atlantic region in the fall, and southern latitudes in the fall. The new coastal-oriented shark, SC1802, followed a similar migration (Figure 5). This juvenile shark stayed primarily on the continental shelf (88% of tag deployment days) while it migrated from its southern location in the winter to the Gulf of Maine in the summer months. Sharks from the Skomal et al. (2017) study that preferred pelagic habitats had a less defined seasonal migration pattern. However, those sharks would become shelf-oriented in the summer months. SC1803 did not seem to follow this pattern and virtually stayed offshore (97.6%) for most of the tag deployment (total days = 375 d). Once tagged off the coast of the southern United States, this sub-adult shark travelled offshore through the Sargasso Sea to northern latitudes as far north and east as Newfoundland, Canada for the summer months and returned to the northern coast of Florida in the winter of the following season (Figure 4). All sharks that migrated offshore (n = 8) moved to different areas in the WNA and did not move to a consistent focal area (Figure 6).

Vertical Movements

Of the 26 sharks that had tracks updated or are new, 22 had data usable for the depth analysis. Four sharks were removed (WS 10-01, WS 10-02, WS 14-25, and WS 09-05) due to incompatible, non-overlapping bins or a lack of data. Of the 22 remaining individuals, six were male, ten were female, and six were of unknown sex. Two tags (WS 13-02 and SC1803) were recovered, and therefore had archival data to be used in the depth portion of this study for a total of 3276 shark days. The deepest dive recorded (1128 m) was from WS 13-05, an adult female, who spent most of her time in pelagic waters (Table 1). Of the 26 sharks, eight recorded depths >800 m, all of which were either adults (n = 5) or sub-adults (n = 3). As a result of the cluster analysis, three dominant diving modes were present. The dendrogram plot (Figure 7) indicates the relative distances between all eight groups and, therefore, the differences in diving behaviors. The three dominant modes accounted for 89.0% of the histogram data. Five other groups were present (groups 1, 2, 3, 7, 8), but only accounted for 0.58%, 1.9%, 2.1%, 4.2%, and 2.3% of the data, respectively (Figure 7).

The dominant diving patterns were not exclusive to one geographical location, sex, or season (Figure 8). The dominant groups are as follows: group 4 (red), group 5 (orange), and group 6 (yellow). All three movement patterns were found both on and off the continental shelf.

Diving offshore was also characterized by of these three behavioral clusters. In this study, diving behaviors were not exclusive to one particular area (Figure 8).

Depth versus time of day queried by cluster was plotted using the archival data from the recovered tags of WS 13-02 and SC1803 (Figures 8, 9, 10). ROD was seen both on and off the continental shelf (Figure 8). During the night hours, sharks were mainly seen in the upper 100 m with heavy concentration in the upper 25 m (Figure 9). From noon until midnight, these sharks exhibited rapid diving patterns by the heat signatures with deeper depths around 100, 300, 400, and 500 m (Figure 9). Compared to the other two dominant groups, this was the only pattern to show dives deeper than 100 m. It also is the only one of the three major patterns to indicate strong differences between day and night vertical distribution.

Cluster 5 was characterized as the ‘Travel’ mode and occurred primarily along the continental shelf. This behavior was also somewhat seen in the pelagic realm, similarly to the ROD behavior (Figure 8). This cluster is distinguished by the animal’s time being spent in the upper 5 m of the water column with some time spent at depths not exceeding 20 m (Figure 10). Sharks in this study spent 44.2% of their time in the upper 5 m of water, 51.9% of their time in the upper 20 m of water, and 3.88% of their time in depths greater than 20 m. Unlike the ROD behavior, this diving pattern did not exhibit day and night depth differences. However, swimming was more concentrated at the surface during the afternoon into dusk hours (Figure 10).

‘Coastal’ mode was described as vertical distribution shallower than 50 m and mostly concentrated in the upper 30 m of water. Like both Travel and ROD, this behavior occurred both on and off the continental shelf (Figure 8). Sharks from this study in the ‘Coastal’ cluster were seen at depths no deeper than 60 m and were similar to the ‘Travel’ mode where there was a heavy concentration of activity at the surface during the daytime to dusk hours. Distribution between depths from 0-30 m was even throughout the 24 h period.

Seasonal differences between the sexes were found for each diving behavior (Figure 12). Male ROD behavior occurred almost exclusively off the continental shelf, but this diving mode was seen rarely on the shelf. During the summer fall and spring months, male ROD behavior was seen mostly in lower latitudes. No winter ROD behavior for males was recorded. Female

ROD behavior occurred almost exclusively off the continental shelf during the summer. Similarly to males, female ROD occurred in lower latitudes. Travel behavior in males during the fall was seen both on and offshore, with concentration in the Gulf of Maine. Winter travelling was seen in lower latitudes while travelling in the summer was seen in higher latitudes in males. Spring and summer travelling was seen both on and offshore with summer travelling in higher latitudes. Similarly, females in the fall saw most of the Travel behavior in the Gulf of Maine. Summer Travel was exclusive to the northern latitudes while spring and winter was seen both on and offshore with a wide range of latitudes. In males, the Coastal behavior was wide-ranging. In the winter, male Coastal behavior occurred in lower latitudes and summer Coastal behavior occurred in higher latitudes. Spring and fall were seen both on and off the shelf in a wide range of latitudes. Lastly, female Coastal behavior had a large number of points in the Gulf of Maine in the Fall and Summer, while winter and spring Coastal behavior was seen both on the shelf and in the pelagic realm in a variety of latitudes.

Differences in size class behaviors were also apparent (Figure 13). There were few juveniles (n = 3) tagged in the Skomal et al. (2017) study and those tagged in 2018, but none of them exhibited ROD behavior. Both adults and subadults who displayed ROD behavior did so primarily on and off the shelf south of Delaware. Subadults in the spring exhibited ROD mostly offshore. Travel behavior in adults in the fall and summer occurred in higher latitudes and in lower latitudes and more offshore in the winter and spring months. Subadults travelling in the fall stayed on the shelf all along the coast of the United States and Canada. The winter and spring travelling occurred mostly offshore. Summer travelling was offshore in higher latitudes when compared to the winter and spring. Juveniles who displayed the Travel behavior did so closer to the continental shelf and in the higher latitudes in the summer/spring/fall months and in lower latitudes in the winter. Coastal behavior in adults was exhibited mostly on the shelf in higher latitudes in the spring/summer/fall months and in lower latitudes in the winter. Subadults were more wide ranging with this behavior, moving to the pelagic realm regardless of the season. Juvenile coastal behavior was similar to the adults, where in the spring/summer/fall months they were mostly on the shelf in higher latitudes. In the winter, they stayed in the lower latitudes.

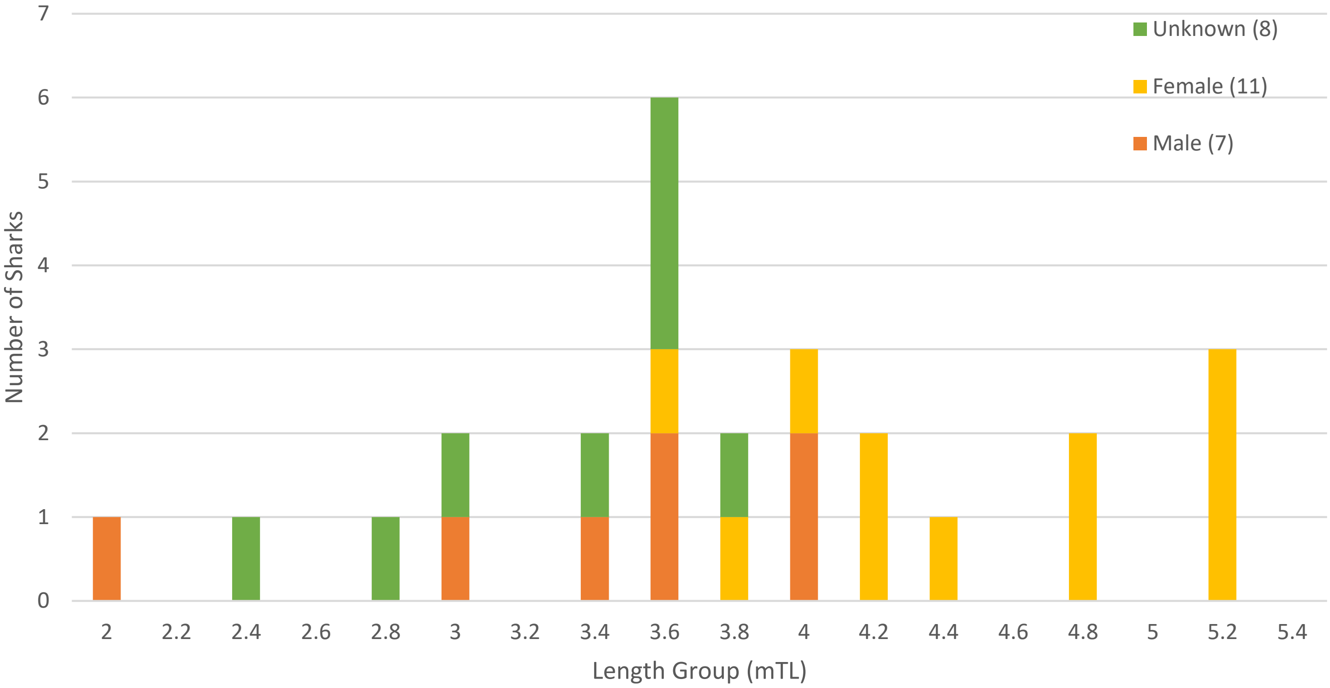

FIGURE 3. Total length frequency distribution of white sharks tagged in the Skomal et al. (2017) study between 2009-2016 and those tagged in 2018. Tagged females (n = 11) were larger with an average total length (TL) of 4.49 m and tagged males (n = 7) were smaller with an average TL of 3.37 m. Sharks with an unidentified sex (n = 8) had an average total length of 3.28 m.

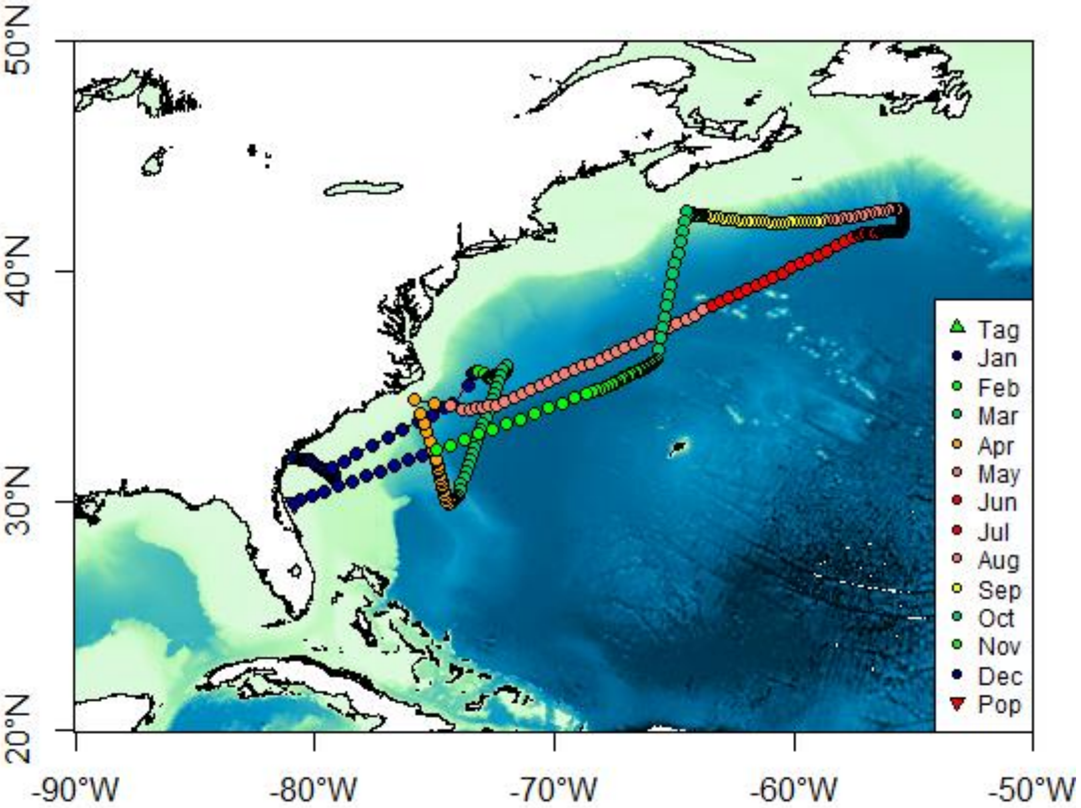

FIGURE 4. Most probable track of SC1803 using the HMMoce model. This animal was tagged in December of 2018 and was recovered in December of 2019. SC1803 travelled offshore through the Sargasso Sea to northern latitudes as far north as Maine and as far east as Newfoundland, Canada for the summer months and returned to the northern coast of Florida in the winter of the following season.

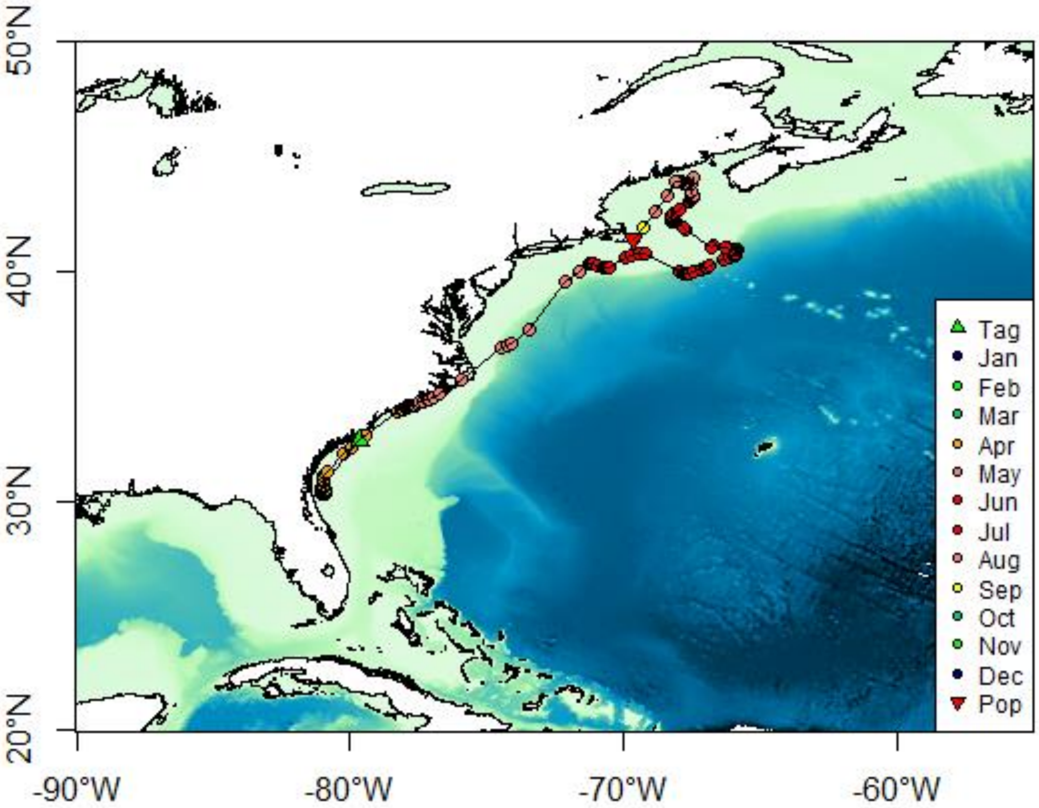

FIGURE 5. Most probable track of SC1802 using the HMMoce model. This juvenile shark was tagged in March of 2018 and stayed primarily on the continental shelf while it migrated from its southern location in the winter to the Gulf of Maine in the summer months.

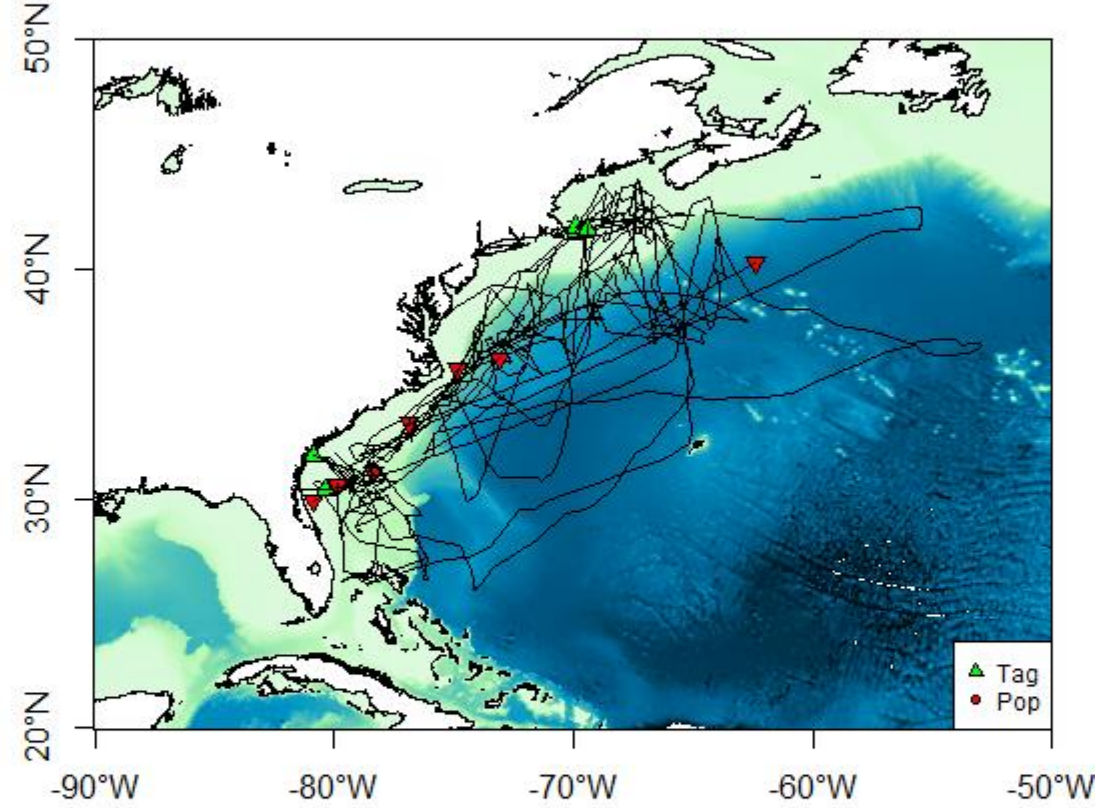

FIGURE 6. Most probable tracks for sharks with movements that are considered pelagic (n = 8). Tracks are plotted as black lines. Tag and pop-up locations are denoted with green and red triangles, respectively. All eight sharks migrated to different areas offshore, showing no offshore focal area.

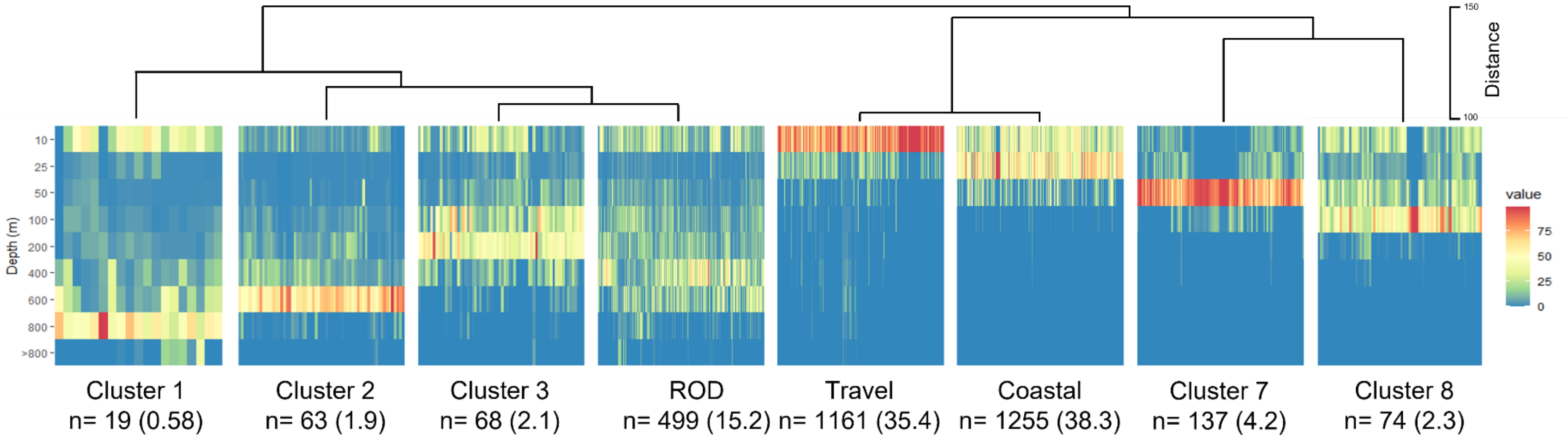

FIGURE 7. Dendrogram depicting white shark depth behaviors from clustering analysis. Each column represents a 24-hour histogram (n = 3276 days from 22 sharks). Color indicates fraction of time. Cluster size is indicated by number of shark days (n) and a percent of the total of shark days (in parentheses). Depth bins are defined along the y-axis.

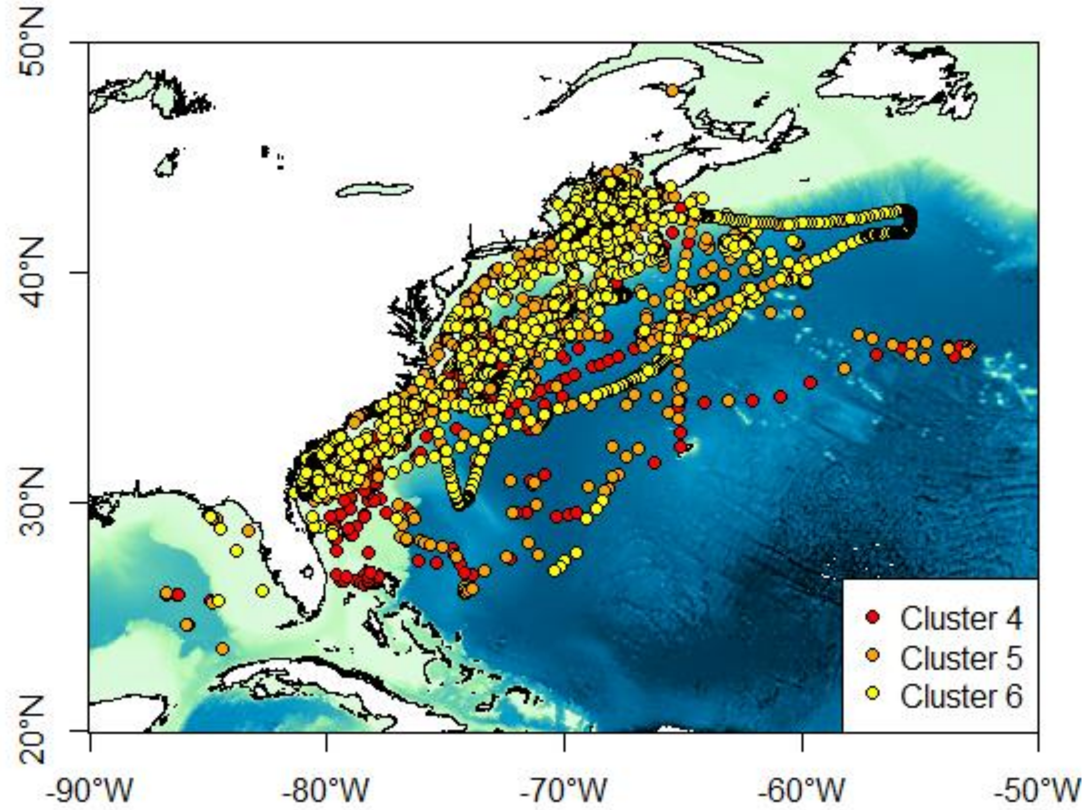

FIGURE 8. Daily white shark position estimates for the three main clusters: "ROD" (Cluster 4: red), "Travel" (Cluster 5: orange), and "Coastal" (Cluster 6: yellow). All three behaviors occurred throughout both the pelagic and offshore areas.

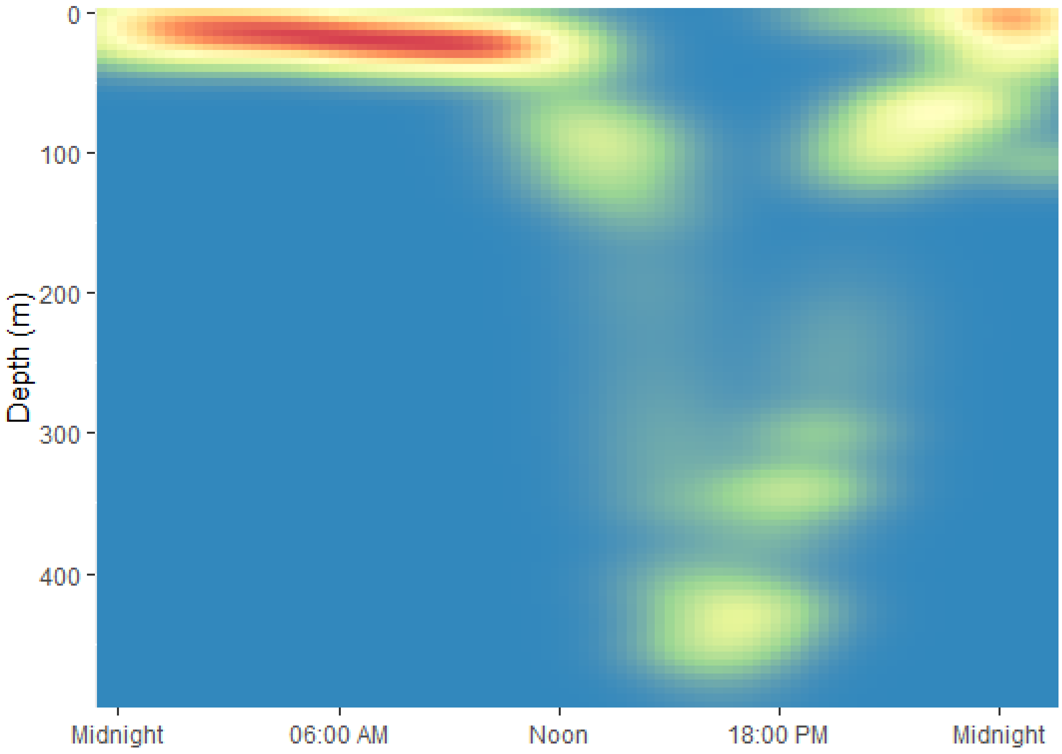

FIGURE 9. ROD diving behavior in white shark SC1803 from archival data queried by cluster over a 24-hour period. Sharks exhibiting this behavior stayed in depths < 20 m during the late evening into mid-morning. Outside of those hours, sharks were seen at depths from 0 m to 500 m. WS 13-02 did not exhibit ROD diving behavior.

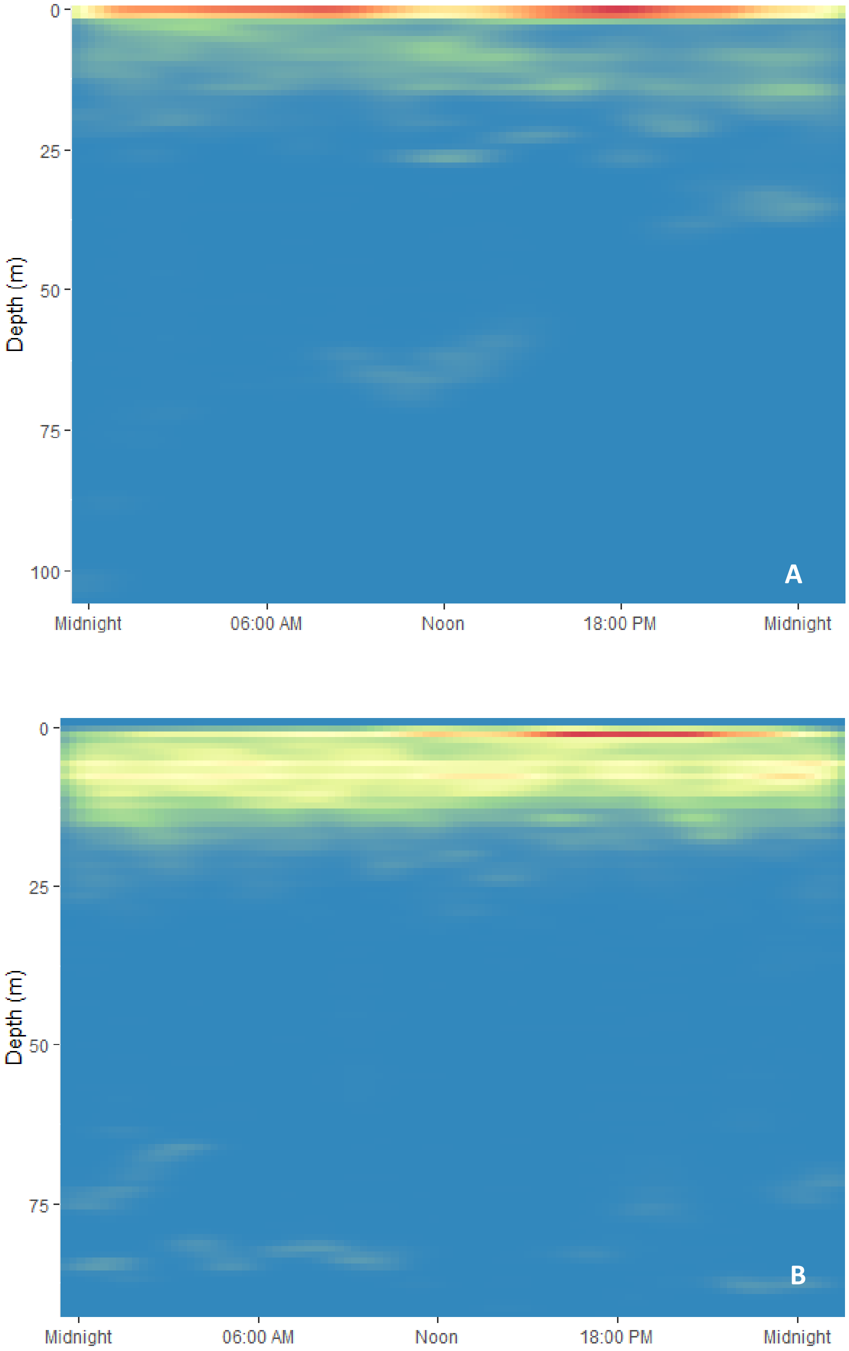

FIGURE 10. (A) Travel diving behavior in white shark SC1803 and (B) WS 13-02 from archival data queried by cluster over a 24-hour period. This behavior shows that shark depth preferences stayed < 15 m.

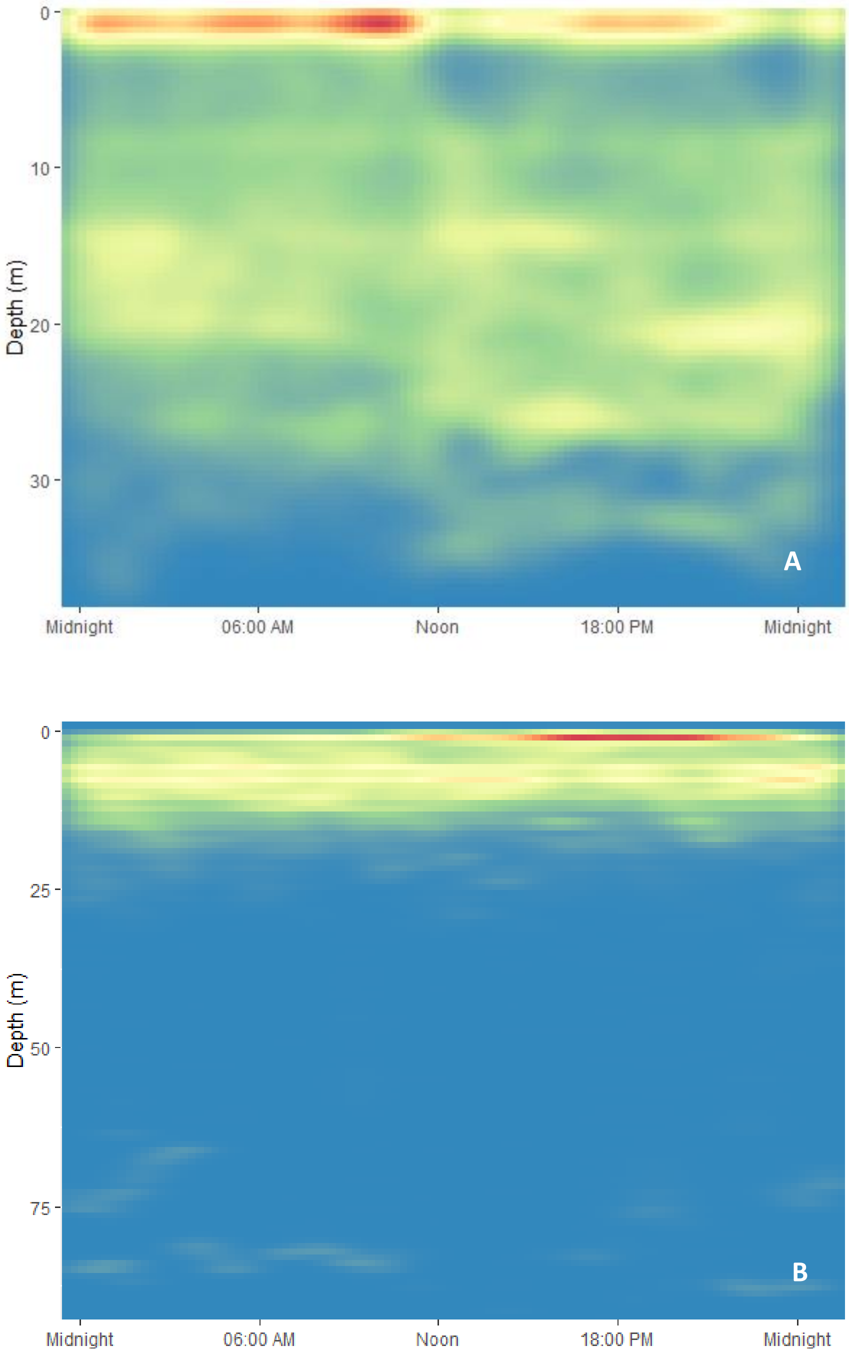

FIGURE 11. (A) Coastal diving behavior in white shark SC1803 and (B) WS 13-02 from archival data queried by cluster over a 24-hour period. Sharks exhibiting this behavior preferred depths < 40 m.

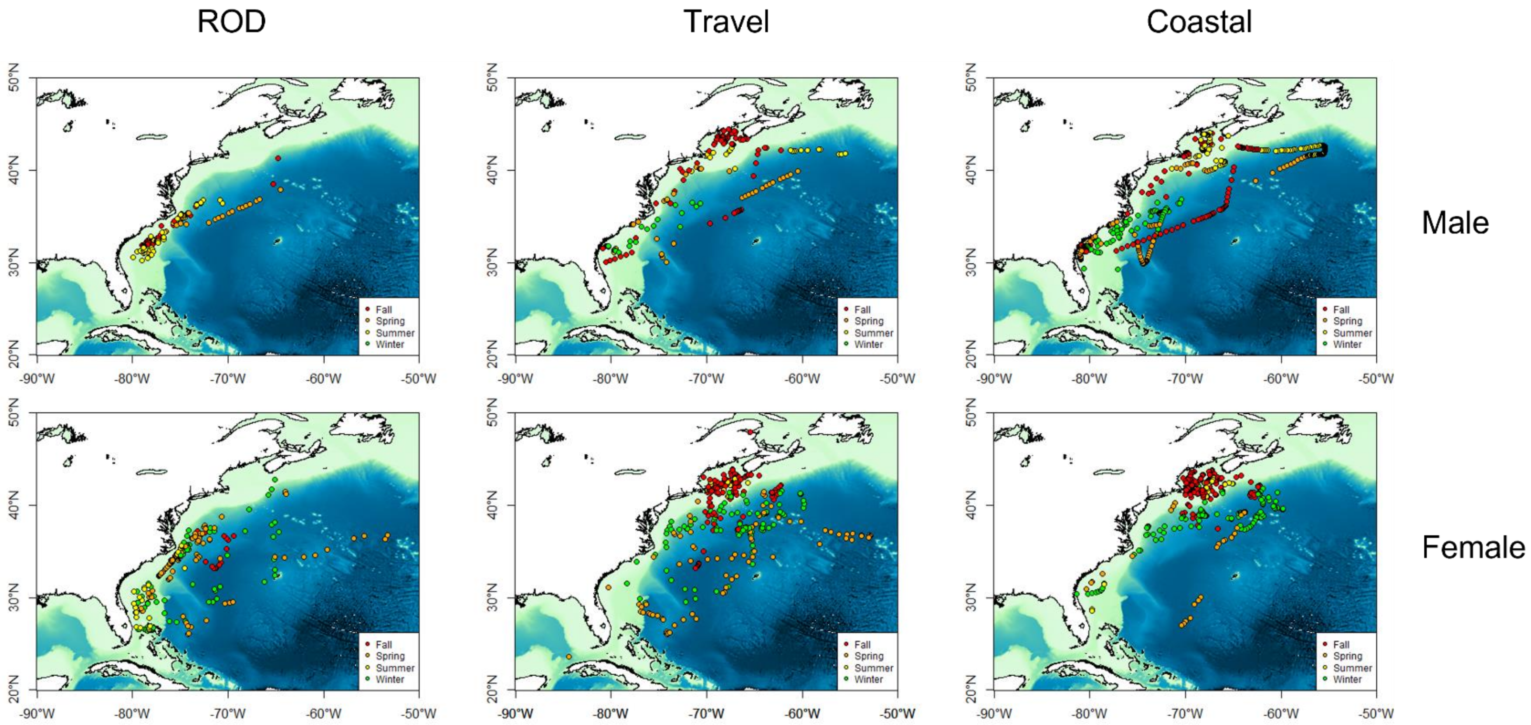

FIGURE 12. Seasonal movements of white sharks in the northwest Atlantic broken down by cluster and sex. Seasons are based on the lunar calendar (mo/d: Spring, 3/20−6/19; Summer, 6/20−9/19; Fall, 9/20−12/19; Winter, 12/20−3/19).

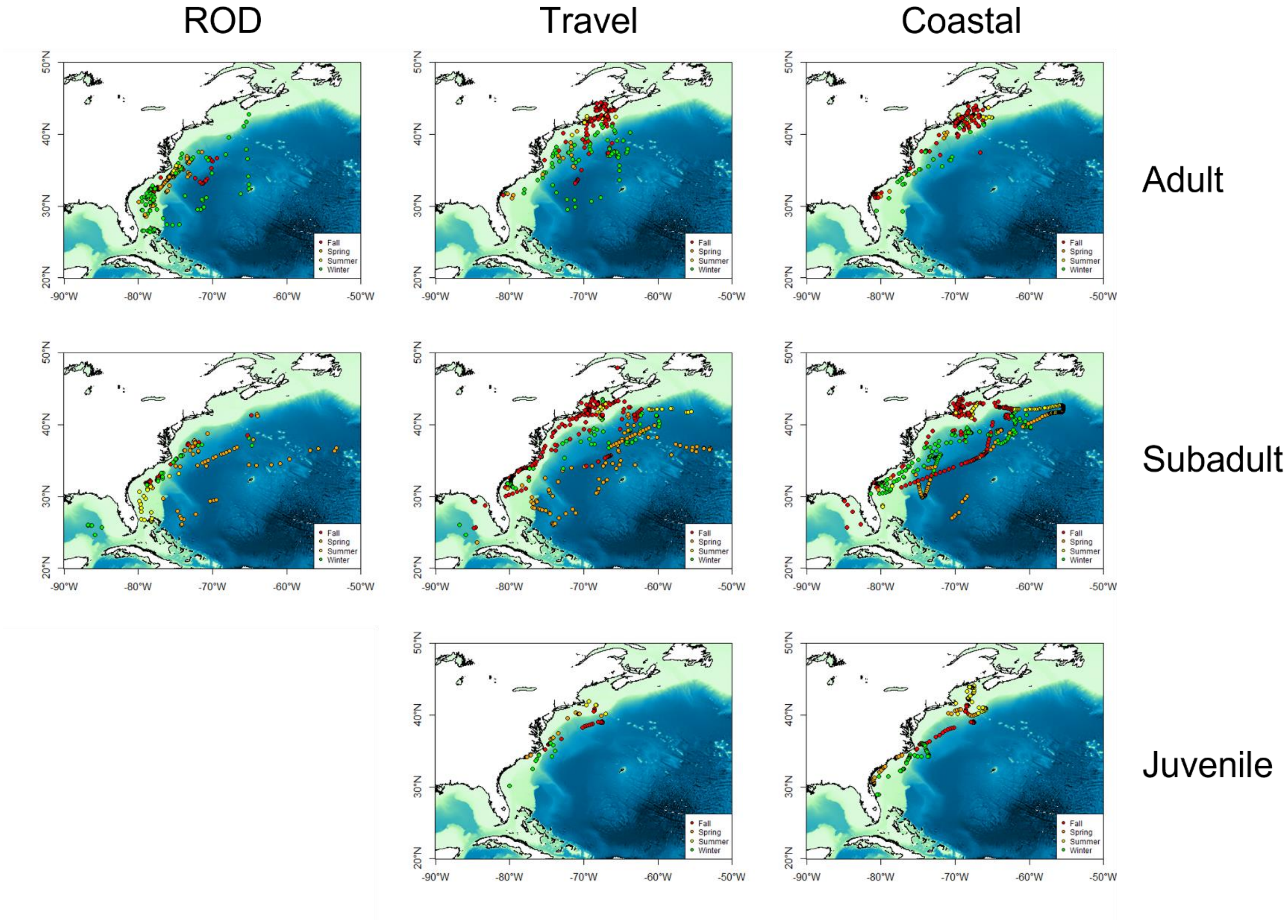

FIGURE 13. Seasonal movements of white sharks in the northwest Atlantic broken down by cluster and size class. Seasons are based on the lunar calendar (mo/d: Spring, 3/20−6/19; Summer, 6/20−9/19; Fall, 9/20−12/19; Winter, 12/20−3/19).

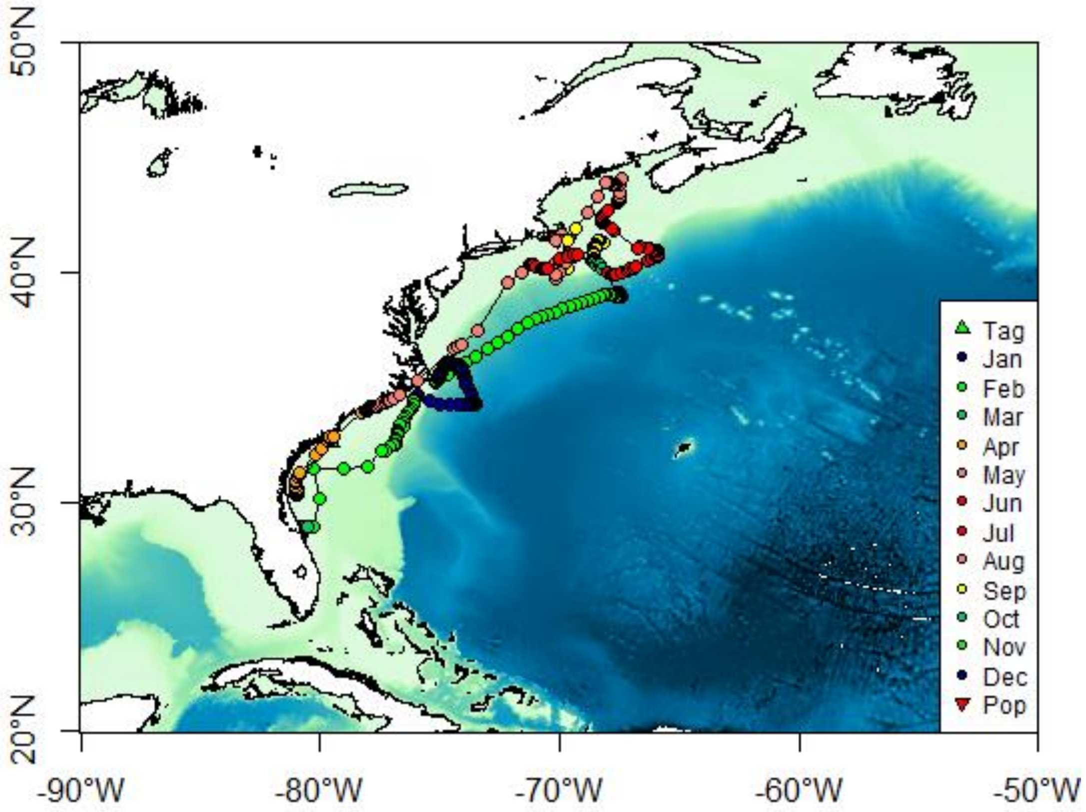

FIGURE 14. Most probable tracks for juvenile white sharks (n = 3). Tag and pop-up locations are denoted with green and red triangles, respectively. Juveniles stayed primarily on the continental shelf throughout their movements.

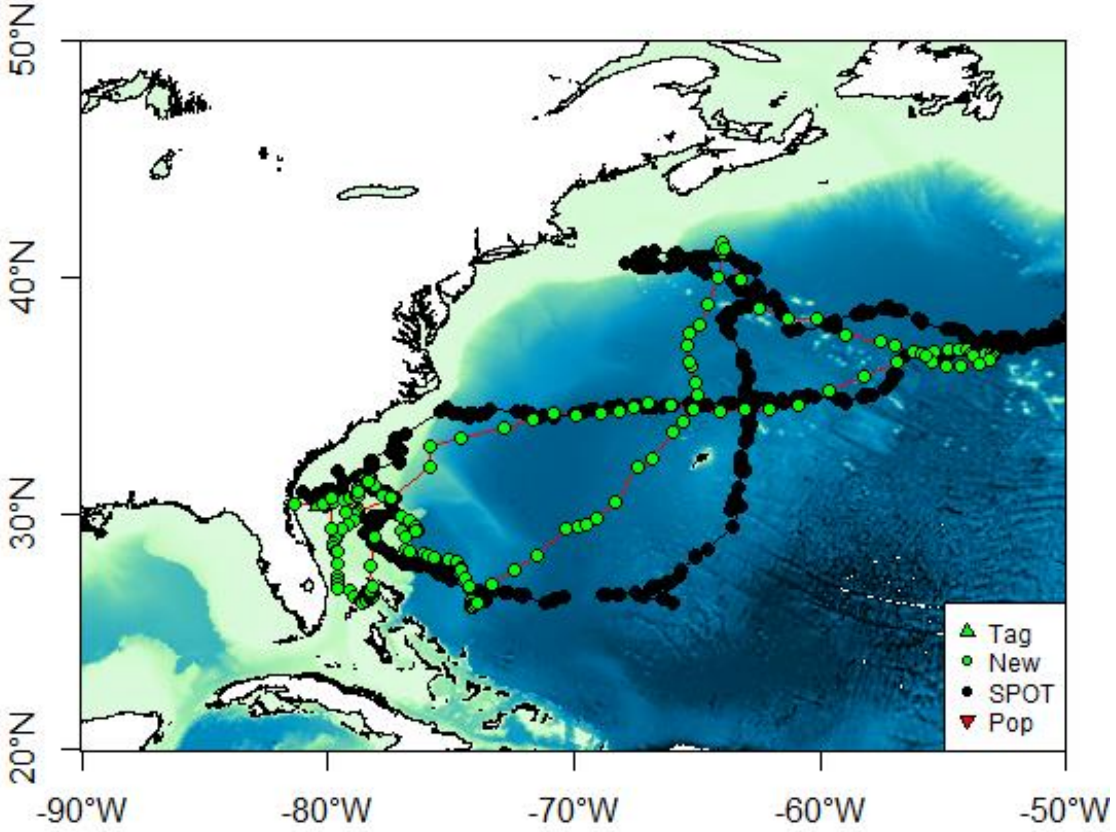

FIGURE 15. WS13-01 original SPOT tag locations (black) compared to the new HMMoce track locations (green). While away from the continental shelf and the Sargasso Sea, the tracks followed a similar pattern. When WS 13-01 returned to the shelf off the coast of Florida, the tracks differed.

Discussion

Pelagic and Coastal Environments

The pelagic environment, which lies beyond the continental shelf, includes the entire ocean water column, and hosts communities that are outlined primarily by differences in water masses (e.g., temperature, salinity; Barton, 2007). The fish fauna in pelagic waters often associate less with the substrate than benthic species and are generally more mobile and wide-ranging (Barton, 2007). Life is found throughout the entire water column, but numbers of both species and individuals tend to decrease with increasing depth. One major variable that affects biodiversity in these waters is productivity. Productivity tends to decline as distance from the continental shelf increases. Species richness tends to decline in areas where productivity is high and seasonally variable (Snelgrove, 2001). In the epipelagic (<200 m) and mesopelagic (200-1000 m) realms, there are multiple larger pelagic fishes that share similar movement patterns and relatively high energetic demands (Barton, 2007). These fishes typically spend most of their time in the epipelagic zone and generally have a broad range of horizontal movements (Itoh et al., 2003; Neilsen et al., 2009). Large sharks have the ability to move many kilometers per day (e.g., Barton, 2007), thus complicating efforts to assess movements in a given community. While previously thought by Compagno (1984) to reside in only coastal waters, adult and sub-adult white sharks *Carcharodon carcharias* have been shown to migrate and spend a proportion of their time beyond the continental shelf (Weng et al., 2007a; Bonfil et al., 2010; Francis et al., 2012; Jorgensen et al., 2012; Skomal et al., 2017). The intent of this migration offshore is unknown and could be due to one or a combination of behaviors such as foraging (Duffy et al., 2012) or parturition (Domier & Nasby-Lucas, 2012).

Unlike the open ocean, coastal environments often have an abundance of sunlight and nutrient-rich riverine sediment as well as upwelling in some regions (Barton, 2007). The continental shelf generally extends in from the coastline to depths of about 200 m deep and includes a broad expanse of relatively shallow habitats (Barton, 2007). From the abundant sunlight and nutrient input, productivity in these waters is relatively high, especially when compared to its offshore counterpart. For the Northeastern United States continental shelf, productivity peaks in the spring and fall months (Barton, 2007). This abundance of nutrients attracts target species important for fisheries, making this an extremely important region (Barton, 2007). This biological productivity also likely draws all size classes of white sharks to this area to forage during the summer and fall months (Weng et al., 2007a; Skomal et al., 2017).

Horizontal Migrations

Large-scale regional movements and diving behaviors are seen in many large pelagic fishes, including thunnid tunas, swordfish, and several shark species (Itoh et al., 2003; Gore et al., 2008; Abascal et al., 2010). White sharks in this study followed many of the movement and diving behaviors seen in other fishes. In this study, data from tagged white sharks in the WNA was run through a different geolocation model from the original in the Skomal et al. (2017) study known as HMMoce (R, R development Core Team) to better estimate their positions. The HMMoce model is generally more reliable due to lower root-square-mean-error values, and when compared to other commonly used models, was shown to produce more accurate tracks (Braun et al., 2018a). Unlike white sharks in the eastern North Pacific, sharks in the WNA did not move to an offshore focal area (Jorgensen et al., 2012). Sharks in the WNA more resembled white sharks in New Zealand and did not show a large pelagic offshore aggregation site; sharks in waters around New Zealand moved to separate areas in the WNA (Duffy et al., 2012).

Two tracks were modelled in this study that were not present in the original Skomal et al. (2017) paper (SC1803; Figure 4, SC1802; Figure 5). SC1803 is a sub-adult male that was tagged off the southern coast of the United States in 2018. This individual moved to pelagic waters during the start of tag deployment in winter months and stayed offshore for almost the entirety (97.6%) of the tag deployment (n = 375 days) gradually moving to northern latitudes during the spring and summer months (Figure 4). SC1803 underwent a vast migration over the deployment period, reaching as far east as Newfoundland, Canada and returned to northern Florida for a total of 7690 km travelled. Vast movements are not uncommon for large pelagic fishes such as swordfish (Abascal et al., 2010), basking sharks *Cetorhinus maximus* (Gore et al., 2008; Braun et al; 2018b), and Pacific bluefin tuna *Thunnus orientalis* (Itoh et al., 2003), all of which are known to make large-scale regional migrations. Similarly, white sharks have also been documented making vast migrations (Bonfil et al., 2005; Bruce et al., 2006; Weng et al., 2007a; Bonfil et al., 2010; Duffy et al., 2012). The other new track, SC1802, was tagged off the coast of Georgia as well in 2018. This shark is a juvenile male who stayed mostly on the continental shelf while the tag was deployed (n = 174 days). This individual demonstrated the common migration to higher latitudes in the summer and lower latitudes in the winter reported in many other species (Itoh et al., 2003; Neilsen et al., 2009; Curtis et al., 2014; Skomal et al., 2017; Figure 5).

In the WNA, there are strong seasonal fluctuations in productivity, driving a plethora of species to migrate to this region in the spring and summer months (Barton, 2007). Most of the white sharks tagged tended to spend their summer months in higher latitudes near Cape Cod. This could be due to a few factors such as the warming of waters around the Cape in the summer, the high abundance of seals in the region, and/or for mating purposes. As noted by Skomal et al. (2017), sharks who spent most of their time confined to the continental shelf occupied temperature ranges between 13-23˚C, which follows the seasonal shift in the 15˚C isotherm. The seal population on Cape Cod has rebounded in recent years, likely drawing white sharks back to this area when the waters start warming (Wood et al., 2009). Lastly, it was previously hypothesized that mating occurs in this area of the WNA (Pratt 1996; Skomal et al., 2017; Verkamp et al., 2021), and if true, could be another reason for the aggregation near Cape Cod during the summer.

Some of the other sharks in this study also demonstrated the latitudinal movement pattern (Figure 5). Like white sharks tagged off New Zealand and in the eastern Pacific, some of the larger individuals moved further offshore before migrating south during the winter months (Figure 4). Two individuals (WS13-01, SC1803) went as far east as Newfoundland, Canada. It was noted in Skomal et al. (2017) that this southern migration allows for overlap between white sharks and other large cetaceans such as North Atlantic right whales *Eubalaena glacialis*, which migrate south for parturition. This movement suggests that these whales could provide a food source for white sharks during the winter months. The winter months are outside of pupping season for harbor seals (*Phoca vitulina*), which make easy targets when they reach their juvenile stage in the summer. This could be a similar scenario to white sharks native to New Zealand waters who are drawn away from the seal rookeries by cetacean migrations as well as searching for warmer waters during the winter months (Skomal et al., 2017). Cetacean migrations drawing white sharks from Cape Cod are a plausible explanation in the WNA because of the ability of white sharks to shift their diet source based on prey availability (Skomal et al., 2012). Prey sources such as smaller cetaceans and other fish species could also be of importance to white shark diet in the WNA. The differences in offshore migrations between sharks in the WNA could indicate region-specific behaviors that are related to foraging (Weng et al., 2007a).

Although sharks in the WNA did not show use of an offshore focal area like their Pacific counterparts, recent findings focusing on white shark movements and populations in the WNA are supported by this study (Bowlby & Gibson, 2020; Bastien et al., 2020). An increase in white shark sightings in Canadian waters has been shown in recent years, which is supported by findings from this study and is likely due to the rebounding population (Curtis et al., 2014; Bastien et al., 2020). Some pelagic sharks from this study (e.g. SC1803) were seen to reach Canadian waters as far north as Newfoundland. Recent population estimates have also shown that conservation measures to protect white sharks have likely been effective in reducing fishing mortality in the WNA (Bowlby et al., 2020).

Understanding crucial life stages is critical to effective management of a species, which is especially true for the juvenile stage in large predators with a low fecundity. Juvenile sharks in this study tended to stay in waters on the continental shelf (Figure 14). One difference from an original track that is interesting was from WS09-03, who originally stayed close to the continental shelf for the duration of the tag. The new track from the HMMoce output indicates that this individual remained in deeper waters while travelling south (Figure 14). Given the lengths of these sharks (2.4 m and 2.1 m; WS09-03 and SC1802, respectively), it would not be out of the realm of possibility for these animals to dive to deeper depths. In Weng et al. (2007b), larger juvenile white sharks would make deeper excursions than smaller juveniles in the summer and autumn months. The smaller of the two (SC1802) did not seem to stray too far from the continental shelf, like younger white sharks in the Pacific, spending 88% of its time on the continental shelf (Weng et al., 2007b).

Position estimates for this study were slightly different than the position estimates in Skomal et al. (2017) for most individuals, but overall trends remained the same. For example, WS13-01 (Pelagic) spent the spring and summer months off the continental shelf as it migrated east to the pelagic realm. After 180 days offshore, this animal returned to the coast of Florida. Compared to its SPOT tag track, the location estimates were similar. As shown in Figure 15, the tracks differed slightly, primarily due to the included parameters such as light-based longitude. SST, and HYCOM data. However, some tracks did not turn out as well, particularly for individuals that migrated into the Gulf Stream and to the western coast of Florida. WS13-02 was shown to migrate along the coast and around Florida to the Gulf of Mexico in the original study (Skomal et al., 2017). When run through the HMMoce model, this track and locations using the best fit model did not accurately reflect the previous trend. Instead of following the coast of Florida around to the Gulf, the track for this individual cut right through the state. This is not only extremely incorrect, but highlights an error previously discussed in Braun et al. (2018). Braun et al. (2018) noted the potential for error when using HYCOM outputs to represent locations of animals in and around the Gulf Stream because of its extremely dynamic nature. Basking sharks tagged from a Braun et al. (2018b) study did not move into waters in the Gulf Stream, making the HYCOM data usable in that study.

Vertical Migrations

Consistency in behavioral clusters were seen between sharks in this study and those in Jorgensen et al. (2012). These methods made it easier to distinguish diving patterns that can then be linked to life history activities such as foraging, mating, and parturition (Jorgensen et al., 2012). Three main diving behaviors (88.9% of sharks days) were identified from the cluster analysis: ROD, Travel, and Coastal. Jorgensen et al. (2012) described these three patterns as well as a fourth, DVM, which was the only difference in clusters. The depth versus time of day queried by cluster that was plotted using the archival data from the recovered tags of WS13-02 and SC1803 gave insight into these diving behaviors (Figures 8, 9, 10).

Rapid oscillatory diving (ROD) which could be attributed to foraging, was seen both on and off the continental shelf (Figure 8). This behavior was not seen in waters surrounding the Cape. Specifically, ROD (Cluster 4) is characterized as even distribution between 30 and 200 m with shallower dives during nighttime hours and this pattern has previously been described for white sharks (Weng et al., 2007a; Jorgensen et al., 2012). During the night hours, sharks were confined to the upper 100 m with heavy concentration in the upper 25 m (Figure 8). From noon until midnight, these sharks exhibited rapid diving patterns shown with deeper depths around 100, 300, 400, and 500 m primarily off the continental shelf (Figure 9). For males and females that exhibited this behavior, % of the shark days occurred off the continental shelf in waters deeper than 200 m. Compared to the other two dominant groups, this was the only pattern to show dives that were deeper than 100 m. Rapid oscillatory diving (ROD) also is the only one of the three major behavior patterns that indicates strong differences between day and evening vertical distribution. This could be due to foraging behavior during the evening hours. White sharks around Cape Cod have been described as occupying shallow depths at night (Winton et al., 2021), which could be due to favorable hunting conditions triggered at crepuscular periods allowing the sharks to remain hidden in shallower waters at night. One interesting observation with the ROD behavior was that it was not seen in any of the juveniles. This could be due to ROD not typically being a behavior exhibited by juveniles, or just due to the low number of juveniles tagged in this study (n = 3). The ROD behavior in juveniles has not been previously examined. In Jorgensen et al. (2012), no juveniles <3 m TL were tagged in that study and in Weng et al. (2007b), no specific diving behavior, except for DVM, was identified.

The Travel behavior seen in this analysis matches a previously described surface swimming pattern with continuous travel (Bonfil et al., 2005; Jorgensen et al., 2012; Weng et al., 2007a). This behavior was seen both on and off the continental shelf like ROD (Figure 8). This behavior is indicated by almost all the animal’s time spent in the upper 5 m of water. There was no difference seen in this behavior over the course of one 24-h period. There are potentially two behaviors exhibited during the Travel phase, mostly dependent on their swimming speed. White sharks are suggested to use different swimming speeds depending on whether they are travelling or foraging (Watanabe et al., 2019). Faster swimming speeds can be associated with travelling while slower swimming speeds can be associated with foraging. This hypothesis indicates that white sharks aggregating near seal colonies adopt slower speeds that may be used to increase encounters with seals while reducing swimming costs (Wantanabe et al., 2019). A slower swimming speed could explain the travel behavior seen around the Cape as well as when sharks migrate out of those waters in the colder months.

In Jorgensen et al. (2012), the ‘Coastal’ mode was described as vertical distribution shallower than 50 m and mostly concentrated in the upper 30 m of water. Similar to both Travel and ROD, this behavior occurred both on and off the continental shelf (Figure 8). Sharks from this study in the Coastal cluster were seen at depths no deeper than 60 m. There was no difference seen in this behavior over the course of one calendar day, and distribution between depths from 0-30 m was even throughout the 24-h period. This behavior is consistent with that seen in white sharks off the coast of California near a known seal rookery (Goldman & Anderson, 1999). White sharks in these waters are ‘patrolling’ for prey by covering the area either swimming close to the bottom or at a distance deep enough to remain hidden (Goldman and Anderson, 1999). Most of the Costal behavior, especially in females, occurred in waters surrounding Cape Cod. Unlike the Costal behavior described in Jorgensen et al. (2012), sharks in the WNA exhibited this behavior both on and off the continental shelf. This behavior was originally described as Coastal because it was a behavior primarily seen along the coast and was attributed to sharks in Pacific waters patrolling for seals near rookeries (Jorgensen et al., 2012). This does not seem to be the case for sharks in the WNA, however. It is plausible that sharks in the WNA could be exhibiting this behavior in pelagic waters for foraging similar to Jorgensen et al. (2012).

Since many more juvenile sharks have been tagged in the WNA since the Skomal et al. (2017) paper was originally published, it would be interesting to include tag data from those sharks into the depth study, which could shed more light onto ROD behaviors in juveniles. It would also be interesting to note how the HMMoce model affects other tracks in the Gulf Stream. From the results discussed here, animals that are known to go through dynamic areas and along the continental shelf around the coast of Florida should not be analyzed with the HMMoce model.

Discovering which areas are essential for foraging, mating, and parturition are critical for the survival of this species. Previous studies have suggested that removals of juvenile white sharks could have resulted in population declines of 60% during the 1970s and 1980s (Bowlby and Gibson, 2020). To conserve the species from similar declines, conservation actions would need to be 100% effective in preventing mortality associated with fisheries for the population in the WNA to have doubled in the past 30 years (Bowlby and Gibson, 2020). This sheds light on the extreme susceptibility of this population to fishing, and reiterates the need of more habitat use, behavioral, and reproductive studies on this species to better protect critical areas.

Conclusions

In this study, tag data were used with both the HMMoce model and a depth analysis to combine both horizontal and vertical movement data into an overall behavior analysis. Original movements that were previously published by including parameters such as known locations from receivers, SST, HYCOM, and light levels. Some tracks did not respond with the HMMoce model well. This is due to the particularly dynamic nature of the Gulf Stream (Braun et al., 2018a). Future studies wishing to use the HMMoce model should be cautious of very dynamic areas and those along the continental shelf. These areas seemed to influence the ability of the HMMoce model to give improved location estimates. General trends remained the same, however. Ultimately, this study identified three swimming behavioral modes in white sharks in the WNA, which were distinguished using a hierarchical cluster analysis to indicate differences in diving behavior. Regional diving behavior in the WNA was previously unidentified. Two new shark (SC1802 and SC1803) tracks were also modeled to give more insight into movement patterns, one of which (SC1802) was a juvenile. This is important because juveniles have not been thoroughly investigated in the WNA.

In the future, increasing the sample size, especially for juveniles would be helpful to determine if ROD is a behavior demonstrated by these sharks. Knowing that information would potentially help clarify if ROD is a behavior related to foraging or mating. Also, being able to find a way to better use the HMMoce model for sharks that migrate along the eastern coast of the United States and through highly dynamic areas would be ideal. It would allow this model to be used more frequently and would help give better position estimates to all tracks regardless of movements. Overall, this research provides a more comprehensive understanding of the temporal and spatial movements in white sharks in the WNA. It also helps establish the diving behaviors of the WNA white shark population and gives more insight into the use of the HMMoce model. While knowledge gaps regarding life history and ecology still exist, these findings help establish the importance of the waters surrounding Cape Cod and those along the continental shelf, to better assist with management of this species.

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