Using Satellite Tagging Technologies to Improve Management and Conservation of the Northwest Atlantic Porbeagle Shark *Lamna nasus*

by

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ABSTRACT

The Northwest (NW) Atlantic porbeagle *Lamna nasus* is overfished and captured as bycatch in fisheries within the region. A comprehensive understanding of the population's life history (e.g., reproduction) and habitat use, and the impact of capture with different gear types (e.g., post-release mortality) is needed to ensure effective fisheries management plans, develop bycatch mitigation strategies, and support stock recovery. This research used satellite tagging technologies to address gaps in knowledge needed to support management and conservation decisions for the NW Atlantic porbeagle. I provided the first estimate of post-release survival and recovery periods for immature porbeagles captured with rod-and-reel. Although survival was high (100%), juvenile porbeagles exhibited a recovery period in surface waters that may make them vulnerable to further fishing interactions. Next, I described the vertical habitat use of young porbeagles to recommend possible fishing modifications to reduce risk of capture. Young porbeagles spent more time in surface waters during summer compared to fall and during the night compared to day, suggesting that risk of capture may be reduced by setting gear deeper during summer and at night when this life stage's behavior is reduced to the upper water column. Then, I provided an analysis of the seasonal and life stage-based habitat use of porbeagles. Space use was concentrated in continental shelf waters around Cape Cod, Massachusetts regardless of season and life stage. Given the relatively small and static high occupancy area overlaps with a high concentration of fishing activity, this region could be considered for spatial management of the NW Atlantic porbeagle. Finally, I used ultrasonography and satellite tagging to describe the three-dimensional habitat use of gravid porbeagles for the first time. Gravid porbeagles demonstrated seasonal differences in horizontal and vertical habitat use but spent most of the pupping season in waters southeast of Cape Cod or on Georges Bank, suggesting this region may be serving as a pupping ground for at least a portion of this population. Conservation efforts should focus on these important habitats to protect the next generation of porbeagles.

DEDICATION

This dissertation is dedicated to my beloved grandmother, Joanne Darline Carlson, who passed away while I was completing this degree.

To my grandmother,

You helped inspire my love of the ocean at an early age and provided unwavering support in the pursuit of my dreams. This dissertation would not exist without your influence. I hope it makes you proud.

I love you, blue skies.

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LIST OF ABBREVIATIONS

AIC	Akaike information criterion
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
CTCRW	Continuous-time correlated random walk
DAL	Days at liberty
DNR	Did not report
EFH	Essential fish habitat
E_2	17β-estradiol
F	Female
FL	Fork length
HR	High rate
ICCAT	International Commission for the Conservation of Atlantic Tunas
J	Juvenile
KDE	Kernel density estimate
KUD	Kernel utilization distribution
LC	Location class
LM	Linear model
LMM	Linear mixed model
LW	Lotek Wireless
M	Male
MA	Massachusetts
MFG	Mature female gravid

MFN	Mature female non-gravid
MFU	Mature female of unknown reproductive state
MM	Mature male
MT	Microwave Telemetry
NA	Not available
NMFS	National Marine Fisheries Service
NOAA	National Oceanic and Atmospheric Administration
NW	Northwest
PBSG	Phosphate buffered saline with 0.1% gelatin
PSAT	Pop-off satellite archival tag
P_4	Progesterone
SD	Standard deviation
SE	Standard error
sPAT	Survivorship PAT
SR	Standard rate
SSM	State-space model
T	Testosterone
TL	Total length
U	Unknown
US	United States
WC	Wildlife Computers
Y	Young-of-the-year
YOY	Young-of-the-year

CHAPTER 1

INTRODUCTION

The porbeagle *Lamna nasus* is a large, regionally endothermic, and highly mobile shark species that inhabits cold-temperate waters of the Atlantic, South Pacific, and southern Indian Oceans (Francis et al., 2008). Similar to most large sharks, the porbeagle has conservative life history traits that make this species particularly susceptible to overexploitation and population depletions (Jensen et al., 2002; Natanson et al., 2002; Natanson et al., 2019). Historically, this species has been targeted commercially or taken as bycatch throughout much of its range (Francis et al., 2008), and population declines have occurred in multiple regions worldwide (Campana et al., 2002; Stevens et al., 2006; Rigby et al., 2019). In particular, the porbeagle is considered to be vulnerable to extinction on a global scale by the International Union for the Conservation of Nature (Rigby et al., 2019). Varying levels of abundance decline have been observed in each region, with the largest decline observed in the Northeast (NE) Atlantic and the smallest decline in the Southern Hemisphere (Rigby et al., 2019).

In the Northwest (NW) Atlantic, a Norwegian (and to a lesser extent, Faroe Islands) commercial pelagic longline fishery targeting a virgin (unfished) population of porbeagles began in 1961 (i.e., www.iccat.com; Campana et al., 2002). This fishery collapsed by 1967 due to low catch rates and a decrease in the size of captures, accompanied by a depletion in the NW Atlantic porbeagle population (www.iccat.com; Campana et al., 2002). The fishery appeared to have low but sustainable catches from the 1970s to the early 1990s (i.e., www.iccat.com; Campana et al., 2002). However, new Canadian and United States (US) commercial pelagic longline fisheries targeting porbeagles appeared in the early 1990s, causing a second collapse in the NW Atlantic porbeagle population, which reached its lowest abundance in 2001 (i.e., www.iccat.com; Campana et al., 2013).

Population dynamics models suggested the recovery time for the stock could vary (between 20 and over 100 years) based on productivity and harvest rates and that fishing mortality must remain low for successful recovery to occur (Campana et al., 2013). Due to the collapses in the NW Atlantic population, the porbeagle was listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora, which limits and controls the international trade of the species (www.cites.org; Curtis et al., 2016). Canada listed the porbeagle as Endangered (COSEWIC, 2004) and prohibited the retention of live captures (Campana et al., 2015). In the US, catch (1 porbeagle per day if tuna or swordfish are not landed) and size limits (> 54 inches or ~137 cm fork length) were enforced in both commercial and recreational fisheries in an attempt to reduce the fishing mortality for porbeagles in the region (NMFS, 2007; ICCAT, 2015). Nevertheless, porbeagles continue to be captured as bycatch (with most individuals being discarded) in numerous commercial (longline, rod-and-reel, trawl, gillnet) and recreational (rod-and-reel) fisheries in the NW Atlantic (Hurley, 1998; Curtis et al., 2016; NOAA, 2019; Haugen, 2020). As such, a complete understanding of the NW Atlantic porbeagles' life history (i.e., growth, reproduction) and habitat use, as well as the impact of capture with different gear types (i.e., post-release mortality) will be needed to help inform effective fisheries management plans and support a timely recovery of this historically overfished stock.

To date, the impact of fishing capture on the NW Atlantic porbeagle has only been quantified for the commercial pelagic longline fishery. Campana et al. (2016) studied the capture and post-release mortality of blue shark *Prionace glauca*, shortfin mako *Isurus oxyrinchus*, and porbeagle bycatch in the Canadian pelagic longline fishery targeting swordfish or tuna. This study found porbeagles to have the highest capture mortality rate (44%) of the three shark species and a post-release mortality rate of 27%, indicating an overall fishing mortality rate (including capture and post-release mortality) of 59%. However, it is important to note that handing methods in this study (bringing sharks on board the fishing vessel) were not representative of standard fishing practices and the sample size for injured sharks (n = 4) was low (Campana et al., 2016). These factors may have impacted the observed mortality rates. For example, Bowlby et al. (2020) also studied the post-release mortality of porbeagles in the Canadian pelagic longline fishery but kept most animals in the water. Bowlby et al. (2020) found the post-release mortality rate (14%) for porbeagles to be about half the rate found by Campana et al. (2016). Moreover, Bowlby et al. (2021) examined the recovery behavior and survival of porbeagles following pelagic longline or trawl capture and found that the species had mean recovery periods of 9.1 days, post-release mortality rate of approximately 17%, and survivorship was reduced for individuals that were foul hooked or hooked in the gut. Regardless, the development of bycatch avoidance strategies will be critical to reducing captures, sub-lethal effects, and fishing mortalities for porbeagles in NW Atlantic. This requires an understanding of movements and habitat use, which will be particularly important for critical life stages such as gravid (pregnant) females and juveniles. Additionally, the significant mortality rates of porbeagles in pelagic longline fisheries highlights the need to study the impact of other fisheries (i.e., rod-and-reel, trawl, gillnet) on porbeagles in the region.

There have been limited studies on the movement patterns and habitat use of porbeagles in the NW Atlantic (i.e., Kohler et al., 2002; Campana and Joyce, 2004; Campana et al., 2010; Kohler and Turner, 2019; Skomal et al., 2021). Kohler et al. (2002) and Kohler and Turner (2019) analyzed mark recapture data for several shark species in the larger North Atlantic, including the porbeagle. These conventional tagging studies indicated that porbeagles traveled between 4 to 1216 nautical miles (nm) from tag to recapture locations, with times at liberty ranging from 1 day to 16.8 years (Kohler et al. 2002; Kohler and Turner 2019). However, most porbeagles traveled less than 500 nm between tag and recapture locations and all of these sharks remained within their respective tagging region (NW or NE Atlantic) in these studies (Kohler et al., 2002; Kohler and Turner, 2019). Moreover, after several decades of conventional and satellite tagging, movement studies have suggested that porbeagles in the larger North Atlantic primarily remain within their respective tagging regions (i.e., Kohler et al., 2002; Pade et al., 2009; Campana et al., 2010; Saunders et al., 2011; Biais et al., 2017; Kohler and Turner, 2019; Skomal et al., 2021), with only one transatlantic movement by a porbeagle ever recorded in over 50 years of tagging (Cameron et al., 2018). Therefore, despite the lack of genetic distinction indicating some level of mixing (Testerman, 2014), these movement data suggest the NW and NE Atlantic porbeagles can be addressed as two populations and they are often assessed, studied, and managed as such.

Campana and Joyce (2004) studied the depth and temperature associations of porbeagles in the NW Atlantic using fishery-dependent data. This study found porbeagles to prefer temperatures of 5-10°C and were primarily captured at depths < 200 m (Campana and Joyce, 2004). However, it is important to note that this study was limited to depths and temperatures of commercial fishing operations, and thus may not entirely represent the habitat preferences of the population. Finally, three studies (Campana et al., 2010; Wang et al., 2020; Skomal et al., 2021) utilized pop-off satellite archival tags (PSATs) to analyze the horizontal and vertical movements of porbeagles in the NW Atlantic. Campana et al. (2010) deployed PSATs on 21 porbeagles in the region, including 11 mature females. This study found that males and immature females primarily occupied continental shelf waters for the duration of the tagging period, while most mature females migrated to the Sargasso Sea during the winter and early spring (Campana et al., 2010). Based on the assumed annual reproductive cycle of the NW Atlantic porbeagle at the time of the study and the disparity in movements between mature females and other life stages, Campana et al. (2010) suggested that the Sargasso Sea served as a pupping ground for this population. However, given the more recent finding that the NW Atlantic porbeagle population has a biennial reproductive cycle (Natanson et al., 2019), it is now uncertain whether the mature females tagged in Campana et al. (2010) were gravid, as no formal assessment of reproductive state was completed. Wang et al. (2020) analyzed the fine-scale diving behavior of one mature female porbeagle in the NW Atlantic over 283 days with high-resolution data recovered from a PSAT. This study found marked seasonal shifts in diel activity patterns that were associated with sea surface and bottom water temperatures, the mixed layer depth, and the occurrence of a hurricane (Wang et al. 2020). During all seasonal periods, the shark occupied shallower warmer waters during the nighttime and deeper cooler waters in daytime, but diel mean, standard deviation, and max depths varied among seasonal periods. Additionally, diving behavior was markedly different during Hurricane Kyle (Wang et al., 2020). As such, the results of Wang et al. (2020) highlight the potential influence of environmental conditions on the diving behavior of porbeagles. Finally, Skomal et al. (2021) deployed PSATs on 20 large juvenile (128-154 cm fork length (FL)) porbeagles in the NW Atlantic and found that this life stage displayed broad horizontal and vertical movements that were seasonally dependent. Similar to mature females tagged in Campana et al. (2010), large juvenile porbeagles migrated into more southern waters off of the continental shelf during the late fall, and returned to shallower continental shelf waters in spring (Skomal et al., 2021). In the summer and early fall, large juveniles primarily occupied water depths < 200 m and spent most of the time in the top 25 m of the water column. When occupying deeper offshore habitat, large juvenile porbeagles displayed one of two diving behaviors, either largely remaining in colder epipelagic waters (0-200 m; termed "non-divers") north of the Gulf Stream, or made frequent deep dives and remained in the mesopelagic zone (200-1000 m; "divers") when in warmer waters within or south of the Gulf Stream (Skomal et al. 2021). Collectively, movement and habitat use studies indicate that NW Atlantic porbeagles exhibit seasonal movements, occupying shallower continental shelf waters during the summer and early fall and deeper offshore habitat in the late fall and winter. However, an understanding of the horizontal and vertical movement patterns of pups and confirmed gravid females will be critical to developing bycatch avoidance strategies for the population.

The life history of the NW Atlantic porbeagle has been relatively well-studied. For example, Natanson et al. (2002) examined the age and growth of the porbeagle in the

NW Atlantic and determined that the population is characterized by late ages at maturity (8 and 13 years for males and females, respectively) and long lifespans (up to 45 years in an unfished population). Additionally, Jensen et al. (2002) assessed the reproductive biology of the population, including the sizes at sexual maturity (162 -185 cm FL for males and 210- 230 cm FL for females) as well as the reproductive cycle. Based on examinations of the reproductive tracts, Jensen et al. (2002) confirmed that the NW Atlantic porbeagle population was oophagous, meaning embryos are nourished by consuming unfertilized eggs ovulated by the mother throughout gestation. This previous study also suggested the population had a gestation length of 8-9 months, a litter size of approximately 4 pups, and an annual reproductive cycle (Jensen et al., 2002). However, a more recent study by Natanson et al. (2019) discovered a geographically segregated group of mature female porbeagles in the NW Atlantic that were not reproductively active, indicating a biennial cycle. This new finding regarding the reproductive cycle has implications for the populations' productivity, decreasing the lifetime reproductive output and rate of population recovery compared to what was previously assumed (Natanson et al., 2019). This further highlights the need to understand the habitats used by critical life stages (pups, gravid females) in order to support conservation and recovery of the population.

Gaps in our current knowledge of porbeagle ecology include the impact of rod-and-reel fishing on immature porbeagles that are released alive, as well as the horizontal and vertical habitat use patterns of porbeagles of all life and reproductive stages. Such information will be imperative to understanding the efficacy of current management measures and contributing data needed for developing strategies to reduce bycatch of porbeagles in the NW Atlantic. Fortunately, the advancement of satellite tagging technologies in recent decades has revolutionized the ability to study the ecology of sharks (Hammerschlag et al., 2011). Satellite tags now offer opportunities to collect such data that are critical to management and conservation needs. For example, estimating the post-release survival of bycatch species is critical to determining total fishing mortality, creating accurate stock assessments, and assessing the efficacy of fisheries management regulations (i.e., Ellis et al., 2017; Musyl et al., 2019). Studying the post-release survival rates of bycatch after discarding can now be done with vertical movement data obtained from PSATs. Additionally, understanding movements and habitat use of sharks can be used to determine the degree of vulnerability to capture in fisheries, identify "hotspots" or areas with high overlap between critical habitat and fishing effort, develop strategies to reduce the capture of sharks (i.e., marine protected areas, changes in fishing practices such as fishing depth), and/or test the efficacy of conservation zones (e.g., Musyl et al., 2011). Historically, fisheries dependent catch data and conventional tags, which require the animal to be recaptured, were the only methods of determining the movements and habitat use of sharks. However, fin-mounted satellite tags (hereafter referred to as "fin-mount tags") and PSATs can now be utilized to remotely study the horizontal and vertical movement patterns, migrations, and behavior of sharks at a finer scale than traditional methods. For example, PSATs can be used to understand the depth and temperature preferences of sharks, as well as large scale movements using light-based geolocation methods in some tag models (Hammerschlag et al., 2011). Additionally, fin-mount tags have been developed to track the horizontal movements of sharks by transmitting location information to passing satellites when the tag (usually attached to the shark's dorsal fin) is above the water’s surface (Hammerschlag et al., 2011). While the use of fin-mount tags is limited to species that frequently swim at the sea surface, these tags provide higher location accuracy than light-based geolocation estimates from PSATs. Collectively, my dissertation utilizes satellite tagging technologies to fill critical gaps in the understanding of the ecology of the NW Atlantic porbeagle that can be beneficial in the context of fisheries management and conservation needs. This research will provide new data that can be used by management to help determine the efficacy of current porbeagle fisheries management plans as well as be used to inform potential strategies for reducing porbeagle bycatch in fisheries in the region. The general objectives for each chapter are as follows:

1. Use PSATs to estimate the post-release survival rate and to observe post-release recovery behavior of immature porbeagles caught with rod-and-reel gear and released alive in the NW Atlantic.
2. Use short-term, high-resolution PSATs to assess fine-scale vertical movement patterns and to identify temporal trends in the depth distribution of young-of-the-year (YOY) and one-year-old porbeagles in the NW Atlantic.
3. Use fin-mount tags to assess seasonal habitat use of porbeagles in the NW Atlantic and compare movement patterns by life stage.
4. Use a combination of tagging technologies to assess horizontal and vertical movement patterns of gravid porbeagles in the NW Atlantic and identify high use areas during the expected pupping season.

CHAPTER 2

ESTIMATE OF POST-RELEASE SURVIVAL OF IMMATURE PORBEAGLES CAUGHT WITH ROD-AND-REEL IN THE NORTHWEST ATLANTIC

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ABSTRACT

The Northwest (NW) Atlantic population of porbeagles *Lamna nasus* is susceptible to capture in rod-and-reel fisheries and most individuals are discarded alive due to catch and size limits. To estimate post-release survival, pop-off satellite archival tags were attached to porbeagles captured with rod-and-reel. Fourteen tags were deployed, of which 13 transmitted. All sharks for which I had data survived, giving a post-release survival rate of 100%. Following release, 6 individuals remained in surface waters for several hours to days, while 2 individuals immediately resumed normal diving behaviors. For the remaining sharks (n = 5), low tag transmission resolution precluded the detection of fine scale post-release behavior. The duration of initial depth-holding behavior was

characterized using a break-point analysis of dive track variance, which suggests porbeagles exhibited a median post-release recovery period of 116 h (10th and 90th percentiles = 68.8 and 280.1 h) following capture and handling. This preliminary study suggests immature porbeagles are resilient to capture and handling, although more data would provide stronger support for management recommendations.

Capture as bycatch is a pressing threat to fish stocks (Davies et al., 2009), and slow-growing shark species with low reproductive output are particularly susceptible to overexploitation (Stevens et al., 2000). Management measures (e.g., catch limits, retention prohibitions, circle hook requirements, wire leader bans) are often employed for overexploited shark species in an effort to reduce fishing mortality (e.g., ICCAT, 2015). Although such management measures may effectively reduce directed landings, incidentally captured sharks may still suffer unintended at-vessel or post-release mortality from injuries and physiological damage (Kneebone et al., 2013). Therefore, computing total catch and assessing the efficacy of management measures require quantification of both components of unintended fishing mortality (at-vessel and post-release mortality; e.g., Musyl and Gilman, 2019).

The Northwest (NW) Atlantic population of porbeagles *Lamna nasus* is particularly vulnerable to population declines (Natanson et al., 2002). Historically, this species was targeted commercially or taken as bycatch throughout much of its range (Francis et al., 2008), and population declines have occurred in multiple locations worldwide (Campana et al., 2002; Stevens et al., 2006). After the introduction of longline fishing pressure in the early 1960s, the NW Atlantic population declined precipitously in abundance, reaching a minimum in 2001 (Campana et al., 2013). Population dynamics modeling suggests fishing mortality must remain low for successful recovery to occur (Campana et al., 2013). In response to declines, catch and size limits have been utilized in the NW Atlantic to reduce rod-and-reel fishing mortality (i.e., Campana et al., 2002; NMFS, 2007; ICCAT, 2015). Despite these management measures, porbeagles remain susceptible to capture in rod-and-reel fisheries targeting tuna and pelagic sharks in the

NW Atlantic (Hurley, 1998; NOAA, 2019) and no study to date has investigated the impact of rod-and-reel capture on porbeagles released alive. Therefore, this study utilized pop-off satellite archival tags (PSATs) to estimate post-release survival and characterize behavior following release for porbeagles caught with rod-and-reel in the NW Atlantic.

METHODS

Porbeagles were caught opportunistically in the NW Atlantic using rod-and-reel with 200 lb Jinkai fishing line set at a strike drag strength of 40 lb. Rods and reels were equipped with 16/0 non-offset Mustad circle hooks or 12/0 Mustad J-hooks baited with locally caught species (i.e., Atlantic mackerel *Scomber scombrus*) alive or dead, and whole or chunked. Fight time (time from when the shark was hooked until it was either secured alongside the vessel or brought onboard), sex, fork length (FL), and handling time (time from when the shark was secured alongside the boat or brought onboard until it was released) were recorded. Sharks were assigned an injury code modified from Marshall et al. (2015) and a release condition adapted from Manire et al. (2001) (Table 2.1). Before release, the hook was removed or the leader was cut.

Different pop-off schedules (in parentheses) characterized the PSATs used to observe post-release survival: Lotek Wireless (LW) PSATLIFE tags (28 d; n = 7), Wildlife Computers (WC) Survivorship PATs (sPATs; 30 d; n = 4), and Microwave Telemetry (MT) High Rate (HR; 30 d; n = 1) and Standard Rate (SR; 9 mo; n = 2) X-Tags. The short-term deployments were assumed to be long enough to detect mortality caused by trauma or stress during capture and handling, while the 2 SR X-Tags were deployed to observe delayed mortality over longer time spans. For 10 porbeagles, tags were attached using a stainless steel dart anchor (Hallprint) inserted into the dorsal musculature. The tags have a buoyancy rating of 8 g and the tag tethers were 2.3 g in water, ensuring tags would float if shed. To reduce the likelihood of premature tag shedding, for 4 porbeagles PSATs were looped through a hole in the dorsal fin (Moyes et al. 2006). In this case, a 5 mm diameter hole was drilled (Ryobi drill) through the dorsal fin, then flexible tubing with 136 kg test monofilament Jinkai fishing line was threaded through the hole and crimped with a stainless steel nicopress crimp sleeve. The PSAT was attached to this loop and centered behind the dorsal fin. PSATs were programmed to collect pressure (i.e., depth) and ambient temperature at 10−90 s intervals and report data at 5 (PSATLIFE, HR X-Tag) or 15−60 (SR X-Tag) min intervals or report daily minimum and maximum data (sPAT). PSATs were programmed to release prematurely if pressure remained constant for a pre-determined number of days (LW: ±5 m for 3 d, MT: ±3 m for 2 d, and WC: ±4 m for 1 d), indicating a mortality or a shed tag floating at the surface or washed ashore. PSATs were programmed to release and transmit prematurely if pressure went below a predetermined threshold (LW: 1500 m, MT: 1250 m, and WC: 1400 m).

Post-release survival was determined using depth profiles from PSAT data downloaded from the ARGOS website (www.argos-system.org). To evaluate changes in diving behavior following release, hourly variance in depth was calculated from the tags transmitting at 5 min intervals (n = 6). A break-point analysis completed in R (v 3.5.1) was used to identify the hour in which variability at the beginning of the dive track differed the most from variability in the latter part of the dive track (Wichern et al., 1976). Extremely low hourly variance only occurred while an individual remained within surface waters, and variance markedly increased once an individual began utilizing a range of depths. The end of the recovery period was identified from a time series of absolute differences between mean variance prior to and after a given sampling hour. The maximum reduction in the absolute difference in variance occurred once an animal ceased any depth-holding behavior and began to move cyclically through the water column, indicating the end of the recovery period. For tags with lower transmission resolution (i.e., sPATs), sharks that exhibited minimal diving behavior following release were identified from the amount of time they remained in the top 50 m of the water column.

RESULTS

Opportunistic capture resulted in a random sample of 14 immature (Jensen et al., 2002) porbeagles tagged with PSATs (mean FL (±SD) 122.4 ± 38.8 cm; Figure 2.1; Table 2.2). Data were successfully transmitted from tags on 13 of these individuals (FL 122.5 ± 40.3 cm). Fight time ranged between 1 and 76 min. All 13 (100%) sharks for which I had data survived until the tags popped off (between 12 and 246 d after release). Two tags attached with dart anchors shed prematurely (12 and 25 d) but these individuals were included in survival analyses, given that most shark mortality occurs within the first few hours to days after release (e.g., Musyl & Gilman, 2019).

Six sharks swam in surface waters (<50 m depth; Figure 2.2) with limited vertical movement immediately following release, suggesting possible recovery periods. During these potential recovery periods, sharks spent 16.4−99.5% of time in the top 10 m and 61.6−100% of time in the top 20 m of the water column. Following the potential recovery periods, these same individuals spent 26.2−79.9% in the top 20 m of the water column, remained below 50 m for 1.2−56% of the time, and made regular dives to ≥100 m. Based on break-point analysis of hourly dive variance for individuals with high transmission resolution (example given in Figure 2.3), recovery times ranged from 49 to 350 h, with a median of 116 h (10th and 90th percentiles = 68.8 and 280.1 h). For some individuals recovery behavior (based on the time spent in top 50 m of water column or breakpoint analysis of dive variance) could not be determined because of tag transmission resolution. In particular, SR X-tags (n = 2; no. 25 516 and 25 514) did not transmit data for the first several days at liberty and 3 sPATs (no. 416, 193, and 819) transmitted daily maximum depths of approximately >50 m for the first day at liberty and therefore shorter duration (<24 h) recovery periods could not be determined. However, the 2 individuals with high transmission resolution tags (no. 1815 and 161 793) that dove to >50 m immediately following release exhibited relatively consistent hourly dive variance throughout monitoring, and therefore did not exhibit depth-holding behavior indicative of a recovery period upon release based on the breakpoint analysis of hourly dive variance.

DISCUSSION

This study suggested high (100%) post-release survival for immature porbeagles captured with rod-and-reel regardless of capture, handling, and release factors (i.e. injury code, release condition). Short-term (28 d) survival was the focus of this study and long-term delayed mortality (i.e., from infection or gut hooking and cessation of feeding) may have been underestimated. However, results from the deployment of two 9 mo tags suggests long-term survival may also be high for porbeagles. The survival rate in this study is consistent with those found for other shark species captured with rod-and-reel, including shortfin mako *Isurus oxyrinchus* (90%; French et al., 2015), blue shark *Prionace glauca* (87%; Howey et al., 2017), and blacktip shark *Carcharhinus limbatus*

(90.3%; Whitney et al., 2017). Additionally, Sepulveda et al. (2015) found post-release survival of rod-and-reel caught common thresher sharks *Alopias vulpinus* to be 100% when mouth-hooked, although survival for tail-hooked individuals was 66%.

The observed depth-holding behavior was consistent with previously documented post-release behavior modification in porbeagles (Hoolihan et al., 2011), other pelagic fishes (Pepperell and Davis, 1999), and other sharks (Campana et al., 2009, Hoolihan et al., 2011). Decreased vertical movement may be a consequence of physiological stress associated with capture and handling (Hoolihan et al., 2011), as porbeagles may need to reallocate energy from normal swimming patterns to restore homeostasis (Marshall et al., 2015). This study suggests porbeagles exhibit a recovery period following capture and handling that typically lasts ~116 h (4.8 d). Given the observed recovery behavior increases time spent in surface waters where rod-and-reel fishing for pelagic species occurs, captured and released porbeagles may be more vulnerable to recapture and/or predation from larger predators in habiting surface waters.

CONCLUSION

These findings suggest immature porbeagles are resilient to capture and handling in rod-and-reel fisheries in the NW Atlantic, and these are the first data of this kind that can be considered in management of this species. Based on these preliminary results, mitigation measures that increase the proportion of porbeagles released alive (i.e., catch limits, size limits) may be viable strategies for minimizing mortality in rod-and-reel fisheries. However, more data is necessary to obtain sufficient statistical power to better support management recommendations (Musyl & Gilman, 2019) and evaluate how mortality rates or recovery periods vary with characteristics of the fishery.

Table 2.1

Injury codes (modified from Marshall et al., 2015) and release conditions (adapted from Manire et al., 2001) assigned to porbeagles captured with rod-and-reel.

Indicator	**Description**
Injury Code	
1	No visible trauma, hooked in jaw
2	Minor abrasions or small lacerations
3	Obvious trauma (i.e., lacerations on body, gut hooking)
4	Moribund
Release Condition	
1	Burst swimming
2	Strong swimming
3	Sluggish swimming
4	Sank with no visible swimming effort

Table 2.2

Summary data for porbeagles captured with rod-and-reel. Fight and handling times are reported to the nearest minute. Note: M = male, F = female, FL = fork length, IC = injury code, RC = release condition, loc = location, DAL = days at liberty, SR = standard rate, HR = high rate, sPAT = Survivorship PAT, DNR = did not report.

[a]denotes a shark removed from survival analysis.

ID	Sex	FL (cm)	IC	RC	Fight Time (min)	Handle Time (min)	Tag Type	Capture Date	Capture Loc	Pop-off Date	Pop-off Loc	DAL	Distance Traveled (km)	Recovery Time (h)	Outcome
25516	-	110	-	-	-	-	SR X-Tag	06/26/2015	43.22, -70.08	02/26/2016	43.03, -67.19	246	236	NA	Survived
25514	F	119	-	-	-	-	SR X-Tag	07/10/2015	43.24, -70.08	03/11/2016	40.07, -68.92	246	365	NA	Survived
161793	F	92	-	-	-	-	HR X-Tag	08/12/2016	43.57, -70.14	09/11/2016	43.56, -70.08	31	5	0	Survived
1815	F	94	-	-	-	-	PSATLIFE	09/10/2016	43.37, -70.12	10/07/2016	42.81, -70.5	28	70	0	Survived
2492	F	90	1	3	2	7	PSATLIFE	08/30/2018	43.40, -70.30	09/10/2018	41.54, -70.31	12	207	NA	Survived
2490	F	90	1	2	3	3	PSATLIFE	09/23/2018	43.40, -70.30	10/17/2018	41.94, -67.15	25	304	117	Survived
416	F	198	3	1	76	13	sPAT	06/12/2019	43.37, -70.13	07/13/2019	43.00, -69.21	31	85	NA	Survived
2498[a]	F	121	1	1	1	7	PSATLIFE	06/17/2019	43.36, -70.12	DNR	DNR	DNR	DNR	DNR	DNR
193	M	127	1	1	1	8	sPAT	06/18/2019	43.36, -70.13	07/19/2019	43.56, -68.27	32	151	NA	Survived
446	-	152	3	2	8	6	sPAT	06/27/2019	42.72, -70.28	07/28/2019	42.66, -70.21	32	10	NA	Survived
2499	F	110	2	1	1	5	PSATLIFE	06/27/2019	42.73, -70.28	07/24/2019	42.60, -70.22	28	15	115	Survived
819	F	209	3	2	23	17	sPAT	07/02/2019	42.90, -70.10	08/02/2019	42.41, -70.54	32	66	NA	Survived
2491	F	88	1	1	8	2	PSATLIFE	07/09/2019	43.38, -70.13	08/05/2019	43.87, -69.10	28	100	49	Survived
2494	M	114	3	1	5	3	PSATLIFE	10/01/2019	42.32, -70.32	10/28/2019	34.42, -65.46	28	975	350	Survived

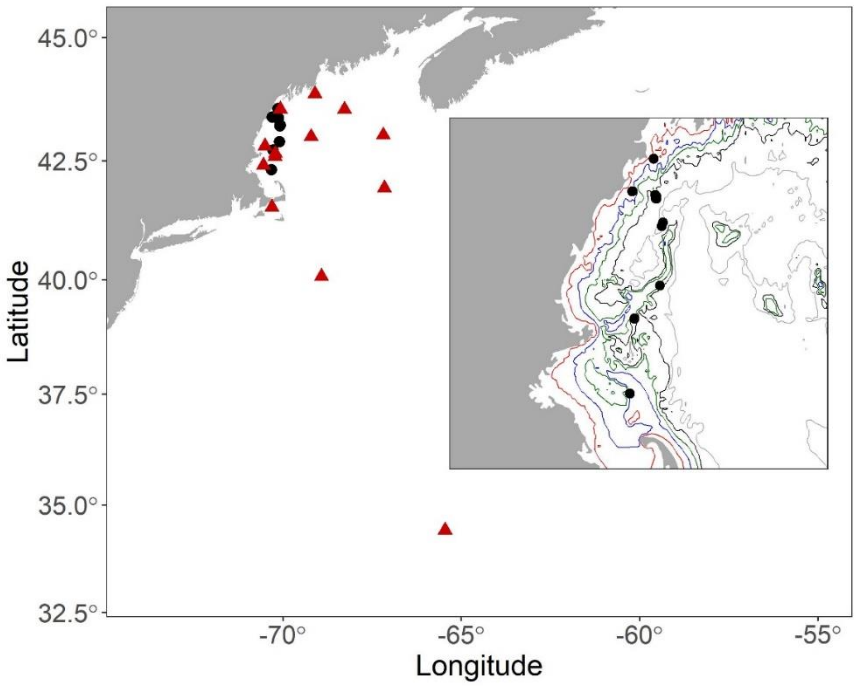

Figure 2.1. Tagging (●) and pop-off (▲) locations for porbeagles captured with rod-and-reel. The inset shows 25 (red), 50 (blue), 75 (green), 100 (black), and 150 (grey) m depth contours at tagging locations.

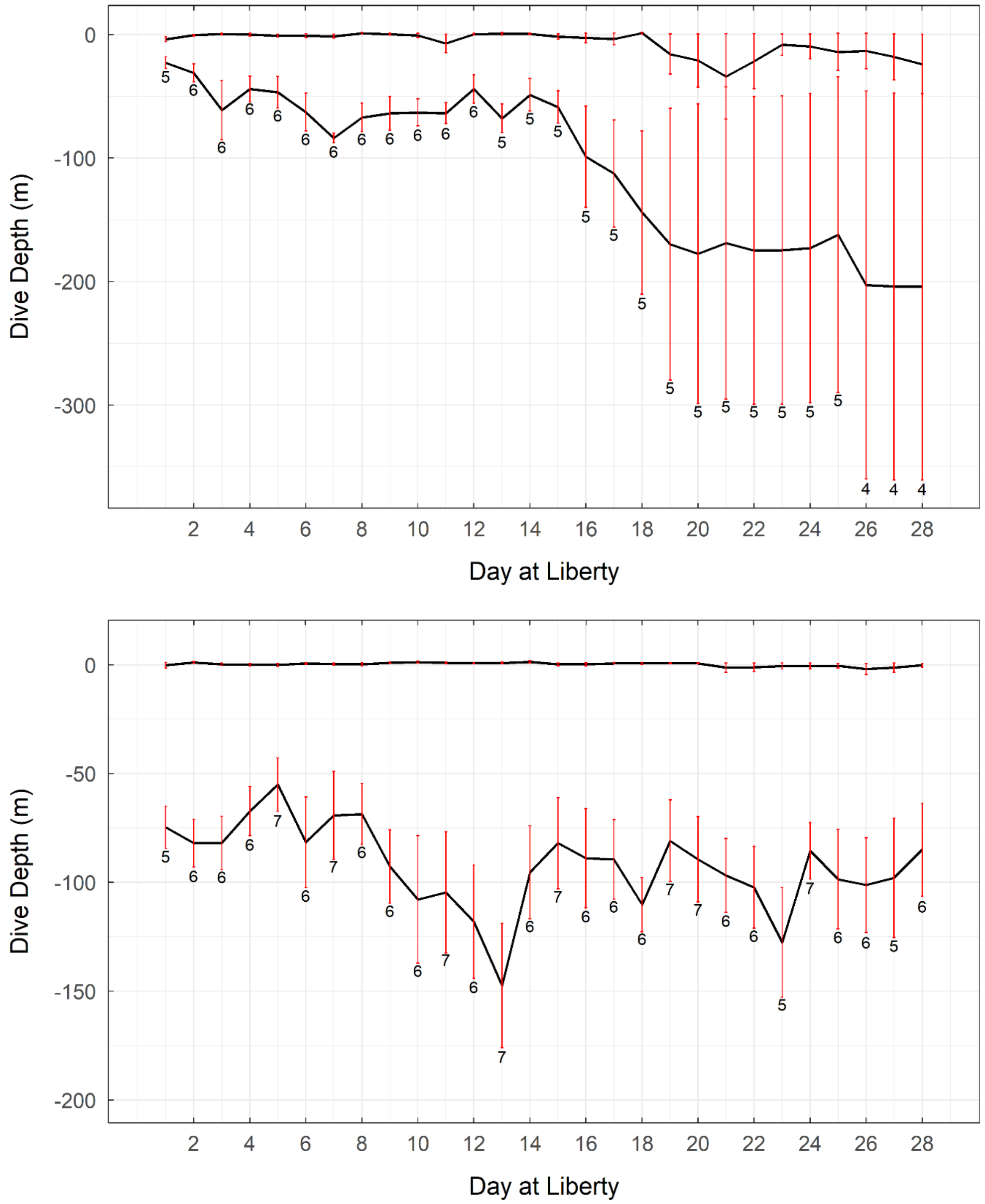

Figure 2.2. Daily mean minimum (top line) and maximum (bottom line) dive depth representing porbeagles captured with rod-and-reel that exhibited a possible recovery period (top panel) or no recovery period (bottom panel). Note the difference in scales of the y-axes. Numbers below error bars indicate sample size. Change in sample size represents tag shedding or change in the number of tags with depth data available. Error bars represent ± 1 standard error (SE).

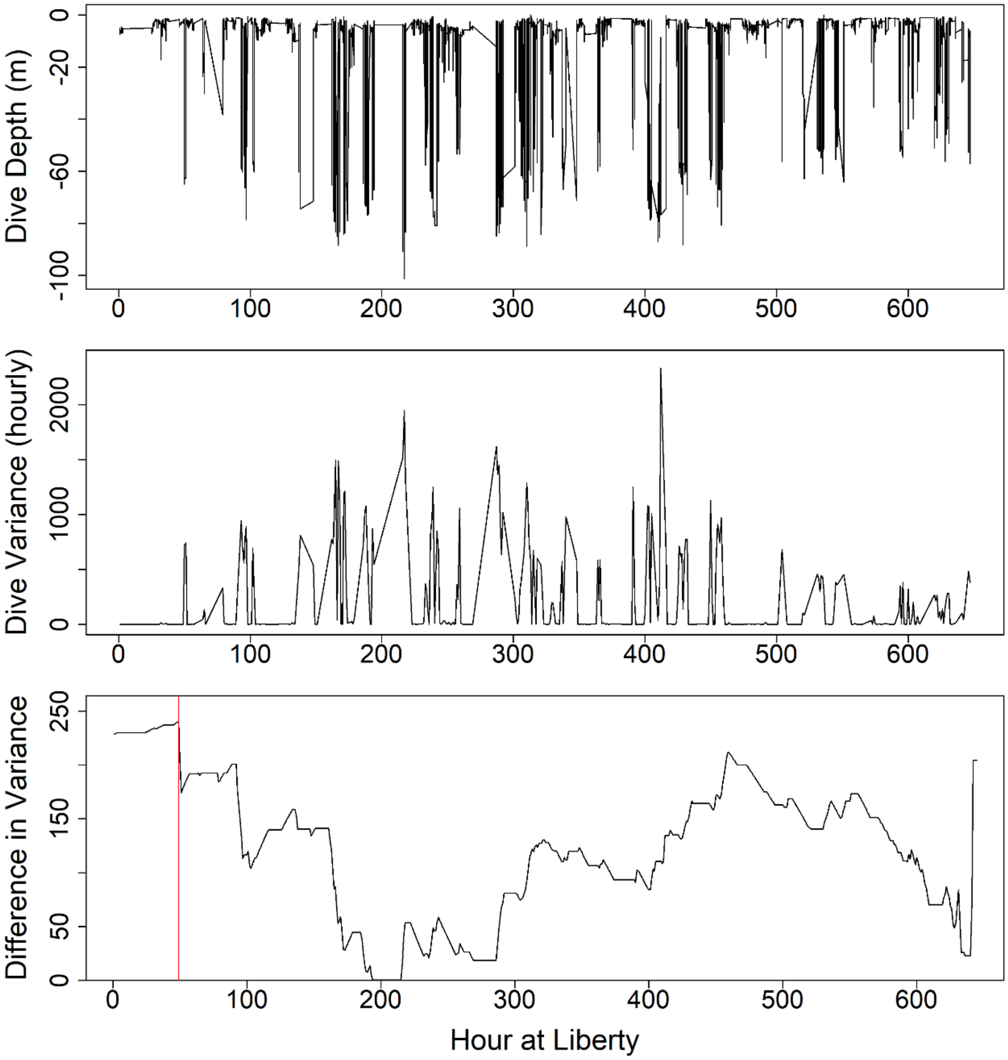

Figure 2.3. Example breakpoint analysis for no. 2491, showing the time series of recorded dive depths (top panel), hourly variance in depth (middle panel), and the absolute difference in mean variance for each successive hour at liberty from the remainder of the dive track (bottom panel). The near-zero variance at the start of the track indicates depth-holding at the surface (middle panel) and the maximum difference in variance between the start and end of the dive track (red vertical line; bottom panel) corresponds to 49 h for this individual.

CHAPTER 3

FIRST INSIGHTS INTO THE VERTICAL HABITAT USE OF YOUNG PORBEAGLES IN THE NORTHWEST ATLANTIC WITH IMPLICATIONS FOR BYCATCH REDUCTION STRATEGIES

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ABSTRACT

For threatened marine species, data on their vertical habitat use patterns can reveal the risk of interactions with fishing gear. These can inform bycatch avoidance strategies, such as modifying the timing and depth of gear deployment. The porbeagle *Lamna nasus* population is overfished (US) and endangered (Canada) in the Northwest Atlantic Ocean. Data on vertical movements of young-of-the-year (YOY) and one-year-old porbeagles is absent, yet these life stages are frequently captured as bycatch in fisheries. I used data from short-term (28-day), high-resolution (5-min interval) pop-off satellite archival tags (PSATs) attached to YOY (n = 11; 80-103 cm fork length) and one-year-old (n = 3; 110-

114 cm fork length) porbeagles to examine temporal patterns in diving and characterize vertical habitat use during summer and fall. Occupied depths of tagged sharks ranged from the sea surface to 679 m, with ambient water temperatures of -0.2 to 26°C. Young (YOY and one-year-old) porbeagles predominantly utilized the epipelagic zone (0-200 m), but several individuals also made brief excursions into the mesopelagic zone (200-1000 m) during the fall. Young porbeagles exhibited a diel activity pattern characterized by more extensive use of the water column during the day, and remained primarily at the surface at night. Vertical habitat use differed between seasons, with summer characterized by greater affinity for surface waters (0-10 m) compared to fall. These results suggest that the risk of interaction with active fisheries on the continental shelf may be reduced by setting gear deeper at night and/or during summer.

Knowledge of movement patterns and habitat use is imperative to understanding species ecology and contributes to effective fisheries management for overexploited marine species (Heard et al., 2017; Hays et al., 2019; Andrzejaczek et al., 2022b). For example, information on vertical habitat use may be useful for (1) understanding the risk of capture in fisheries and (2) mitigating capture risk by adjusting the depths of fishing gear during temporal periods of high potential overlap (Cortés et al., 2010; Musyl et al., 2011a; Andrzejaczek et al., 2019; Bowlby et al., 2020b). Such information has historically been difficult to obtain for highly mobile sharks that occupy wide geographic and vertical (depth) ranges (Carlisle et al., 2015; Queiroz et al., 2016; Queiroz et al., 2019). Fortunately, the advancement of satellite tagging technologies has revolutionized our abilities to monitor fine- and large-scale movements, behavior, environmental preferences, and habitat use of sharks (Hammerschlag et al., 2011; Renshaw et al., 2023). Studies using satellite telemetry have found the dynamics of shark movements and behavior to be highly variable depending on a multitude of factors, including (but not limited to) time of day (Comfort and Wang, 2015; Tyminski et al., 2015; Coffey et al., 2017; Andrzejaczek et al., 2022b), season (Shepard et al., 2006; Hoffmayer et al., 2021; Skomal et al., 2021), age/size (Afonso and Hazin, 2015; Thorburn et al., 2019; Ajemian et al., 2020; Kock et al., 2022), sex (Campana et al., 2010; Stehfest et al., 2014), region (Santos et al., 2021; Bowlby et al., 2022), and changes to oceanic conditions (Vedor et al., 2021b; Hammerschlag et al., 2022). Research that considers multiple spatial and temporal scales, as well as different patterns by life stage, is most likely to appropriately describe the complex spatiotemporal dynamics of shark habitat use.

Despite technological advancements, the majority of studies to date have focused on adult or subadult life stages. Data on movement patterns for young individuals, especially young-of-the-year (YOY) sharks, is limited or absent for most highly migratory or pelagic species (Carlisle et al., 2015; Curtis et al., 2018; Nosal et al., 2019; Shaw et al., 2021). However, young individuals are generally the most vulnerable life stage to both natural (Smith et al., 1998) and fishing induced mortality (Coelho et al., 2012; Bowlby et al., 2021). Moreover, there is often a strong relationship between YOY survival and population persistence for sharks (Kinney and Simpfendorfer, 2009; Carlisle et al., 2015). These facts demonstrate the importance of understanding movement patterns and habitat use for early life history stages to help inform conservation and management decisions for highly mobile shark species (Carlisle et al., 2015). In particular, identifying critical habitats (i.e., pupping grounds, nursery grounds) that facilitate future recruitment of individuals into a stock has become a mandated priority for fisheries management (NMFS, 1996; NMFS, 1999; Driggers et al., 2008; Kinney and Simpfendorfer, 2009) and can be used as a basis for establishing spatial protection strategies for overexploited species (Heupel and Simpfendorfer, 2005; Kinney and Simpfendorfer, 2009).

The porbeagle *Lamna nasus* is a large, highly-mobile, and endothermic shark species that inhabits cold-temperate waters of the Atlantic, South Pacific, and southern Indian Oceans (Francis et al., 2008). Similar to most large sharks, the porbeagle has conservative life history traits (i.e., slow growth, low reproductive output) that make this species particularly susceptible to overexploitation (Jensen et al., 2002; Natanson et al., 2002; Natanson et al., 2019). The porbeagle was historically a commercially targeted species and has also been captured as bycatch throughout much of its range (Francis et al., 2008), which led to declines in multiple populations (Campana et al., 2002; Stevens et al., 2006). For example, following the introduction of a targeted pelagic longline fishery in the early 1960s (Aesen, 1963), the Northwest (NW) Atlantic population of porbeagles declined by an estimated 75%–80%, and the population reached its lowest abundance in 2001 (Campana et al., 2013). The population was designated as endangered in Canada (COSEWIC, 2004) and retention of live porbeagles has been prohibited since 2014 (Campana et al., 2015). Additionally, petitions have been filed twice for the species to be protected under the United States (US) Endangered Species Act, although listing was ultimately deemed unwarranted given the stable or increasing stock numbers and the implementation of fisheries management strategies (catch limits, minimum size limits) designed to reduce fishing mortality (Curtis et al., 2016). Nevertheless, stock analyses predict population recovery may take 100 years (NOAA, 2022) and the NW Atlantic porbeagle is still subject to capture as bycatch in pelagic longline, rod-and-reel, trawl, and gillnet fisheries throughout the NW Atlantic (Hurley, 1998; Campana et al., 2015; Curtis et al., 2016; Haugen, 2020; NOAA, 2022). Although survival is reported to be high in rod-and-reel fisheries (Anderson et al., 2021; Chapter 2), survival is relatively low in pelagic longline fisheries (Campana et al., 2016), an estimated 35.6% of captured porbeagles were discarded dead in the US otter trawl fishery in 2020 (NOAA, 2022), and survival is currently unknown following gillnet capture, although it is likely that gillnet survival is low due to suffocation in the net (Bendall et al., 2012; Cortés et al., 2020; NOAA, 2022; Chapter 5).

None of the studies on the movement patterns and habitat use of porbeagles in the NW Atlantic (i.e., Campana and Joyce, 2004; Campana et al., 2010; Kohler and Turner, 2019; Wang et al., 2020; Skomal et al., 2021) included tagging of YOY (< 107 cm fork length (FL); Natanson et al., 2002) and one-year-old juveniles (107-119 cm FL; Natanson et al., 2002). Only one study to date has focused its efforts on understanding the movement patterns of juvenile porbeagles in the NW Atlantic (Skomal et al., 2021), yet tagged individuals ranged in size from 128-154 cm FL and were estimated to be 2-6 years old (Natanson et al., 2002). These older juveniles displayed wide-ranging horizontal and vertical movements that were seasonally dependent. Similar to mature females tagged by Campana et al. (2010), larger juvenile porbeagles migrated into more southern waters off of the continental shelf during late fall, returning to shallower continental shelf waters in spring (Skomal et al., 2021). In the summer and early fall, these larger juveniles primarily occupied water depths < 200 m and spent the majority of their time in the top 25 m of the water column. When occupying deeper offshore habitat in late fall and winter, these larger juvenile porbeagles displayed one of two diving behaviors, either predominantly remaining in colder epipelagic waters (0-200 m; termed “non-divers”) north of the Gulf Stream or making frequent deep dives and remaining in the mesopelagic zone (200-1000 m; termed “divers”) when occupying warmer waters within or south of the Gulf Stream (Skomal et al., 2021). Given the vulnerability of YOY and one-year-old juveniles to fishing mortality (Cortés et al., 2020; Cortés and Semba, 2020) and the potential for ontogenetic changes in movement patterns as individuals age (Afonso and Hazin, 2015; Thorburn et al., 2019; Ajemian et al., 2020; Kock et al., 2022), research on early life stages remains a key knowledge gap for this species. Dive information would need to be at higher-resolution than 6-12 h intervals (per Skomal et al., 2021) to identify diel patterns and seasonal changes in individual behavior (e.g., Wang et al., 2020).

PSATs developed for studies on post-release mortality offer high-resolution data over shorter time scales, as compared to those typically employed for habitat use studies which are designed to monitor longer time periods, usually at the expense of resolution (Musyl et al., 2011b). Accordingly, I analyzed data from short-term (28 d), high-resolution (5 min interval) PSATs deployed on young (YOY and one-year-old) porbeagles in the NW Atlantic to assess fine-scale vertical movement patterns and to identify potential temporal trends (i.e., hourly, daily, seasonal scales) in their depth distribution.

METHODS

Capture & tagging techniques.

Young-of-the-year and one-year-old porbeagles were opportunistically caught between August 2016 and October 2019 in the NW Atlantic Ocean using rod-and-reel, research pelagic longline gear, or in the swordfish *Xiphias gladius* pelagic longline fishery as detailed in Bowlby et al. (2020a) and Anderson et al. (2021). All sharks were captured during the summer or fall. Captured sharks were either left in the water or brought onboard the fishing vessel and measured or estimated over the body FL (cm) and geographic location were recorded. The age of each shark was determined from a length-at-age relationship for this population (Natanson et al., 2002): individuals with FL < 107 cm were considered YOY and individuals 107-119 cm FL were considered one-year-old. Sex was recorded for the majority (13 of 14) of individuals. However, sex was unknown for one YOY shark that was captured in the swordfish pelagic longline fishery and tagged in the water with a pole. Prior to release, the hook was removed or the line was cut close to the hook for all animals brought onboard.

Sharks were equipped with a PSATLIFE manufactured by Lotek Wireless, Inc. Prior to release, tag attachment was done using a stainless-steel dart anchor (https://hallprint.com/fish-tag-products/tag/Shark+Tags) inserted into the dorsal musculature, engaging the pterygiophores. The PSATs collected pressure (i.e., depth, hereafter referred to as depth) and ambient water temperature at 10 s intervals for the pre-programed 28 d deployment period, after which the tag is designed to release from the animal, float to the sea surface and transmit archived data. Due to battery life and satellite throughput limitations, the full time-series at 10 s intervals are not transmitted by the tags. Instead, a subset of the recorded time-series, in 5 min rather than 10 s intervals, is sent to the satellites. All tags also had some further reduction of time-series resolution, where transmitted data was not at 5 min intervals for the entire time-series, likely due to battery reduction over time or limited satellite coverage during the transmission period. Additionally, PSATs were programmed to release and/or transmit data prematurely if depth remained constant (±5 m) for 3 days, indicating a mortality or a shed tag floating at the surface or washed ashore. One tag (shark 2; ID 175805) was recovered after pop-off and the full time-series dataset at 10 s resolution was available to download.

Data analyses.

Minimum horizontal displacement of each porbeagle was calculated from the recorded tagging location and the first satellite-transmitted location after the tag pop-off (Figure 3.1) and was plotted using the R package ‘ggmap’ (Kahle and Wickham, 2013). Prior research has demonstrated that porbeagles can exhibit post-release recovery behavior characterized by extended surface swimming following capture and handling (Hoolihan et al., 2011; Anderson et al., 2021; Bowlby et al., 2021; Chapter 2). Any such post-release recovery behavior was removed prior to analyses to eliminate potential biases on our understanding of natural diving behaviors. Recovery periods were identified using a breakpoint analysis of dive variance (Anderson et al., 2021; Bowlby et al., 2021; Chapter 2). Any depth values <0 (i.e., above the sea surface, which can occur due to the error margin of depth readings) were converted to zero.

For each shark, dominant temporal periodicities of vertical movements (i.e., patterns of diving and ascending over a common temporal interval) were investigated using continuous wavelet analysis with a Morlet wavelet transform for the time series of swimming depths. This analysis has been previously used to examine temporal patterns in diving for elasmobranchs when high-resolution data was available (Thorburn et al., 2019; Burke et al., 2020). The continuous wavelet analysis decomposes a time-series into time-frequency space to identify dominant temporal frequencies of cyclical functions, or the amount of time between successive peaks in a wave cycle (Cazelles et al., 2008). In this case, the wavelet analysis identifies time periods with organization in diving behavior such as repeated movement to similar depths, and the temporal trends in this behavior such as diel vertical migration occurring over a 24 h period (Thorburn et al., 2019; Burke et al., 2020). A benefit of the continuous wavelet analysis compared to traditional methods of addressing cyclical patterns in a time-series (such as the Fast Fourier Transform) is that it does not assume stationarity of the periodicities (Cazelles et al., 2008). As such, the continuous wavelet analysis can detect variations in the dominant dive cycle periodicities across the time-series (Cazelles et al., 2008), or intra-individual variability in the temporal patterns of diving behavior. Moreover, another benefit of the continuous wavelet analysis is that it can be used to evaluate a customizable range of temporal periodicities, on the order of minutes to days depending on the length of the time-series intervals and the objectives (Rösch and Schmidbauer, 2014).

The continuous wavelet analysis was completed using the R package ‘WaveletComp’ (Rösch and Schmidbauer, 2014) with parameters set as follows: a loess span of 0, a sampling resolution (dt) of 0.5 h, a frequency resolution (dj) of 1/250, a lower period for the wavelet function of 1 h, an upper period for the wavelet function of 128 h, and the number of simulations (n.sim) of 100 (details in Rösch & Schmidbauer, 2014) based on the temporal resolution of my data, periodicities of interest, and related previous work (Thorburn et al., 2019; Burke et al., 2020). The continuous wavelet analysis returns a plot of the wavelet power spectrum which identifies dominant dive periodicities (in hours; y-axis) over the duration of the tag deployment (x-axis). The wavelet power level (color) in the fitted plot reflects the strength of the cyclical pattern detected.

To overcome discontinuities in the datasets associated with PSAT transmission and to standardize temporal resolution, each time-series was binned in 30 min windows to calculate a mean depth prior to wavelet analyses. Missing values were interpolated from the nearest average depth values in the binned time-series. Interpolated values represented a range of 0.3-42.9% (median = 10.5%) of the data. A period of 30 min represented the optimal tradeoff to reduce discontinuities in the dataset while maintaining high-resolution information on dive periodicity for use in the wavelet analysis (Thorburn et al., 2019). I evaluated sensitivity to the binning interval from the recovered tag (shark

2; ID 175805). The wavelet power spectrum for the satellite-transmitted time-series (5 min interval) was compared to the high-resolution downloaded time-series (10 s interval) for shark 2 (ID 175805), where both were binned into 30 min windows. 42.6% of values from the satellite-transmitted series needed to be interpolated prior to this comparison. Additionally, I analyzed and plotted the wavelet coherence of the downloaded and transmitted time-series, where both were binned into 30 min windows. The wavelet coherence provides a measure of correlation in oscillatory behavior between two time-series, in this case identifying how similar the transmitted time-series wavelet analysis is to the downloaded time-series wavelet analysis.

While the continuous wavelet analysis identifies high-resolution temporal patterns of cyclical diving throughout each individual track, it does not provide information on environmental covariates with depth. As such, linear mixed models (LMMs) with Gaussian distributions were used to investigate the influence of diel period (day vs. night) and season (summer vs. fall) and their interaction on the depth distribution of YOY and one-year-old porbeagles. The response variable was either the log-transformed average depth (an indicator of overall depth preference) or the log-transformed standard deviation (SD) of depth (an indicator of vertical activity levels), where the raw depth data was used for calculating averages and standard deviations over each diel period (i.e., 2 averages and SDs of depth per day per shark). Both response variables were log-transformed prior to model fitting to meet the assumption of normality. Additionally, the corAR1 function was used to account for temporal autocorrelation. Categorical predictors were diel period (day and night) and season (summer and fall). Given the exact time of sunrise and sunset changes based on location and day of the year and the tags did not have light-based geolocation data, I opted to standardize diel periods into approximate timeframes for day (06:00-17:59 local time) and night (18:00-5:59 local time) at the tagging location. This categorization of diel period is similar to those used in previous studies (i.e., Weng and Block, 2004; Afonso & Hazen, 2015). The summer and fall seasons were differentiated based on the equinoxes of the tagging year (summer = June 20-Sep 21 and fall = Sep 22-Dec 20 in 2016 and 2017; summer = June 21-Sep 21 and fall = Sep 22-Dec 20 in 2018; summer = June 21-Sep 22 and fall = Sep 23-Dec 20 in 2019) to align with Skomal et al. (2021) and allow the most appropriate comparison with this study. Linear mixed models were compared to linear models (LMs) via likelihood ratio tests to determine if individual shark identifier should be included as a random effect. Models were fitted using the R package 'nmle' (Pinheiro et al., 2022). Akaike information criterion (AIC) and backward selection were used to determine the most parsimonious model (Akaike, 1973).

RESULTS

Data from a total of 11 YOY porbeagles measuring (mean ± SD) 93.9 ± 6.7 cm FL and three one-year-old porbeagles measuring 111.3 ± 2.3 cm FL tagged in the NW Atlantic were used for this analyses (Table 3.1). The sex ratio was female-biased with 11 females, 2 males, and 1 individual of unknown sex tagged. Six of the PSATs transmitted after completing the entire programmed deployment period (28 days), while 8 others transmitted early with deployments ranging from 8 to 27 days in duration. Premature tag transmissions were due to tag shedding rather than mortality, as the time-series of depth and temperature data indicated all sharks were alive immediately prior to tag pop-off (Anderson et al., 2021; Chapter 2). Regarding seasons, 4 tag deployments occurred exclusively in the summer, 5 exclusively in the fall, and 5 spanned portions of both seasons; overall, approximately 40% of depth and temperature data were from summer and approximately 60% were from fall. For sharks whose PSAT transmitted after completing the entire programmed deployment period, the minimum horizontal displacement ranged from 75 to 962 km (mean ± SD = 527 ± 377 km) (Figure 3.1; Table 3.1). For sharks whose PSAT popped early, estimated minimum horizontal displacement ranged from 15 to 975 km (Figure 3.1; Table 3.1). However, it is important to note that for these tags that detached prematurely, the first satellite transmission occurred 1-3 days after initial shedding from the shark. Sharks tagged in this study moved in multiple directions from the tagging to pop-off location and one individual (shark 14; ID 175808), a 114-cm one-year-old male, appeared to move as far south as 35°N. All other porbeagles appeared to remain north of 40°N based on tagging and tag pop-off locations, although locations used by sharks between tagging and tag pop-off were unknown.

Vertical & thermal habitat use.

Following the removal of behavioral recovery periods, which ranged in length from 0 to 282 h (median = 30 h), depth and ambient water temperature data were available for time periods ranging from 8 to 28 days. Collectively, young porbeagles occupied a wide range of depths (Figure 3.2; Figure A.1) from the sea surface to a maximum of 679 m by a 114-cm one-year-old male (shark 14; ID 175808). Associated water temperatures ranged from -0.2 to 26°C (Figure 3.2; Figure A.1). Porbeagles reached an average maximum depth of 275 ± 194 m (range = 72-679 m) during the tag deployments (Table 3.1). Collectively, tagged sharks spent approximately 95% of time in the epipelagic zone (0-200 m) and 5% in the mesopelagic zone (200-1,000 m).

Young porbeagles displayed rapid oscillatory dives, repetitively descending and ascending through the water column, for the majority of the tag deployments (Figure 3.2; Figure A.1). However, there appeared to be underlying diel and seasonal patterns in the relative depths of these oscillations and in overall vertical habitat use. Deep oscillatory dives occurred most frequently during the day (Figure 3.3); average depth was deeper and SD of depth was greater during the day than night (Figure 3.4). On average, approximately 14% of the day was spent at depths >100 m, whereas approximately 5% of the night was spent at depths >100 m (Figure 3.5). In comparison, oscillatory diving in surface waters was more common during the nighttime (Figure 3.3); on average, approximately 38% of nighttime was spent at depths of 0-10 m and approximately 28% of daytime was spent at depths of 0-10 m (Figure 3.5). Accordingly, the diel time at temperature profile showed that young porbeagles also spent more time at warmer ambient water temperatures during the night than during the day (Figure 3.6). On average, approximately 68% of the night was spent in ambient water temperatures of 15-21°C, whereas approximately 47% of the day was spent in ambient water temperatures of 15-21°C (Figure 3.6). The time spent at colder temperatures (<12°C) did not appear to be related to the size of tagged porbeagles (Figure 3.7). In regard to season, young porbeagles exhibited a more restricted depth distribution in the summer (Figure 3.4; Figure 3.8). They displayed a clear affinity for surface waters during the summer, with over 50% of their time spent at 0-10 m (Figure 3.8). In comparison, young porbeagles spent less than 20% of their time at 0-10 m and spent more time at deeper depths during the fall (Figure 3.8). For example, dives into the mesopelagic zone (200-1,000 m) occurred almost exclusively in the fall; only one individual, a 95-cm YOY female (shark

6; ID 163396) that was tagged offshore of the Grand Banks, made mesopelagic dives during the summer (Figure A.1F).

Continuous wavelet analysis.

The sensitivity analysis for shark 2 (ID 175805) revealed that patterns in the diving time-series (Figure A.2) as well as trends in diving periodicities determined by the wavelet power spectra were well-preserved with both the satellite-transmitted time-series (5 min intervals) binned and interpolated into 30 min windows and the downloaded time-series (10 s intervals) binned into 30 min windows (with the downloaded data having slightly higher wavelet power (stronger cyclical pattern detected); Figure 3.9). When considering all tagged sharks, there was substantial intra- and inter-individual variability in the periodicities of cyclical diving patterns throughout the tracks (i.e., how often individual sharks dove and ascended; Figure 3.2; Figure A.1). However, the most prevalent periodicity in diving detected by continuous wavelet analysis was approximately 24 h (i.e., diel pattern; Figure 3.2; Figure A.1). Shorter periodicities in cyclical diving (approximately 1.5-8 h; i.e., yo-yo diving) were also commonly observed in many tagged porbeagles (i.e., Figure 3.2; Figure A.1). Taken together, the two dominant periodicities suggest diel activity patterns consisting of relatively rapid cyclical diving occurring throughout both diel periods, but at differing depth distributions (i.e., deeper oscillations during the day, shallow oscillations during the night; Figure 3.3).

Linear mixed models.

Based on the results of AIC and likelihood ratio tests, incorporating the random effect of individual shark identifier improved the fit for the model of log average swimming depth (LR = 377.3; $p < 0.001$) and log SD of depth (LR = 232.5; $p < 0.001$)

and thus LMMs were used (Table 3.2). The most parsimonious model of log average swimming depth for young porbeagles included the fixed effects of both diel period and season, as well as their interaction (Table 3.2; Table A.1). Log average depth was significantly deeper both during the day compared to night and during the fall compared to summer for young porbeagles (Figure 3.10). For the model of log SD of depth, the most parsimonious model included only the fixed effect of diel period (Table 3.2; Table A.1). Log SD of depth was significantly greater during the day compared to night (Figure 3.11).

DISCUSSION

The analyses of short-term, high-resolution PSATs deployed on YOY and one-year-old porbeagles provided the first insights into vertical habitat use of the youngest life stages of this species during summer and early fall in the NW Atlantic Ocean. These data revealed common temporal patterns in vertical habitat use for these young porbeagles, ranging from rapid oscillatory (or “yo-yo”) diving to seasonal differences in water column usage. While more detailed examination of dive shapes and individual dive durations was not the focus of this work, this represents another potential avenue for future research with this fine-scale data. Nevertheless, the results of this study underscore the benefits of using high-resolution PSATs to examine variability in swimming depths at a fine temporal scale, which has not be done in most studies unless PSAT tags were physically recovered. For example, results of LMMs indicated these young porbeagles not only dove significantly deeper during the day compared to the night, but also had greater dive variability. None of the shorter periodicities in dive behavior (1.5 to 8 h) would have been evident from data binned at 6 or 12 h intervals, nor would the behavioral tendency to exhibit greater dive variability during the day as compared to night. Such behavioral flexibility forms an important component to the understanding of vertical habitat use, and indicates these young sharks were not only shifting their average swimming depths from nighttime to daytime, but also their vertical activity levels (the amplitude and/or frequency of oscillatory movement). In most cases, young porbeagles tagged in this study maintained a degree of affinity for surface waters or near surface waters during both diel periods. However, they made repeated oscillatory dive excursions between surface (or near surface) waters and deeper depths during the day, whereas the amplitude of oscillatory diving was restricted to surface (or near surface) waters during the night. Collectively, these findings suggest young porbeagles were not often following the traditional definition of diel vertical migration, in which animals remain at deep depths during the day and shallow depths during the night (Francis et al., 2015; Andrzejaczek et al., 2019). Instead, young porbeagles were most commonly exhibiting a “diel activity pattern” in which dive distributions had different variance during the day and the night, yet overlapped in depth (Arostegui et al., 2017). While this diel activity pattern of shifting the depths and amplitudes of oscillatory dives is quite common in pelagic predators (e.g., Goodyear et al., 2008; Andrzejaczek et al., 2019; Nasby-Lucas et al., 2019; Vedor et al., 2021a; Andrzejaczek et al., 2023) most other work characterizing diving behavior of porbeagles suggested the traditional diel vertical migration pattern to be most common for larger life stages of the species (Campana et al., 2010; Francis et al., 2015). Only one previous study that had obtained high-resolution data from a recovered PSAT also found similar evidence of a diel activity pattern (greater average depth and dive variability during the day than night) during the summer for a mature female porbeagle tagged in the NW Atlantic (Wang et al., 2020). Although it's possible that data resolution in most previous studies (i.e., Pade et al., 2009; Campana et al., 2010; Francis et al., 2015; Skomal et al., 2021) restricted the calculation of dive variability over shorter time scales for larger porbeagles, I cannot rule out that this diel activity pattern is more characteristic of the earliest life stages.

Although tag deployments were short, sample size was low, and geolocation tracks could not be constructed, there appeared to be differences in habitat use and depth distributions of these young porbeagles between summer and fall. Several young porbeagles in this study appeared to move into deeper waters off of the continental shelf during fall (based on dive depths >200 m and locations of tag pop-off), a migration that occurred earlier in this study compared to the previously documented seasonal movements for larger porbeagles tagged in the NW Atlantic (Campana et al., 2010; Skomal et al., 2021). These young porbeagles tagged in this study moved into deeper waters by late October, whereas mature females moved offshore in December to March (Campana et al., 2010) and larger juveniles in late November to December (Skomal et al., 2021). Young porbeagles in this study also exhibited greater use of surface waters in the summer and greater use of deeper depths in the fall. For example, the most frequent depth bin used by young porbeagles was 0-10 m (approximately 56% of time) during summer and 20-40 m (approximately 33% of time) during the fall. Moreover, some young porbeagles (i.e., shark 12 (ID 175892), shark 14 (175808)) that moved into deeper waters off of the continental shelf in the fall completely avoided surface waters, remaining below 50-150 m and reaching maximum daytime depths of over 500 m. Similar transitions to deeper depths when occupying offshore habitat was also observed in larger porbeagles (Campana et al., 2010; Skomal et al., 2021), yet the maximum depth observed for young porbeagles tagged in this study (679 m) was much shallower than the maximum depth reported for larger conspecifics (~1300 m) (Campana et al., 2010; Skomal et al., 2021). While this difference in maximum depth between studies could be due to the shorter tag deployments in this study, it is possible that the youngest life stages of porbeagles do not dive as deep as older life stages (Campana et al., 2010; Skomal et al., 2021). Moreover, while the seasonal patterns observed in this study are fairly consistent with previous work on larger life stages (Campana et al., 2010; Skomal et al., 2021), it is important to consider that differences in habitat and depth use between seasons for young porbeagles in this study could be at least partially impacted by the short deployment durations and tagging location. For example, most individuals with summer deployments were tagged in coastal waters where maximum dive depths may be constrained by bathymetry. I cannot discount the possibility that diving patterns or depth distributions may have differed if these individuals were tagged in deeper habitats, as shark 6 (ID 163396) was tagged offshore of the Grand Banks and did make a couple of mesopelagic dives during late summer. More regionally widespread tagging efforts and longer tag deployments would be needed to fully disentangle seasonal depth use patterns for the youngest life stage.

Shark diving behaviors are thought to be primarily related to prey distribution and availability within different habitats (Nakamura et al., 2011; Francis et al., 2015; Heard et al., 2017; Andrzejaczek et al., 2019). Thus, the diel vertical activity pattern and seasonal differences in depth distribution of young porbeagles in this study suggests a need for different prey search tactics (Pade et al., 2009) in different habitats as their distribution changes seasonally. Stomach sampling suggests that juvenile porbeagles <150 cm consume mainly groundfish, cephalopods, and pelagic fishes during summer and fall (Joyce et al., 2002). Given the opportunistic diet of young porbeagles during the summer and fall, and varying distribution of these prey within the water column, I hypothesize that the diel activity pattern exhibited by young porbeagles likely functions as a foraging strategy that maximizes the amount of prey that can be encountered (Sepulveda et al., 2004; Pade et al., 2009; Madigan et al., 2021; Santos et al., 2021). For example, the observed diel activity pattern (remaining in surface waters at night and yo-yo diving between the surface and deeper waters during the day) has also been documented in other pelagic species including Atlantic blue marlin *Makaira nigricans* (Goodyear et al., 2008), juvenile shortfin makos *Isurus oxyrinchus* (Sepulveda et al., 2004), and white sharks *Carcharodon carcharias* (i.e., Weng et al., 2007a, b; Andrzejaczek et al., 2022a). These diel activity patterns were suggested to be related to daytime visual feeding in shortfin makos (Sepulveda et al., 2004), white sharks (Andrzejaczek et al., 2022a), and blue marlin (Goodyear et al., 2008). It is possible that searching an extensive portion of the water column for prey may be more advantageous during the day when light levels are highest (Sepulveda et al., 2004; Goodyear et al., 2008; Andrzejaczek et al., 2022a). At night it may be more efficient to reduce the extent of the water column used while hunting under the cover of darkness (Andrzejaczek et al., 2022a), especially given many small pelagic species, including prey of porbeagles, migrate to shallow depths at night (Hays, 2003; Francis et al., 2015; Andrzejaczek et al., 2019). The shift to deeper waters in the fall by some individuals was also likely influenced by the seasonal shifts in prey distribution, as cephalopod and pelagic teleosts are known to migrate to or overwinter in offshore habitats in our study region (e.g., Hendrickson, 2004; Van Beveren et al., 2023). Previous work suggested that the diet of juvenile porbeagles shifts to a higher proportion of cephalopods and pelagic teleosts during winter and spring (Joyce et al., 2002), and this diet shift likely coincides with the transition into deeper offshore habitat (Skomal et al., 2021). When the young porbeagles migrated offshore they may have begun to occupy deeper depths, at least in part, to follow the vertical movement patterns of their mesopelagic prey, as has been suggested for larger porbeagles occupying mesopelagic environments (Saunders et al., 2011; Francis et al., 2015; Skomal et al., 2021).

Another potential driver of the diel and seasonal vertical movement patterns is the need to remain within an optimal temperature regime and ontogenetic differences in thermal tolerance. Like other lamnid sharks, porbeagles are regionally endothermic and thus can maintain warmer internal temperatures relative to ambient water (Carey et al., 1985). However, given smaller sharks have a higher surface area to volume ratio than larger conspecifics (Carlisle et al., 2015; Shaw et al., 2021), it is likely that YOY and one-year-old porbeagles have a reduced endothermic capacity compared to older individuals and prefer warmer temperature regimes than larger individuals, as has been suggested for YOY salmon sharks *L. ditropis* (Carlisle et al., 2015) and YOY white sharks (Shaw et al., 2021). Given the diel activity pattern observed in this study appears to be more prevalent in young porbeagles, this behavior may be reflecting their need to return to the surface more frequently and for more extended periods to maintain their internal temperature when in colder waters on the continental shelf. For example, while there was no apparent size-based difference in in the amount of time spent at cold temperatures (<12°C) for sharks in this study, these YOY and one-year-old porbeagles spent less time at temperatures <12°C than larger juveniles tagged by Skomal et al. (2021). In particular, larger juveniles were observed to spend approximately 40-50% of time during the summer and 50-60% of time during the fall at temperatures <12°C (Skomal et al., 2021), while the young porbeagles tagged in this study spent on average only 20% of time during the summer and 15% of time during the fall at temperatures <12°C. That said, it is also possible that the difference in time at temperature found between studies could be due to differences in deployment durations, as Skomal et al. (2021) had year-round data while data for this study was limited to late June through early November.

While the tracking period was relatively short, the young porbeagles did not seem to make use of water temperatures in excess of 22-26°C; collectively, less than 1% of their time was spent in water temperatures within this range. Moreover, the switch to submergence behavior in deep habitats during fall coincided with when maximum ambient water temperatures recorded by the tags were within this range. Submergence behavioral responses to sub-optimal water temperatures has previously been documented in larger porbeagles (Campana et al., 2010; Skomal et al., 2021), salmon sharks (Coffey et al., 2017), shortfin makos (Loefer et al., 2005), and a YOY white shark (Shaw et al., 2021). During periods in which young porbeagles primarily used deeper depths, ambient water temperatures at the sharks' minimum swimming depths approached the upper end of the species' known thermal tolerance (Francis et al., 2008; Campana et al., 2010; Saunders et al., 2011; Francis et al., 2015; Skomal et al., 2021). As such, it is possible that submergence behavior observed in a few of the young porbeagles tagged in this study was at least partially associated with the avoidance of excessively warm surface waters (Campana et al., 2010; Skomal et al., 2021).

Predation risk and inter- or intra-specific competition could also be affecting dive behavior (Andrews et al., 2009; Queiroz et al., 2012). For example, predation risk is a widely documented factor influencing ontogenetic shifts in habitat use of sharks (Morrissey and Gruber, 1993; Grubbs, 2010; Speed, 2010; Queiroz et al., 2012; Vianna et al., 2013; Carlisle et al., 2015). Competition has also been suggested to be mitigated via spatial, temporal, and/or dietary partitioning among life stages or species (Weideli, 2023). The vertical movement patterns observed in young porbeagles in this study may be related to predation risk or competition given the diel activity pattern appears to be more common in YOY and one-year-old sharks (Campana et al., 2010; Skomal et al., 2021). Moreover, young porbeagles tagged in this study spent more time at shallow depths during the summer and fall compared to larger conspecifics (Campana et al., 2010; Skomal et al., 2021). Species that have the potential to be predators and/or competitors of young porbeagles include larger conspecifics and other large coastal and oceanic shark species (i.e., white shark, Curtis et al., 2016; tiger shark *Galeocerdo cuvier*, Hammerschlag et al., 2022), although predation of porbeagles is currently undocumented. During the summer and fall when this study occurred, larger porbeagles (Campana et al., 2010; Chapter 4; Chapter 5), white sharks (Franks et al., 2021; Bowlby et al., 2022), and (to a lesser extent) tiger sharks (Hammerschlag et al., 2022) are known to inhabit the NW Atlantic continental shelf, thus overlapping with young porbeagle habitat. Given this horizontal overlap, it is possible that the diel vertical activity pattern we observed in young porbeagles is a mechanism to reduce interactions with potential predators/competitors (Andrews et al., 2009; Speed et al., 2010; Queiroz et al., 2012; Vianna et al., 2013; Bond et al., 2015). It is also possible that the greater preference for surface waters and the transition into off-shelf habitats occurring earlier in the year in some young porbeagles compared to larger conspecifics could be beneficial for reducing intra-specific competition. However, understanding the role of predation and competition in shaping spatiotemporal movement patterns is challenging and more information (i.e., more high-resolution dive data for mature porbeagles) is needed to discern the influence of these factors on ontogenetic habitat use of this species.

Conservation implications.

The tracking period of this study coincides with the most active US commercial and recreational rod-and-reel fishing season (summer and autumn), primarily targeting bluefin tuna (NOAA, 2022), and also overlaps with commercial trawl and gillnet fisheries targeting benthic species (NOAA, 2022). Reported porbeagle catches in the US recreational rod-and-reel fishery include an estimated 4.9 metric tons (mt) of landings and 68 individuals discarded (NOAA, 2022). While porbeagle catch data for US trawl and gillnet fisheries are limited to observed sets, this species is one of the most frequently bycaught highly migratory shark in these fisheries in the Northeast region (NOAA, 2022). In 2020, 118 porbeagles were caught in 115 observed otter trawl sets and approximately 77 individuals were caught in 177 observed gillnet sets (NOAA, 2022). Reported Canadian catches include an estimated 4.2 mt in trawl fisheries and 1.4 mt in longline fisheries in 2020 (www.iccat.int). In general, however, catches are predicted to be substantially underreported for this species (ICCAT, 2020).

Given the predicted slow rate of recovery and continued incidental capture in multiple fisheries in the region, the NW Atlantic porbeagle population would benefit from reduced fisheries interaction. The data observed in this study suggest young porbeagles are most active during the day, when presumably feeding throughout the water column, yet primarily remain within surface waters at night. Based on this preliminary data, young porbeagles appear to be most at risk to surface gear deployed during the night and summer, providing a potential avenue for adjusting the timing and depth of fishing gear for reducing interactions. Based on this diel depth distribution, setting surface gear deeper during the nighttime and limiting bottom gear to night sets while young porbeagles appear to have an affinity for surface waters may reduce risk of interactions with this life stage, especially during the summer. When young porbeagles move off the continental shelf into deeper waters in the fall, they would be less at risk to shallow water fisheries (rod-and-reel, gillnet, trawl). The pelagic longline fishery is the main fishery occurring in deeper waters off of the continental shelf. Given fisheries data suggest captures of porbeagles by pelagic longline gear have been minimal (12 kg reported catch in the US pelagic longline fishery in 2020; www.iccat.int) in recent years (NOAA, 2022; www.iccat.int), current pelagic longline fishing techniques appear to successfully limit interactions with porbeagles.

Table 3.1

Summary of results from pop-off satellite archival tags (PSATs) deployed on young-of-the-year (YOY) and one-year-old porbeagles in the Northwest (NW) Atlantic. Fork length (FL) was rounded to the nearest cm, maximum (max) depth to the nearest m, minimum (min) and max temperatures (temp) and temp range to the nearest 0.1°C, and min distance travelled to the nearest km. Note: F = female, M = male, U = unknown, DAL = days at liberty, * indicates a tag that popped prematurely and the first satellite transmitted location occurred 1-3 days after initial tag pop-off.

Shark #	**ID**	**Sex**	**FL (cm)**	**Tag Date (m/d/y)**	**DAL**	**Max depth (m)**	**Min temp (°C)**	**Max temp (◦C)**	**Temp range**	**Distance travelled (km)**
1	175887	F	80	10/8/2018	8	283	9.0	20.1	11.2	332*
2	175805	F	88	7/9/2018	27	117	5.9	21.2	15.3	100*
3	175806	F	90	8/30/2018	10	72	9.0	20.6	11.7	207*
4	175804	F	90	9/23/2018	24	145	7.2	17.6	10.4	304*
5	163391	F	94	9/10/2016	28	104	4.9	18.4	13.5	74
6	163396	F	95	9/5/2016	22	389	3.1	20.4	17.3	209*
7	163395	M	95	9/19/2016	28	236	-0.2	16.1	16.3	482
8	163393	F	96	9/19/2016	28	238	1.8	20.6	18.8	962
9	175888	F	100	10/9/2018	23	542	6.2	21.4	15.2	379*
10	163397	F	102	9/13/2016	28	218	1.3	17.9	16.5	938
11	175809	F	103	7/13/2019	28	141	5.7	22.7	17.0	145
12	175892	U	110	10/9/2018	28	565	5.7	26.0	20.3	562
13	175813	F	110	6/27/2019	27	121	5.2	21.7	16.5	15*
14	175808	M	114	10/1/2019	27	679	5.7	25.7	20.0	975*

Table 3.2

Model comparison using Akaike's Information Criterion (AIC). ∆AIC indicates difference between AIC scores and top-ranked model. All models are linear mixed models with shark identity as a random variable and temporal autocorrelation. Mean depth (m) and standard deviation (SD) of depth (m) were both log-transformed prior to analysis to meet assumptions of normality.

Model	**DF**	**AIC**	**∆AIC**
1. Mean depth ~ diel period*season	575	1246.47	
Mean depth ~ diel period + season	576	1251.309	4.839
Mean depth ~ diel period	577	1256.121	9.651
Mean depth ~ 1	578	1495.245	248.775
2. SD of depth ~ diel period	577	1397.293	
SD of depth ~ diel period + season	576	1400.763	3.47
SD of depth ~ diel period*season	575	1405.568	8.275
SD of depth ~ 1	578	1500.932	103.639

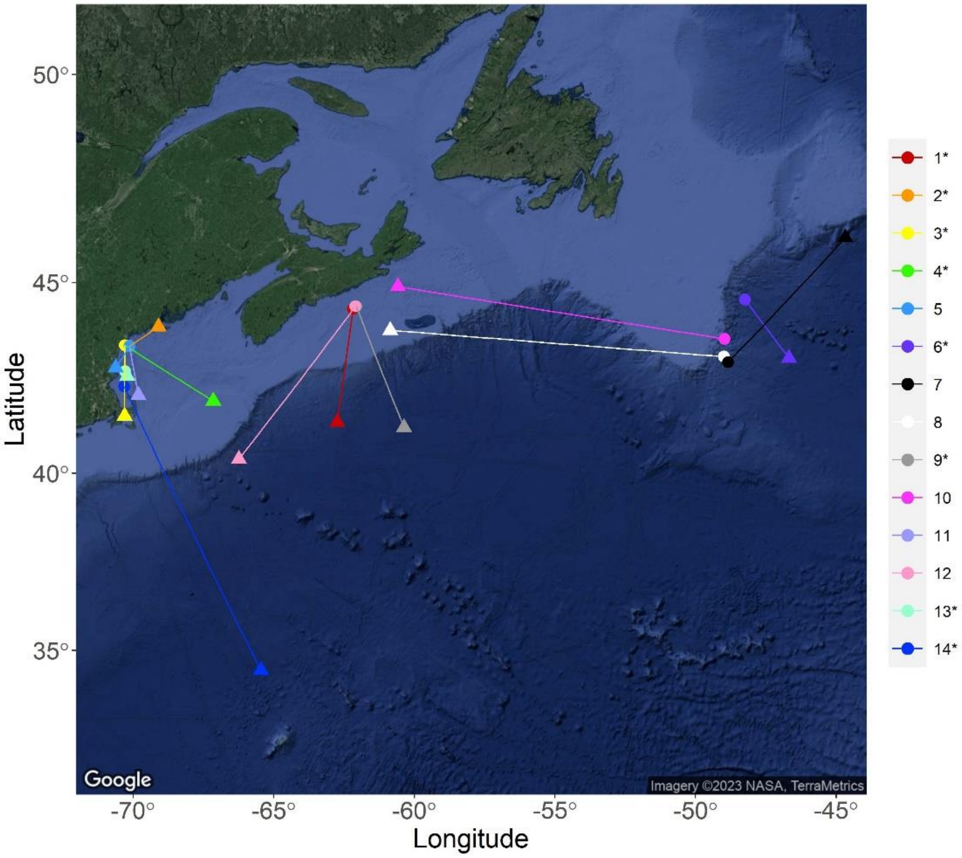
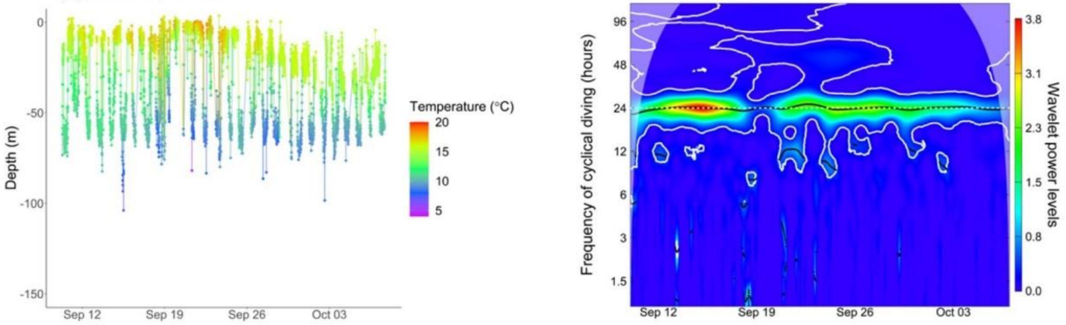
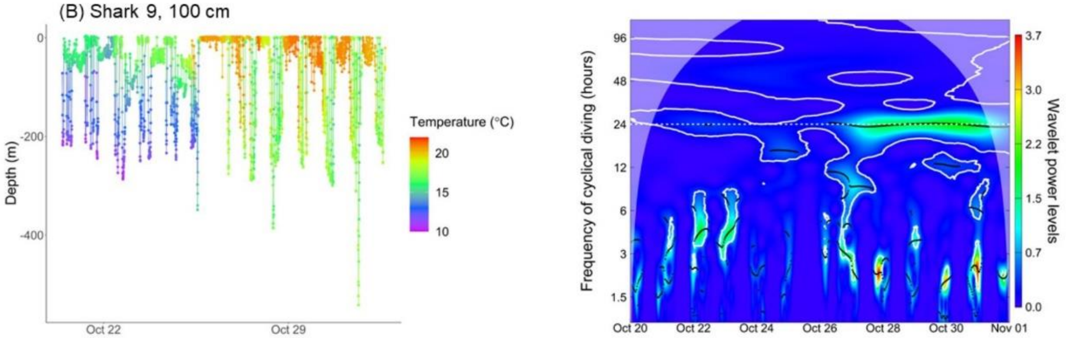


Figure 3.1. Map of the study site with deployment location (circle) and the location of the first satellite transmission after pop-off (triangle) for pop-off satellite archival tags (PSATs) affixed to young-of-the-year (YOY) and one-year-old porbeagles in the northwest (NW) Atlantic. * indicates a tag that popped prematurely and the first satellite transmitted location occurred 1-3 days after initial tag shedding.

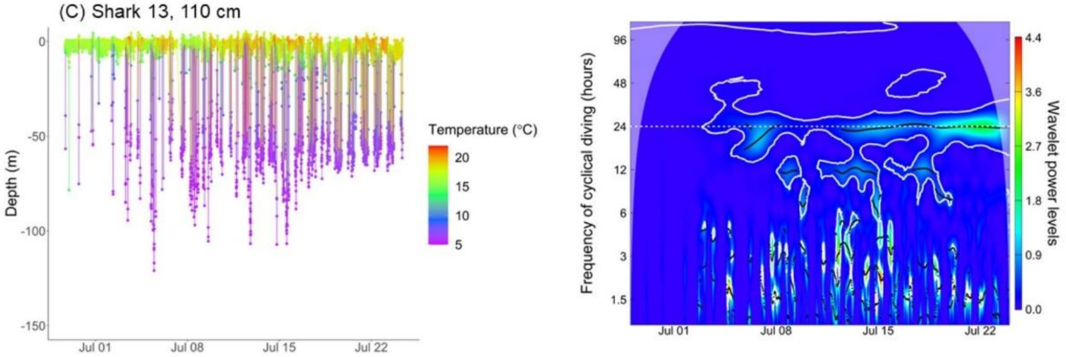
(A) Shark 5, 94 cm



(B) Shark 9, 100 cm



(C) Shark 13, 110 cm



(D) Shark 14, 114 cm

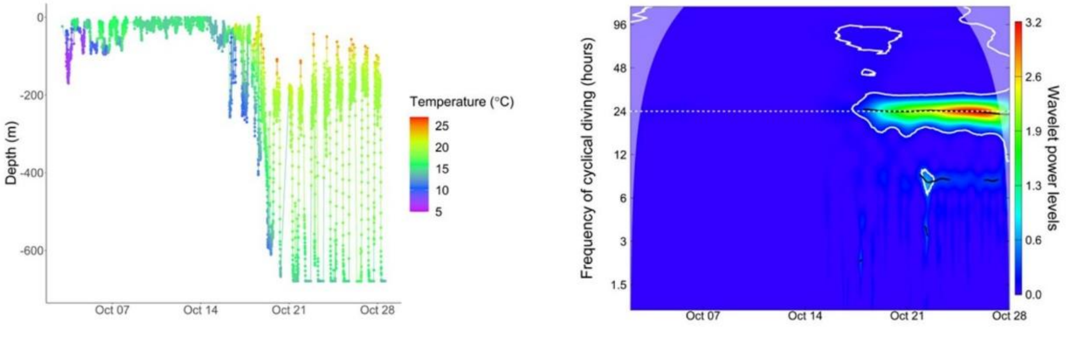


Figure 3.2. Representative time-series of temperature-integrated dive profiles (left) and corresponding continuous wavelet power spectra (right) for four young-of-the-year (YOY; n = 2; A and B) and one-year-old (n = 2; C and D) porbeagles over the duration of the tag deployment. For the wavelet power spectra, areas encircled in white represent time periods with significant cyclical patterns ($p < 0.05$). Within the white encircled areas, the wavelet power level (color) reflects the strength of the cyclical pattern detected, with red representing the strongest cyclical pattern. The black lines represent wavelet power ridges, or the local maxima of wavelet power. The frequencies (y-axis) reflect the time interval over which a cyclical diving pattern is detected. The white dashed reference line identifies the periodicity of 24 h. Shaded areas outside of the cone of influence should not be interpreted. Note the differences in scales of axes and legends among individual plots. Temperature-integrated dive profiles and continuous wavelet power spectra for all 14 individuals can be found in the Supplemental Information (Fig. S1).

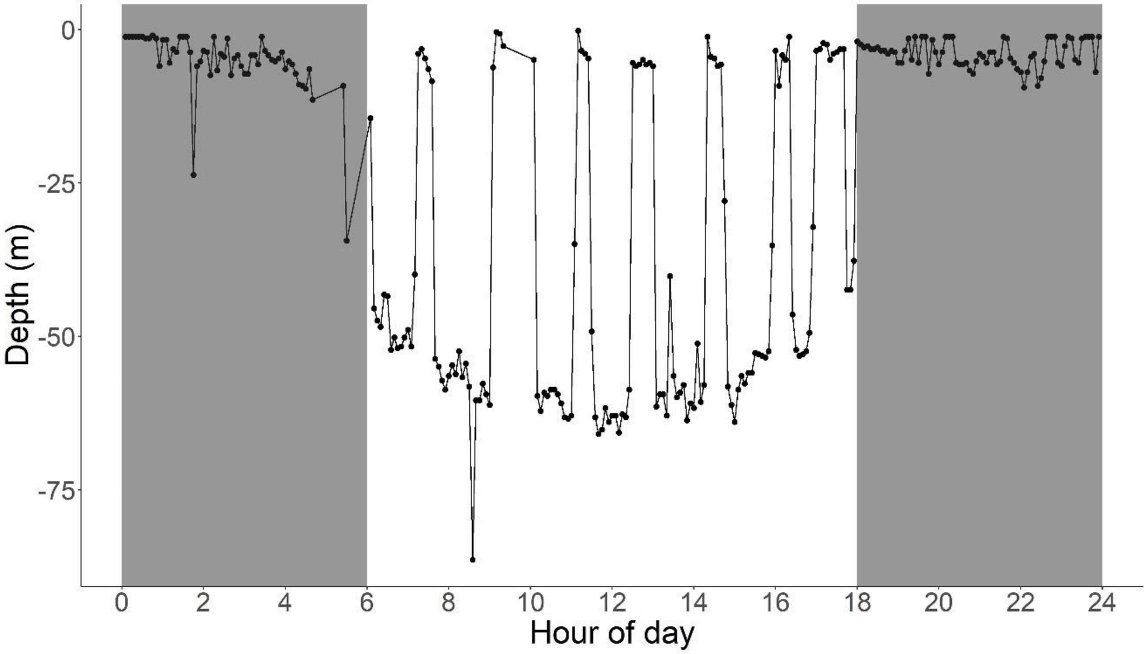


Figure 3.3. Example of a diving profile over a 24 h period (August 5 2019) for shark 11 (ID 175809), a 103-cm young-of-the-year (YOY) female, showing a representative diel activity pattern of surface-oriented oscillatory diving during the night (shaded region) and deeper oscillatory diving during the day (unshaded region).

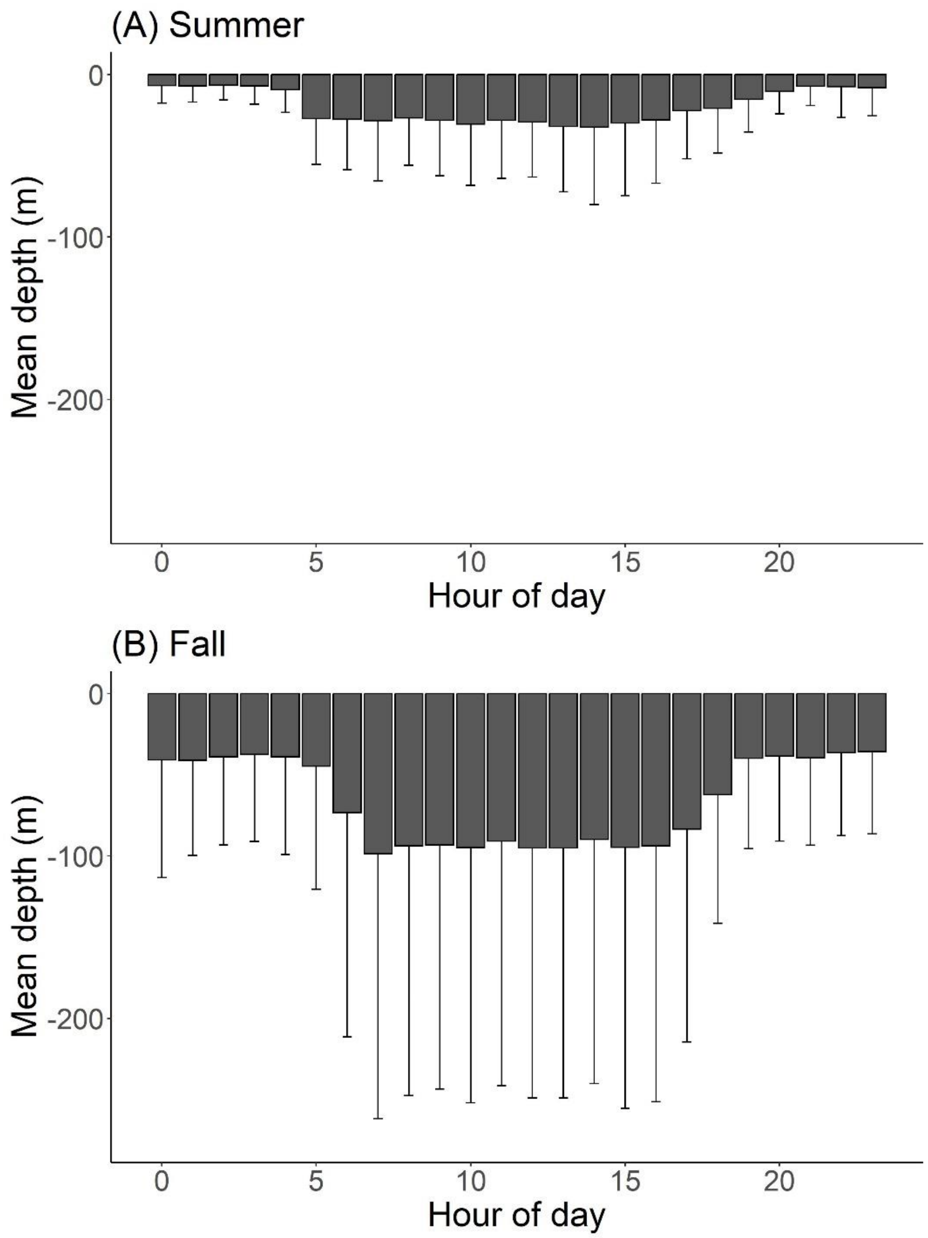


Figure 3.4. Average depth (m) + standard deviation (SD) at each hour of day for all young-of-the-year (YOY) and one-year-old porbeagles combined during the summer (A) and fall (B).

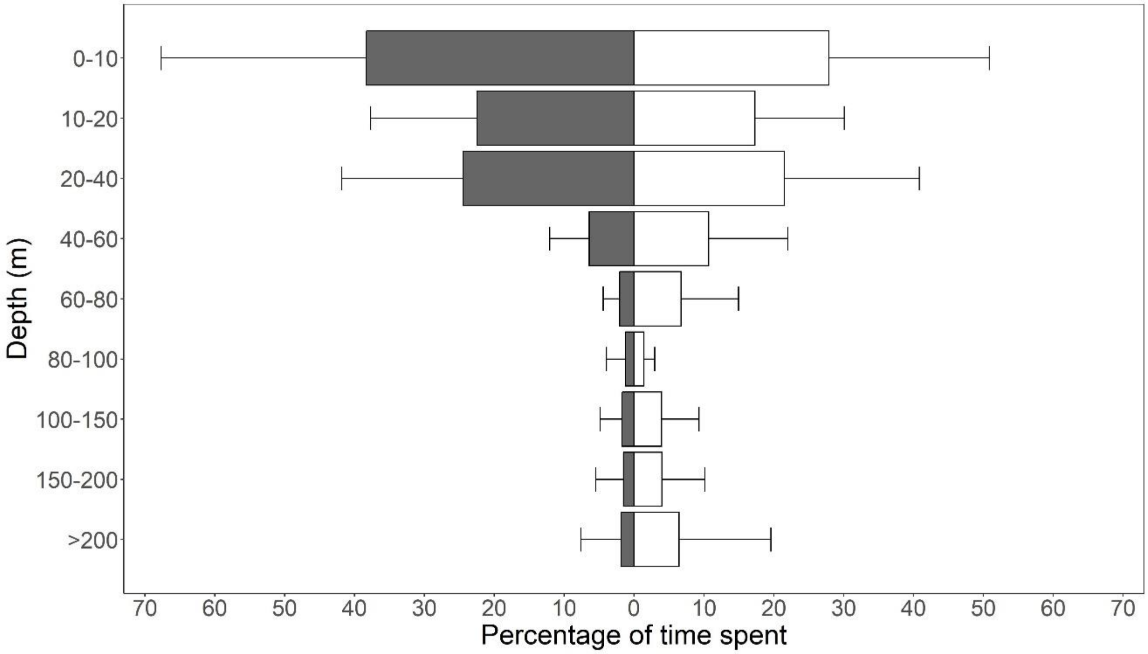


Figure 3.5. The average percentage of time spent at depth (m) during the day (white bars) and night (grey bars) for young-of-the-year (YOY) and one-year-old porbeagles. The error bars represent standard deviations.

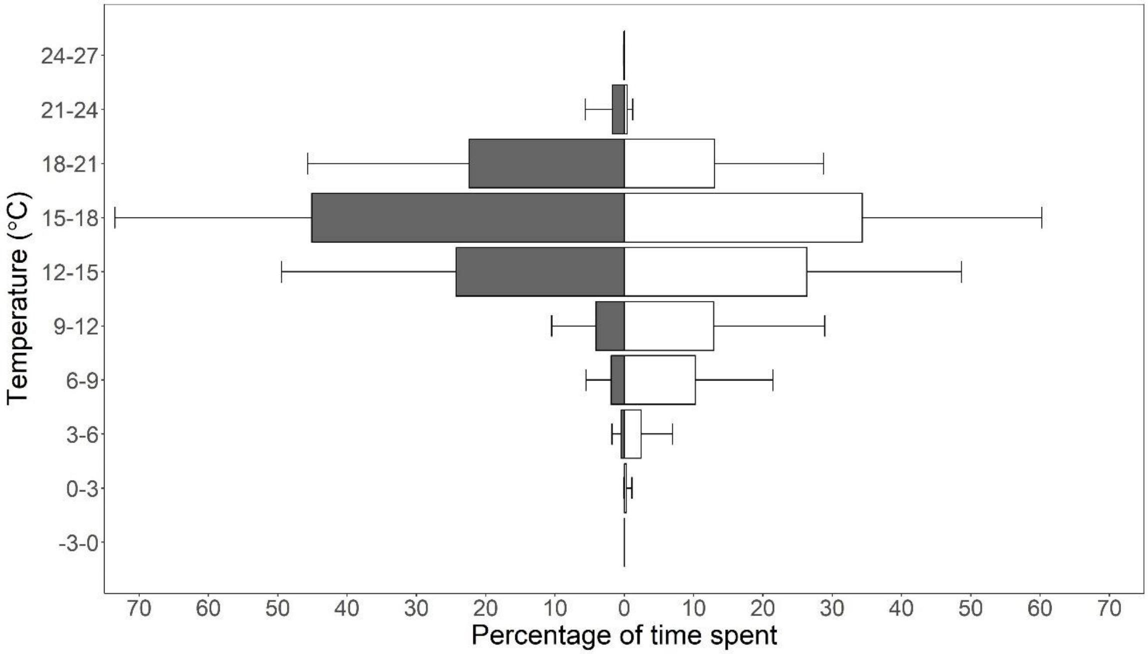


Figure 3.6. The average percentage of time spent in ambient water temperatures (°C) during the day (white bars) and night (grey bars) for young-of-the-year (YOY) and one-year-old porbeagles. The error bars represent standard deviations.

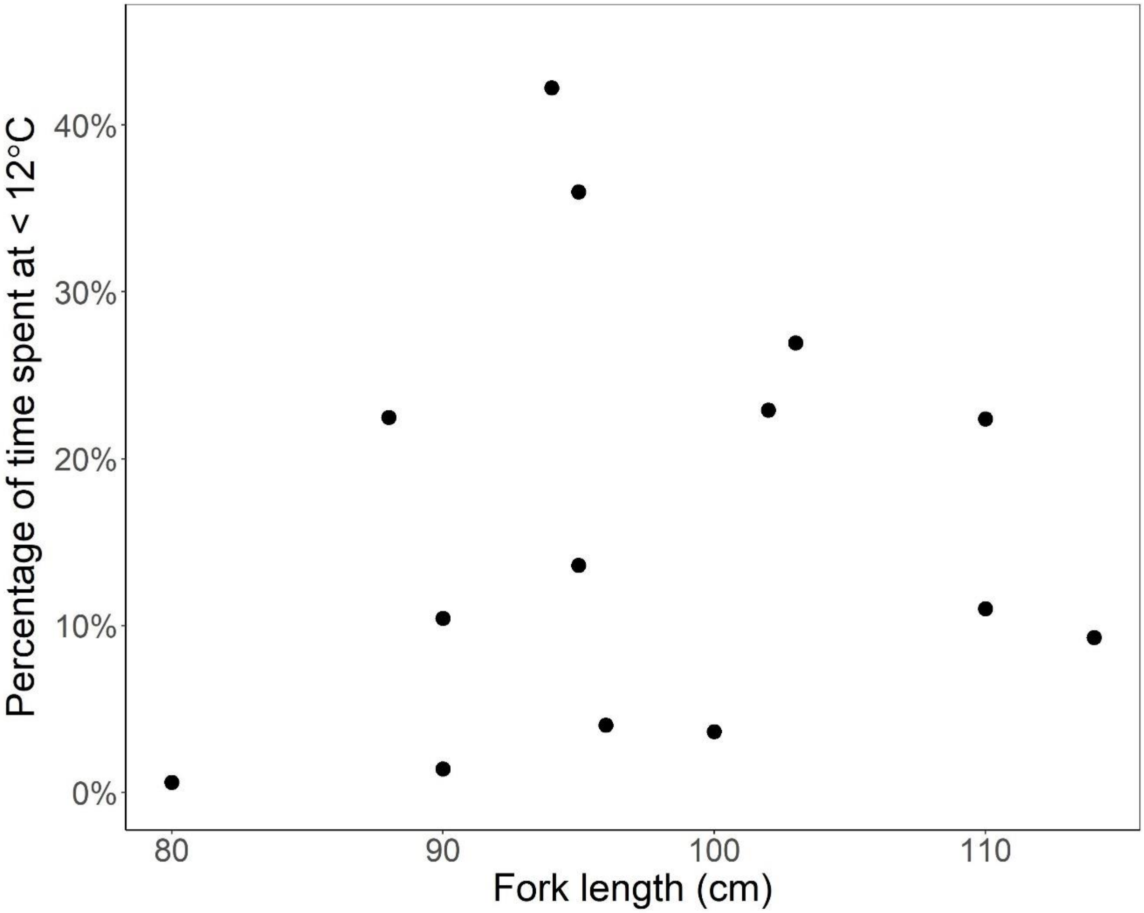


Figure 3.7. The percentage of time spent at cold temperatures (<12°C) by fork length (FL; cm) for young-of-the-year (YOY) and one-year-old porbeagles.

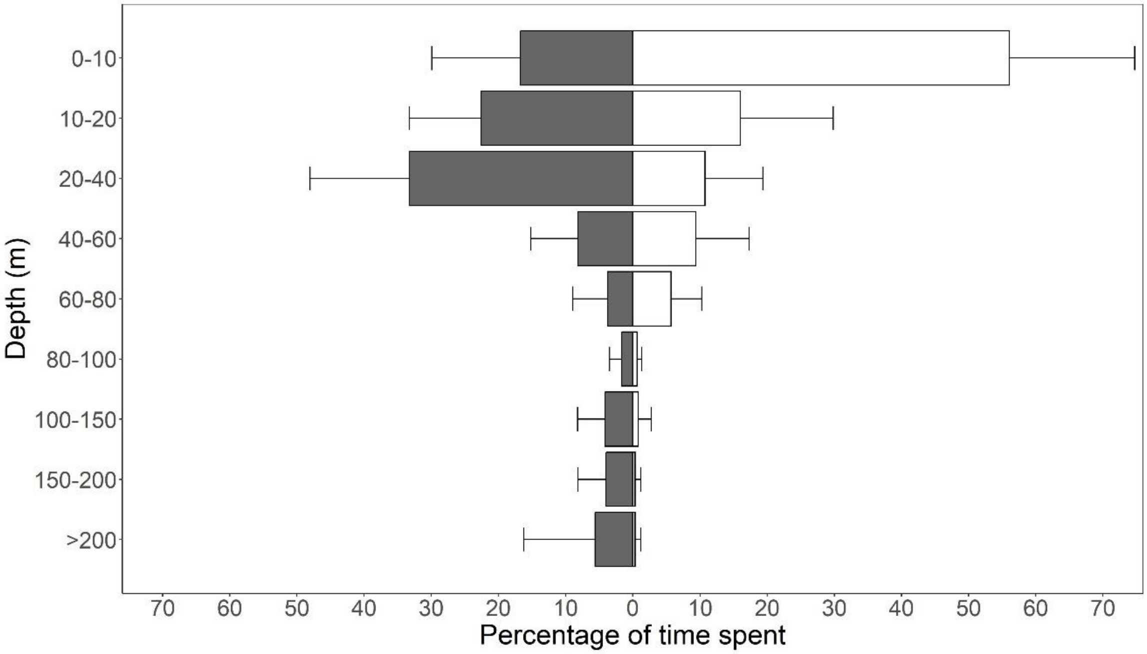
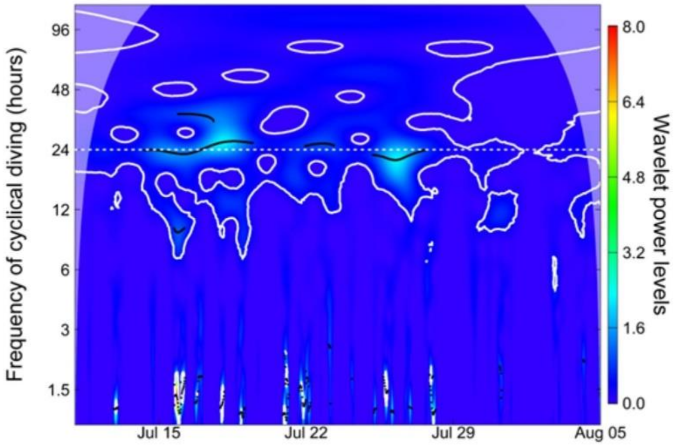
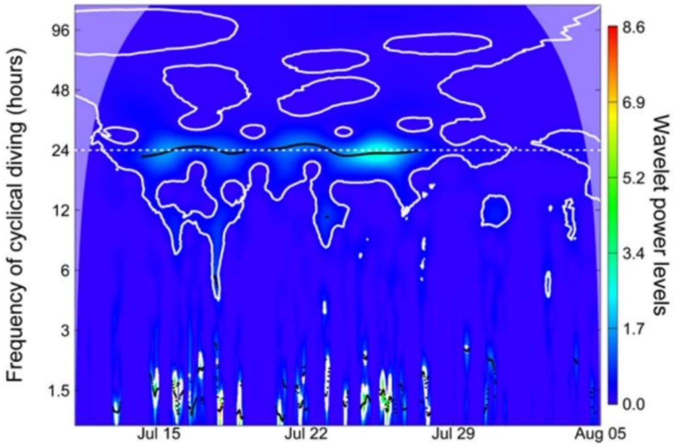


Figure 3.8. The average percentage of time spent at depth (m) during the summer (white bars) and fall (grey bars) for young-of-the-year (YOY) and one-year-old porbeagles. The error bars represent standard deviations.

(A) Transmitted record



(B) Archived record



(C) Wavelet coherence

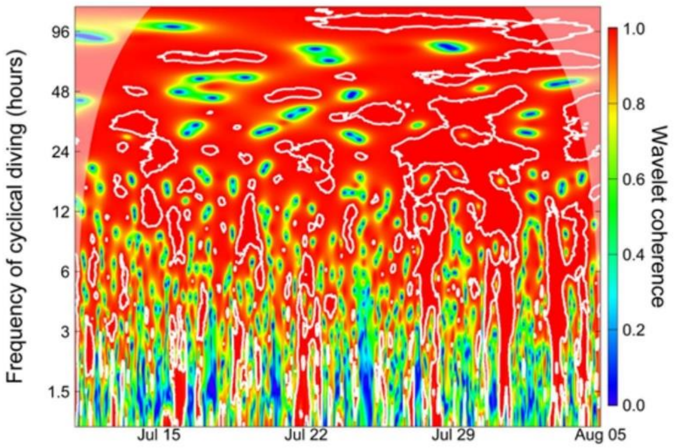


Figure 3.9. Comparison of the wavelet power spectra for the satellite-transmitted data binned and interpolated into 30 min intervals (A) and the recovered, full archived data binned into 30 min intervals (B), and a plot of the wavelet coherence between both time-series (C) for shark 2 (ID 175805). For the wavelet power spectra (A and B), areas encircled in white represent time periods with significant cyclical patterns ($p < 0.05$). Within the white encircled areas, the wavelet power level (color) reflects the strength of the cyclical pattern detected, with red representing the strongest cyclical pattern. The black lines represent wavelet power ridges, or the local maxima of wavelet power. The frequencies (y-axis) reflect the time interval over which a cyclical diving pattern is detected. Shaded areas outside of the cone of influence should not be interpreted. Note the difference in scales of the wavelet power level legends between plots A and B. For the plot of wavelet coherence (C), areas encircled in white represent time periods with significant wavelet coherence ($p < 0.05$). The wavelet coherence (color) reflects the level of similarity in the oscillatory patterns between the two time-series, with red representing the strongest similarity.

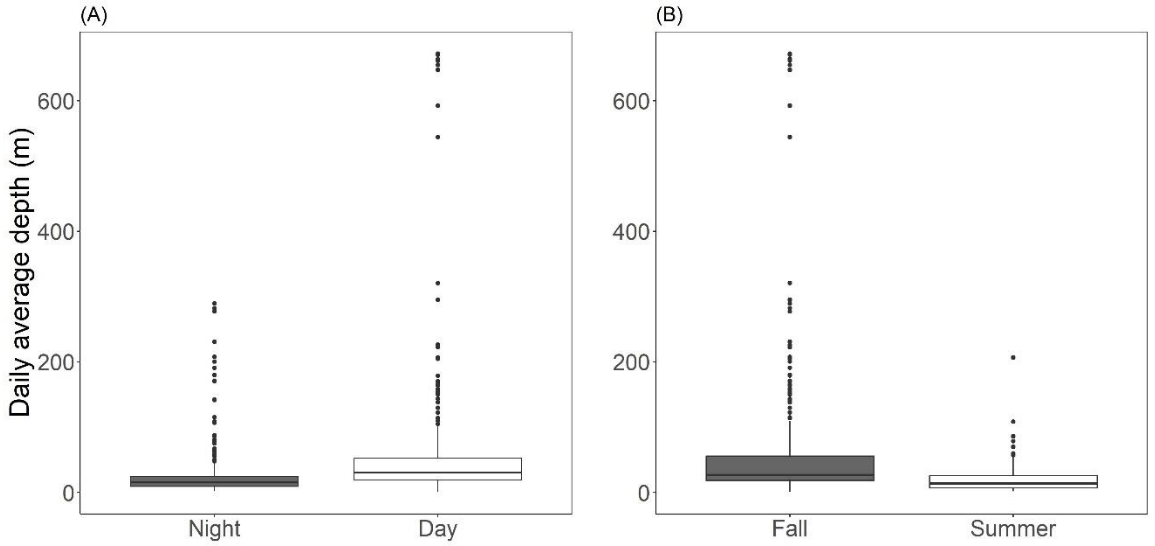


Figure 3.10. Boxplots of daily average depth (m) by diel period (A) and season (B) for all young-of-the-year (YOY) and one-year-old porbeagles. The circles represent outliers.

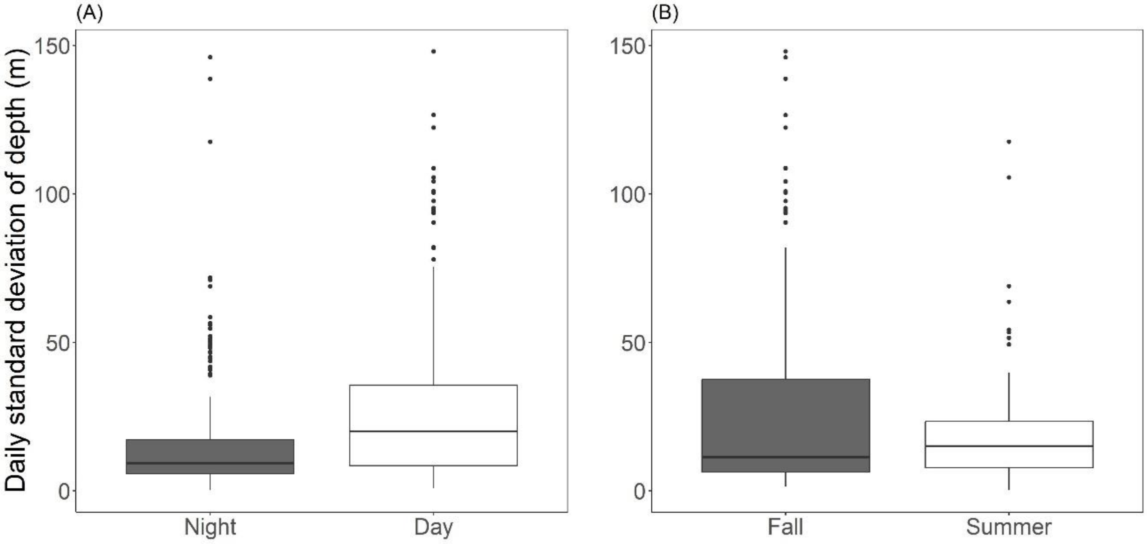


Figure 3.11. Boxplots of daily standard deviation (SD) of depth (m) by diel period (A) and season (B) for all young-of-the-year (YOY) and one-year-old porbeagles. The circles represent outliers.

CHAPTER 4

INFLUENCE OF LIFE STAGE ON THE SEASONAL HABITAT USE OF PORBEAGLES IN THE NORTHWEST ATLANTIC

ABSTRACT

For highly mobile marine species such as pelagic elasmobranchs, the development of effective spatial management requires a comprehensive understanding of movement ecology. Research incorporating movement data across seasons and life stages, including reproductive states, is valuable for informing spatial management, yet is absent for most species. In the Northwest (NW) Atlantic, the porbeagle *Lamna nasus* is a pelagic shark species that is overfished, has a live retention ban (Canada) or strict harvest regulations (United States), and is also commonly captured as bycatch. Research on the spatiotemporal dynamics of NW Atlantic porbeagle habitat use is limited, with all previous research utilizing pop-off satellite archival tags (PSATs) which are prone to large errors in location estimates. This study used 38 higher-accuracy fin-mount satellite tags to identify patterns in habitat use for porbeagles across life stages and seasons in the NW Atlantic. During the summer and fall, the activity space (95% kernel density estimate) of tagged porbeagles occurred almost exclusively on the continental shelf in the Gulf of Maine and Georges Bank. Activity space expanded and shifted southwards to include mesopelagic environments during the winter and spring for juveniles, mature non-gravid females, and mature females of unknown reproductive states, while the activity space of mature males and gravid females remained in shelf waters year-round. This finding differs from the previous assumption that southward migrations are linked to reproduction for NW Atlantic porbeagles. Tagged porbeagles were also found to have a

relatively small high occupancy area (50% kernel density estimate) located around Cape Cod, Massachusetts that was well-conserved across life stages and seasons. This relatively static, small high occupancy area has implications for the population’s conservation given the high amount of fishing activity (rod-and-reel, trawl, gillnet) occurring within this region. Given the overlap between porbeagle high occupancy area and fishing activity, the coastal waters around Cape Cod, Massachusetts could be considered for spatial management of the NW Atlantic porbeagle.

Global declines in elasmobranch populations (Dulvy et al., 2021) have driven widespread prioritization of research and development of conservation strategies (Jorgensen et al., 2022). A relatively common approach to elasmobranch conservation is spatial management, in which critical habitats are protected from anthropogenic impacts, albeit with varying degrees of efficacy (i.e., Edgar et al., 2014; Jaiteh et al., 2016; White et al., 2017; Birkmanis et al., 2020; Crear et al., 2021; Shea et al., 2023). Not only does the highly mobile nature of many elasmobranch species challenge effective spatial management, the tendency for elasmobranch species to segregate by sex, size or maturity, and/or reproductive states further confounds this effort (Cartamil et al., 2010; Bansemer and Bennett, 2011; Chapman et al., 2015; Sulikowski et al., 2016; Maxwell et al., 2019). Space use may be related to a combination of many factors, including competition and predation, food availability, reproduction, energetic constraints, and abiotic needs (Bowler and Benton, 2005; Shaw, 2020; Bowlby et al., 2022). For example, some coastal elasmobranch species, including bull sharks *Carcharhinus leucas* (Heupel and Simpfendorfer, 2011), sandbar sharks *C. plumbeus* (Grubbs and Musick, 2007), cownose rays *Rhinoptera bonasus* (Rangel et al., 2018) and several others (i.e., Castro, 1993; Parsons and Hoffmayer, 2007), have specific nursery areas linked to food resources and/or predator avoidance to help maximize survival during the first few years of life (i.e., Heupel et al., 2007; McMillan et al., 2021). While much less is known about the habitat use of young pelagic elasmobranchs, a few studies have documented larger-scale movements compared to coastal species; for example, early life stage blue shark *Prionace glauca* and shortfin mako *Isurus oxyrichus* habitat use spans 18 and 11 degrees of latitude, respectively, in the eastern North Pacific (Nosal et al., 2019). Additionally, habitats used by gravid females during gestation may be segregated from habitats used by mature males in order to reduce mating attempt harassment or to seek optimal abiotic conditions. For example, gravid tiger sharks *Galeocerdo cuvier* (Sulikowski et al., 2016), soupfin sharks *Galeorhinus galeus* (Nosal et al., 2021), and leopard sharks *Triakis semifasciata* (Nosal et al., 2014) have been observed to aggregate in female-dominated sites with warm water, presumably to accelerate gestation. Collectively, these factors make spatial management decisions inherently complex and highlight the value of comprehensive data on movement patterns across all life stages of a population in order to identify and prioritize the most critical conservation areas. In fact, a recent survey of experts identified making tagging studies more applicable to elasmobranch conservation as a key research priority and suggested that using representative life-history sampling schemes was essential to accomplishing this goal (Jorgensen et al., 2022).

The porbeagle *Lamna nasus* is a large, pelagic, and endothermic shark species that inhabits cold-temperate waters in the North Atlantic and the Southern Hemisphere (Francis et al., 2008). Like most large sharks, the porbeagle exhibits life history characteristics (long lifespans, slow growth, low reproductive output) which make the species vulnerable to overexploitation and population depletion (Jensen et al., 2002; Natanson et al., 2002; Natanson et al., 2019). Furthermore, although the Northwest (NW) Atlantic population was originally suggested to have an annual reproductive cycle (Jensen et al., 2002), a more recent study found evidence of a biennial cycle in some individuals (Natanson et al., 2019), which suggested lower reproductive productivity and greater risk of population decline. The NW Atlantic porbeagle population was once the target of a commercial longline fishery (Aesen, 1963; Campana et al., 2002). However, overexploitation led these stocks to be designated as an endangered species in Canada (COSEWIC, 2004; COSEWIC, 2014), and an overfished species in the United States (US) (Curtis et al., 2016). Conservation concern for the population also led to harvest restrictions, including a ban on live retention in Canada (Campana et al., 2015) and catch and size limits in the US (NMFS, 2007; ICCAT, 2015). Despite these efforts to minimize fishing mortality, porbeagles continue to be captured as bycatch in numerous commercial (longline, rod-and-reel, trawl, gillnet) and recreational (rod-and-reel) fisheries in the region (Hurley, 1998; Curtis et al., 2016; NOAA, 2023; Haugen, 2020). The NW Atlantic porbeagle may benefit from spatial management strategies given the predictions of stock assessments which suggested population rebuilding could take up to 100 years (NOAA, 2023).

A limited number of studies have used pop-off satellite archival tags (PSATs) to explore the spatiotemporal dynamics of horizontal habitat use for NW Atlantic porbeagles (Campana et al., 2010; Skomal et al., 2021; Braun et al., 2023). Skomal et al. (2021) tagged 17 large juveniles on Georges Bank in 2006 to observe their seasonal movements and found that these sharks were shelf-oriented in the summer and early fall and made more extensive movements into offshore habitat in the winter and spring. In comparison, Campana et al. (2010) tagged 21 porbeagles in 2001-2008, including large juvenile females and allegedly mature sharks of both sexes, on Georges Bank, the Scotian Shelf, and the Grand Banks and found large juvenile females predominately utilized shelf-waters (although tag deployments were more limited to summer through early winter). Of the two mature males tagged by Campana et al. (2010), one utilized shelf-waters while another made southeasterly offshore movement in the winter. All mature females moved to offshore habitats in winter and several of these sharks migrated as far south as the Sargasso Sea in the spring (Campana et al., 2010). Based on the assumed annual reproductive cycle of the population during the time of the study (Jensen et al., 2002) and the apparent disparity in movements between mature females and other life stages, Campana et al. (2010) suggested that the Sargasso Sea was a pupping ground for the population. However, there are two key assumptions which limit the validity of these conclusions. First, the tag deployment periods limited the comparisons of habitat use among life stages during all seasons, as most data from late winter and spring was from mature females. Second, more recent data indicate that at least a portion of the NW Atlantic porbeagle population reproduces biennially (Natanson et al., 2019). As mature females tagged by Campana et al. (2010) were not confirmed to be gravid by any recognized method, their reproductive states remain uncertain, and therefore it is possible that movement patterns differ by reproductive state.

A more directed study of seasonal movement that spans all life stages, including all reproductive states, would provide a more comprehensive understanding of the spatiotemporal dynamics of porbeagle habitat use in the NW Atlantic and could also provide a model to test the efficacy of representative life-history sampling schemes for future telemetry work. Moreover, all previous telemetry work on porbeagles have used PSATs to estimate geolocation. There are numerous recognized trade-offs associated with the type of tags used in telemetry studies. While PSATs provide regular, daily light-based geolocation estimates, it is at the expense of reduced location accuracy (i.e., Wilson et al., 2007; Winship et al., 2023), with error on the order of several hundred km (Wilson et al., 2007). In comparison, fin-mount satellite tags transmit more accurate location information, with error on the order of hundreds of m to <5 km (i.e., Tougaard et al., 2008), but at irregular intervals (reviewed by Hammerschlag et al., 2011; Renshaw et al., 2023). Successful transmission by fin-mount satellite tags is dependent on the animal being at the sea surface and in proximity to an orbiting satellite (i.e., Winship et al., 2012). Given that porbeagles spend a large proportion of time at the surface (Pade et al., 2009; Skomal et al., 2017; Chapter 2), this species could be a suitable candidate for using the more accurate fin-mount satellite tags to study its habitat use. Here I advance the study of movement ecology of porbeagles found in the NW Atlantic by using high-accuracy finmount satellite tags. Specifically, I used satellite-tag derived data to advance several overarching goals: (1) assessing seasonal habitat use of porbeagles in the NW Atlantic; (2) identifying the extent of residency and transient phases in seasonal habitats; and (3) comparing movement patterns by life stage by integrating empirical reproductive data.

METHODS

Capture & tagging.

Porbeagles were captured using rod-and-reel in the NW Atlantic from 2017 to 2022, in locations spanning shelf waters from southern Maine (ME) to southern Massachusetts (MA) (Table 4.1). Captured sharks were either left in the water and secured alongside the vessel or brought onboard the vessel. For sharks that were brought onboard the vessel, a saltwater pump was placed in the mouth to facilitate respiration throughout sampling. Sex, fork length (FL; cm), total length (TL; cm), and capture location were recorded. The life stage of each shark was determined based on a length-at-age relationship (Natanson et al., 2002) and the size at 50% maturity (174 and 218 cm FL for males and females, respectively; Jensen et al., 2002) for this population, and/or ultrasonography for some females (described below). Individuals with FL < 107 cm were considered young-of-the-year (YOY; Natanson et al., 2002). Males were considered juveniles if FL was 107-174 cm or mature if FL was >174 cm (Jensen et al., 2002). For females that were not formally assessed for reproductive stage (described below), sharks were considered juveniles if FL was 107-218 cm or mature if FL was >218 cm (Jensen et al., 2002). However, ultrasonography was performed on most females near or above the size range at maturity (210-230 cm FL; Jensen et al., 2002) to determine the reproductive stage (immature, gravid, or non-gravid) following Sulikowski and Hammerschlag (2023). An Ibex EVO II portable ultrasound (E.I Medical Imaging) with a 60 mm curved linear array 5-2.5 MHz transducer (model 290470) capable of a 24 cm scan depth was used to obtain images of the reproductive tract. Scanning was performed on the ventral surface from the pectoral to the pelvic fin in both a transverse and longitudinal orientation to obtain cross-sectional and lengthwise images of the uterus and ovary, respectively.

One of a variety of fin-mount satellite transmitters was fitted to the first dorsal fin of each shark following established protocols (i.e., Hammerschlag et al., 2012; Gibson et al., 2021). Tag models included: Sirtrack K2F transmitter (Lotek Wireless; n = 15), Sirtrack F6F FastGPS Argos transmitter (Lotek Wireless; n = 2), Sirtrack Kiwisat K4 transmitter (Lotek Wireless; n = 2), Sirtrack K2F 176D dive transmitter (Lotek Wireless; n = 4), or SPOT 6 transmitter (Wildlife Computers; n = 15). Additionally, a subset of porbeagles (n = 14) were also tagged with a 365-day PSATFLEX (Lotek Wireless) for another study (Chapter 5; Anderson and Sulikowski, unpublished data).

Data processing & analyses.

Porbeagle position estimates were downloaded from Argos satellites (CLS America, Inc.). Argos provides location accuracy using the following location classes (LC): 3, 2, 1, 0, A, B, and Z (in decreasing accuracy). These LCs are associated with the following error estimates: LC3 < 250 m, 250 m < LC2 < 500 m, 500 m < LC1 < 1500 m, and LC0 > 1500 m. Argos does not provide error estimates for LC A or B, but LC A and LC B have been found to be accurate to > 1 km and > 5 km radius, respectively (Tougaard et al., 2008). The lowest accuracy category transmissions (LC Z) are poor, unreliable location estimates and were removed from the dataset (<1% of all transmissions; Figure B.1).

Due to irregular surfacing of sharks (and thus irregular transmission rates) and variation in satellite coverage at any given time, satellite tracking data often have large data gaps, and may also be subject to autocorrelation and spatial biases. Therefore, all positional data were regularized and interpolated following an approach comparable to Hammerschlag et al. (2022). Specifically, using the R package 'aniMotum' (Jonsen et al., 2023), a continuous-time correlated random walk (CTCRW) state-space model (SSM), with a 2 m/s speed filter (per Skomal et al., 2021), was used to interpolate and regularize positional data along an estimated movement path of each shark. Data were regularized to daily position estimates. The SSM applied also associated each estimate location with a behavioral mode using a move persistence model (see Appendix B for details). Since interpolating track sections with large temporal gaps increases uncertainty in the location estimates (Jonsen et al., 2023), I did not interpolate gaps in the data that exceeded 10 days (Figure B.2). Instead, full tracks with gaps exceeding 10 days were segmented into multiple sub-tracks prior to model fitting and interpolation was completed separately for each sub-track. Additionally, I did not interpolate sub-tracks with <10 positions.

To examine habitat use, kernel utilization distributions (KUDs) were calculated with the interpolated positions using the ‘adehabitatHR’ R package with the “href” bandwidth estimator (Calenge, 2015). Kernel density estimates (KDEs) were used to quantify areas of higher and lower shark use within the KUDs (Worton, 1989). Specifically, I calculated 95% and 50% density volume contours from the KDEs, with the 95% KDE volume contours representing areas with the lowest densities of shark position estimates (referred to as an “activity space”) and the 50% KDE volume contours representing areas with the highest densities of shark position estimates (referred to as “high occupancy area”). First, movement data from all interpolated tracks were combined to make an overall KUD. Then, to examine seasonal differences in habitat use, seasonal KUDs were calculated using interpolated tracks. Seasons were defined as follows: winter: December-February, spring: March-May, summer: June-August, and fall: September-November. Finally, differences in activity space and high occupancy areas by life stage were observed by calculating life-stage based KUDs with the interpolated tracks. The position estimates and 95% and 50% KDE volume contours were plotted using the R package ‘ggmap; (Kahle and Wickham, 2013). Distance of each SSM-estimated location from the tagging location was calculated for each shark included in habitat use analyses. Dispersion from the tagging location was subsequently plotted by life stage and as a function of time since tagging. Additionally, the proportion of time spent within different national boundaries were determined using exclusive economic zone (EEZ) data from Flanders Marine Institute (2019).

RESULTS

Life stage distribution.

A total of 38 porbeagles were tagged with fin-mount satellite transmitters between June 2017 and October 2022 (Table 4.1). Tagging locations were concentrated off the northeastern coast of the US, particularly offshore of Gloucester and Cape Cod, Massachusetts (MA), as well as offshore of southern Maine (ME). Tagged sharks ranged in size from 81.2 to 244 cm FL and included 10 males (3 YOY, 3 juvenile, 4 mature) and 28 females (4 YOY, 8 juvenile, 3 mature but not assessed for reproductive stage, 3 mature non-gravid, 10 mature gravid), representing all life stages.

Tag reporting & fate of tagged sharks.

Thirty-one of the tagged sharks (81.6%) appeared to survival post-release. Post-release mortality was evident at some point in the tag deployment for seven (18.4%) of the tagged sharks and four of these mortalities were related to capture in fisheries. Immediate mortality was confirmed in shark 37 (175434, gravid female) based on depth data provided by a PSAT attached to the shark and failure of the finmount tag to report. Shark 37 was foul hooked in the ventral surface and experienced an extended fight time (47 min) on rod-and-reel before reaching the boat. Predation was inferred in shark 36 (207870, gravid female), approximately five months after tagging, based on the depth and temperature data transmitted by a PSAT attached to the shark. Approximately four days before the PSAT attached to shark 36 floated to the sea surface and transmitted southwest of Bermuda on 03/29/2021, depth data showed that the tag continued to ascend and descend in the water column while the temperature increased by approximately 8°C and remained elevated at several hundred m depth, indicating tag ingestion (i.e., Kerstetter et al., 2004; Beguer-Pon et al., 2012; Cosgrove et al., 2015). The fin-mount tag attached to shark 36 failed to transmit messages after 12/05/2020. Shark 38 (221129, mature non-gravid female) died south of Bermuda on 12/15/2022, approximately 50 days after tagging, based on depth data provided by the PSAT attached to the shark. The other four sharks appeared to be recaptured and harvested during their tag deployment. Shark 23 (33148, mature non-gravid female) appeared to be harvested approximately 71 days after tagging based on satellite transmissions occurring on land north of Gloucester, MA for a month before the tag stopped transmitting. Shark 31 (33098, YOY) appeared to be harvested based on satellite transmissions continually occurring on land (on Cape Cod, MA) for the entire deployment. Shark 35 (234533, gravid female) is known to have been recaught in a monkfish gillnet south of Cape Cod, MA on 03/27/2023, 154 days after tagging. Depth data from a PSAT attached to shark 35 suggested the shark was in the gillnet for approximately 48 hours before removal. Both the fin-mount and PSAT tags from shark 35 were returned. Finally, shark 8 (175793, juvenile female) is known to have been recaught in a bottom trawl targeting squid south of Cape Cod, MA on 06/26/2023, 244 days after tagging, and suffered at-vessel mortality.

Overall, tags reported a total of 10,941 Argos locations, with most locations assigned a LC of B (27%) or 3 (21%) (Figure B.1). The number of days at liberty (days between tagging and the last tag transmission received) for tagged porbeagles ranged widely, from 0 to 963 days (mean = 240 days, median = 170 days) with 24 sharks tracked for ≥100 days. Following the removal of non-reporting tags and tags with limited transmissions, tracks segments were available from 26 out of the 38 tagged porbeagles (68%) for data regularization and interpolation with the SSM. For the 12 sharks that could not be used in the SSM and habitat use analysis, one shark died immediately (shark 37; 175434), one was predicted to have been harvested shortly after tagging (shark 31; 33098), one had a tag that failed to transmit (shark 27; 33111), five were YOY sharks that had very short tag deployments (sharks 28, 29, 30, 32, 33), three had transmissions that were too infrequent before they were harvested (shark 35; 221533) or died (shark 36, 38), and one had infrequent transmissions and a sub-track that did not converge in the SSM (shark 34).

The 26 sharks incorporated into the SSM included 1 YOY, 9 juveniles, 4 mature males, 7 gravid females, 2 mature non-gravid females, and 3 mature females of unknown reproductive states. The SSM produced a total of 4,159 positions estimates for habitat use analyses. The number of days with regularized positions for tagged porbeagles ranged between 25 and 457 days (mean = 160 days, median = 121 days). Track data was most limited for YOY porbeagles, with only one YOY shark (shark 1; 220902) providing enough data for track interpolation. As such, the interpolated track from the single YOY shark was included with the tracks from larger juveniles for further analyses. Additionally, location estimates were limited for mature non-gravid females due to the sample size of individuals and short track durations for this group. There were no location estimates for mature non-gravid females during the winter. Otherwise, location estimates were relatively evenly distributed across life stages and seasons (Figure B.3).

Overall habitat use.

Tracks generated from regularized daily position estimates were largely concentrated on the northeastern US continental shelf, ranging from ME to southern MA between latitudes of approximately 39°N to 45°N and longitudes of approximately 71°W to 65°W (Figure 4.1). A limited number of tracks extended outside this range. One mature male (shark 13; 175432) made excursions north into the Bay of Fundy two years in a row. One mature female of unknown reproductive state (shark 26; 220982) migrated to waters southeast of Bermuda. Two juveniles (shark 7; 221136, shark 8; 175793) and two mature females (one non-gravid (shark 22; 33131), one of unknown reproductive state (shark 24; 172014)) made excursions to the continental shelf region near Long Island, New York and New Jersey (NJ). Finally, one juvenile (shark 8; 175793) and one mature female of unknown reproductive state (shark 26; 220982) moved east of 60°W. When considering national boundaries, 89.0% of porbeagle location estimates occurred within the US EEZ, 10.3% occurred within the Canadian EEZ, and less than 1% of location estimates occurred in the high seas (international waters).

In regards to activity space, the overall KDE (95% KDE, including all regularized tracks) was approximately 257,432 km^2 and encompassed the continental shelf ranging from the lower Bay of Fundy to NJ, with an extension into mesopelagic habitat along the eastern and southern edges of Georges Bank (black polygon, Figure 4.1). The overall high occupancy area (50% KDE) was approximately 44,131 km^2 and included only continental shelf waters east of Cape Cod, MA, and in a region ranging from 40.2° to 42.7°N latitude and 70.5° to 67.7°W longitude (white polygons, Figure 4.1).

Influence of season.

When considering the amount of time spent seasonally in national boundaries, the highest proportion of time spent in US waters occurred during the fall and winter, with 93.1% of fall and 89.6% of winter spent in US waters. In comparison, 88.2% of summer and 86.7% of spring were spent in US waters. The proportion of time spent in Canadian waters was highest during the summer and spring, with 11.8% of summer and 11.5% of spring spent in Canadian waters. In comparison, only 8.8% of winter and 6.9% of fall were spent in Canadian waters. Finally, the highest proportion of time spent in the high seas occurred during the spring and winter, with 1.9% of spring and 1.6% of winter spent in the high seas, respectively. There were no location estimates in the high seas during summer or fall.

Seasonal level KUDs demonstrated year-round use of the Gulf of Maine, Georges Bank, and particularly the shelf-waters surrounding Cape Cod, MA (Figure 4.2; Figure 4.3). The size of activity spaces (95% KDEs) and high occupancy areas (50% KDEs) were greatly reduced during the summer and fall (Table 4.2), with habitat occurring almost exclusively on continental shelf waters from ME to MA (Figure 4.2C; Figure 4.2D). During the winter and spring, activity space and high occupancy areas expanded to approximately 1.5-3 times the size of those in the summer and fall (Table 4.2), and activity space shifted southward to include portions of the mesopelagic environment along the edge of Georges Bank and east of NJ (Figure 4.2A; Figure 4.2B). During the spring, a second activity space area appeared southeast of Bermuda at approximately 31°N, 56°W (Figure 4.2B). High occupancy area was located in the vicinity of Cape Cod, MA year-round (Figure 4.2; Figure 4.3), and spatial overlap in seasonal high occupancy area was located southeast of Cape Cod, MA (Figure 4.3). Specifically, during the summer there was a high occupancy area encompassing shelf waters southeast, east, and north of Cape Cod and a smaller high occupancy area on the northern edge of Georges Bank. During the fall, there was a high occupancy area southeast and east of Cape Cod and a smaller high occupancy area northeast of Cape Cod. However, high occupancy area expanded southward in the winter and spring and also rotated eastward to include most of Georges Bank in the spring (Figure 4.2B).

Influence of life stage.

Based on SSM location estimates, most tagged porbeagles (85%; n = 22) stayed within approximately 500 km of their tagging location (Figure 4.4). However, the maximum dispersal distance from the tagging location ranged from 84.0 to 1,662 km and differed among life stages, with juveniles and mature females of unknown reproductive states dispersing farthest from the tagging location. In particular, the maximum dispersal distance from the tagging location was 1,622 km (shark 26; 220982) for mature females of unknown reproductive state, 971 km (shark 8; 175793) for juveniles, 538 km (shark 18; 175785) for gravid females, 498 km (shark 13; 175432) for mature males, and 455 km (shark 22; 33131) for non-gravid mature females.

Regarding national boundaries, non-gravid mature females and mature females of unknown reproductive states spent the highest proportions of their time in US waters, 100% and 95.8% respectively. Gravid females, juveniles, and mature males spent similar proportions of time in US waters, 88.1%, 88.4%, and 85.4%, respectively. Alternatively, mature males, gravid females, and juveniles spent higher proportions of time in Canadian waters (14.6%, 11.8%, and 11.3%, respectively) compared to females of unknown reproductive state and non-gravid mature females (0.8% and 0% respectively). Finally, mature females of unknown reproductive state spent the highest proportion of time in the high seas (3.5%), followed by juveniles (0.3%) and gravid females (0.1%). Mature males and non-gravid mature females did not have any SSM location estimates in the high seas.

Although the geographic ranges of porbeagles tagged in this study were relatively similar among life stages and were restricted in general, seasonal latitudinal and longitudinal movements were most prevalent in juveniles and mature females that were either non-gravid or were of unknown reproductive state (Figure 4.5). In particular, these life stages occupied more southern latitudes during the winter and/or spring, and more northern latitudes during the summer and fall (Figure 4.4). Additionally, these life stages occupied larger longitudinal ranges during the winter and/or spring compared to the summer and fall (Figure 4.5). On the other hand, mature males and gravid females exhibited relatively minor latitudinal and longitudinal shifts throughout the year compared to the other life stages, and gravid females had the smallest and most consistent latitudinal range in this study (Figure 4.5).

A high occupancy area was concentrated around Cape Cod, MA for all groups (Figure 4.6). There was some degree of spatial overlap in high occupancy area among all life stages except between gravid and non-gravid mature females (Figure 4.6). Activity space overlapped between life stages but varied in size (Figure 4.7; Table 4.3). Mature males (Figure 4.7B) and gravid females (Figure 4.7E) had the smallest activity spaces and gravid females had the smallest high occupancy areas (Table 4.3). The activity spaces for these life stages were almost exclusively in continental shelf waters from ME to southern MA (Figure 4.7B; Figure 4.7E). High occupancy area was concentrated northeast and southeast of Cape Cod, MA for mature males (Figure 4.7B) and southeast of Cape Cod, MA for gravid females (Figure 4.7E). Non-gravid mature females had the next largest activity space (Table 4.3), ranging from southern ME to NJ and extending south of Georges Bank into mesopelagic environments (Figure 4.7D). High occupancy area for this life stage was exclusively in shelf waters north of Cape Cod, MA (Figure 4.7D). Juveniles (Figure 4.7A) and mature females of unknown reproductive states (Figure 4.7C) had the largest activity spaces and high occupancy areas (Table 4.3). The juvenile activity space encompassed the entire Gulf of Maine, the continental shelf region from southern ME to NJ, and extended south of Georges Bank into mesopelagic environments (Figure 4.7A). Juvenile high occupancy area was surrounding Cape Cod, MA as well as the northern edge of Georges Bank (Figure 4.7A). Mature females of unknown reproductive state had three main activity space areas (Figure 4.7C). The largest area encompassed the continental shelf region from southern ME to southern MA and extended south of Georges Bank into mesopelagic habitat (Figure 4.7C). A second area included waters surrounding the Delaware Bay, and a third area occurred southeast of Bermuda at approximately 31°N, 56°W (Figure 4.7C). However, the high occupancy area of this group was southeast of Cape Cod, MA (Figure 4.7C).

DISCUSSION

This study provides one of the first comparative analyses on the movements and habitat use of a large elasmobranch across all of its life history stages, including female reproductive states. It is the first study to do so for porbeagle sharks within the NW Atlantic. While sample size was limited among life history stages (particularly YOY), these data help address knowledge gaps for the population and can be incorporated into future large-scale comparative studies. Results indicate that despite a high degree of overlap in habitat use among life stages and seasons, there was evidence of population structuring in the extent and location of activity space and high occupancy areas for porbeagles in this region. Tagged porbeagles were present on the continental shelf surrounding the northeastern US year-round, although movements into mesopelagic environments did occasionally occur in the winter and spring for some life stages. Larger-scale movements were mainly made by juveniles and mature females that were of unknown reproductive state. Overall, these results differ from previous work on NW Atlantic porbeagles by Campana et al. (2010), as described below.

Juvenile habitat use.

Many previous studies on the movement ecology of sharks have found evidence of ontogenetic differences in habitat use, including changes in environments used (i.e., shifts from estuarine nurseries to coastal or oceanic habitats, latitudinal shifts; Bansemer and Bennett, 2011; Ajemian et al., 2020; Frank et al., 2021; Kock et al., 2022) and/or by expansions in space use as sharks grow (e.g., Speed et al., 2010; Bansemer and Bennett, 2011; Franks et al., 2021; Kock et al., 2022). Interestingly, activity space and high occupancy area were actually greater for juveniles compared to many mature life stages in this study. While the ecological driver of this finding is uncertain, it could be related to resource competition and/or abiotic needs (Bowler and Benton, 2005). For example, the diet of juvenile porbeagles greatly overlaps with that of mature conspecifics (Joyce et al., 2002). Thus, resource competition could cause juveniles to make more frequent or more extensive movements in order to meet their food requirements if larger sharks are competitively superior (e.g., Bowler and Benton, 2005). On the other hand, smaller sharks are predicted to have reduced endothermic capacity and in turn, reduced thermal tolerance compared to larger conspecifics (Carlisle et al., 2015; Shaw et al., 2021). The predicted narrower thermal threshold could have an influence on the activity space of juvenile porbeagles, as they may choose to move further or more often in search of tolerable environments (Carlisle et al., 2015). For example, larger-scale latitudinal and longitudinal movements by juvenile porbeagles were made during the winter and spring when water temperatures would be reduced in the Gulf of Maine, and these sharks may have been seeking more preferred thermal habitats. However, thorough investigation into the environmental correlates of porbeagle movements (in three dimensions) would be needed to help support this hypothesis.

Two previous studies have tagged juvenile porbeagles in the NW Atlantic to assess habitat use. Campana et al. (2010) found juvenile porbeagles to predominantly occupy continental shelf habitats, although tag deployments were limited to summer through early winter and thus may have missed offshore movements for this life stage. In comparison, Skomal et al. (2021) found large juveniles to be relatively shelf-oriented in the summer and fall, but make seasonal offshore movements into mesopelagic environments during the winter and spring. Results from this study most closely align with those found by Skomal et al. (2021), although the KUDs for juvenile porbeagles tagged in this study were smaller and did not overlap with the regions used by juvenile porbeagles tagged in Skomal et al. (2021). Juvenile porbeagles in this study were tagged in US coastal waters from ME to MA, whereas juvenile porbeagles were tagged on Georges Bank in Skomal et al. (2021), and on Georges Bank, the Scotian Shelf, and the Grand Banks in Campana et al. (2010). Tagging location could thus have a large influence on any comparison among juvenile habitat use from these three studies, as they potentially sampled from different components of the juvenile porbeagle population in the NW Atlantic.

Mature male habitat use.

Mature male porbeagles had the second smallest activity space in this study, which appeared to be restricted. to the Gulf of Maine, Georges Bank, and shelf waters south of MA. High occupancy areas included continental shelf waters north and east of Cape Cod, MA, as well as discrete areas southeast of Cape Cod, MA. There were a very limited number of location estimates in offshore, mesopelagic habitats for this subset of tagged individuals. Although tracking data for mature male porbeagles is limited globally, the spatial patterns of mature male porbeagles tagged in this study were similar to previous tracking data for this life stage in the NW Atlantic (Campana et al., 2010) and the South Pacific (Francis et al., 2015). For example, Francis et al. (2015) found no evidence of a seasonal latitudinal migration for the two mature males tagged in the study. Of the two mature males tagged by Campana et al. (2010) in the NW Atlantic, one remained in continental shelf waters for the duration of the tag deployment while another moved southeast to approximately 37°N, 55°W (northeast of Bermuda) in January. Most of the mature males tagged in this study remained in continental shelf waters year-round, although raw, unfiltered location estimates suggested one mature male (shark 24; ID 175432) tagged in this study migrated south to approximately 33°N, 65°W (north of Bermuda) during late December. Collectively, mature male porbeagles appear to be mostly shelf-oriented in the NW Atlantic, but further tagging effort is needed to determine the frequency of southward migrations for this life stage.

The reason for the relatively small activity space of mature male porbeagles in this study is uncertain, but could be related to foraging efficiency and/or endothermic capacity. Other endothermic lamnids such as white sharks (Franks et al., 2021) and shortfin mako sharks (Vaudo et al., 2017; Kohler and Turner, 2019), as well as ectothermic blue sharks (Campana et al., 2011; Kohler and Turner, 2019) are known to make extensive southward migrations to warmer habitats during winter months in the NW Atlantic. Of the endothermic sharks within this region, porbeagles are predicted to have the highest endothermic capacity (Carey et al., 1985), and endothermic capacity is expected to increase with increasing body size (Carlisle et al., 2015; Shaw et al., 2021). Given this consideration, it is possible the mature male porbeagles are taking advantage of their superior thermoregulatory abilities to remain within colder, productive waters near mating grounds year-round to exploit food resources, while most of their competitors (i.e., white sharks, shortfin makos, blue sharks, juvenile porbeagles) move farther south to occupy more moderate thermal habitats (Carey et al., 1985). Although the exact water temperatures occupied by mature male porbeagles during this study are unknown, sea surface temperature data collected from a NOAA buoy (Station CHTM3) near Cape Cod, MA ranged from -1.6-11.0°C (average = 5.0°C) during winter (Dec-Feb) months and from 1.2-24.0°C (average = 9.9°C) during spring (Mar-May) months of 2020-2023 (National Data Buoy Center; https://www.ndbc.noaa.gov/station_history.php?station=chtm3).

Gravid female habitat use.

Campana et al. (2010) found that mature female porbeagles (which were assumed gravid, but not confirmed) made extensive southward migrations to the Sargasso Sea during the spring. Based on the timing and the disparity in movements between those mature females and other life stages, Campana et al. (2010) suggested that mature females were migrating to the Sargasso Sea for parturition. However, YOY porbeagles are found in the continental shelf waters of the US and Canada by early July (Natanson et al., 2002; Anderson et al., 2021; Chapter 3). The suggestion that gravid porbeagles migrate 2,000 km to give birth in unproductive subtropical waters, followed by a return migration for the post-partum females and neonates within a couple months of parturition (Campana et al., 2010), lacks substantiated metabolic and evolutionary rationale (i.e., McMillan et al., 2021). The tracking data collected from confirmed gravid female porbeagles in this study differ from the previous claim regarding the gestation and pupping habitats of the NW Atlantic porbeagle population, as described below.

Gravid females had the smallest activity space and high occupancy area of all life stages tagged in this study. Activity space for this reproductive stage was concentrated in the Gulf of Maine and Georges Bank, while high occupancy area included the region southeast of Cape Cod, MA. Overall, the relatively limited space use of gravid female porbeagles in this study may have been related to the energetic costs of gestation. Oophagy is likely associated with relatively high maternal energetic demands and may therefore place limitations on the behavior of gravid females (Gilmore et al., 2005; Chapman et al., 2013). For example, gravid porbeagles may choose to reside in a small area with ample resources to support foraging efficiency during gestation to maintain metabolism and produce large quantities of nutritive yolk for embryonic consumption (Gilmore et al., 2005). Moreover, while tracking data during the expected pupping season (April through June) were limited to a few individuals, gravid females did not appear to migrate to the Sargasso Sea during this time. In fact, only a limited number of location estimates were observed in offshore mesopelagic habitats, and none of the gravid females tagged in this study were observed to move south of approximately 39°N (NJ). As such, it is possible that the at least some of the gravid females tagged in this study did not migrate to give birth.

Non-gravid mature female habitat use.

Although tag data was very limited for this reproductive stage, the non-gravid mature female porbeagles in this study had a relatively large activity space and high occupancy area over their short tag durations (1-3 months) and one non-gravid mature female dispersed over 450 km within 8 days of tagging. The activity space and high occupancy area of non-gravid mature females were two and 1.5 times larger, respectively, than those for gravid females. The activity space of non-gravid mature females included the southwestern Gulf of Maine, western Georges Bank, shelf waters near New York and NJ, and mesopelagic habitat south of Georges Bank. The relatively large activity space of non-gravid mature females in this study may have been related to energetics and resource acquisition. For example, differences in space use among reproductive states, with non-gravid females occupying larger areas than gravid females, has also been documented in other taxa (e.g., Henry et al., 2005; Marshall et al., 2006; Gilman et al., 2010). The non-gravid female porbeagles in this study may have occupied a larger area to acquire sufficient resources in a prey patchy environment in order to support future reproduction.

The high occupancy area for non-gravid mature females was north of Cape Cod, MA, including Stellwagen Bank, and did not overlap with the high occupancy area of confirmed gravid females in this study. A previous study (Natanson et al., 2019) performed dissections on several female porbeagles caught in the area of Stellwagen Bank to assess maturity and reproductive state. The subset of mature female porbeagles were found to be reproductively resting (i.e., not actively undergoing vitellogenesis, ovulation or gestation), suggesting that Stellwagen Bank was a geographically segregated habitat used by mature females during this resting phase of the reproductive cycle (Natanson et al., 2019). Although sample size is limited, the tracking data from non-gravid mature females in this study support the previous work suggesting Stellwagen Bank may be an important habitat for non-gravid mature porbeagles (Natanson et al., 2019).

Mature females of unknown reproductive state habitat use.

Three female porbeagles tagged in this study were above the size at 50% maturity but were not formally assessed for reproductive state. These porbeagles made the most extensive movements and had the largest activity space in this study. For example, two of the three mature females of unknown reproductive states dispersed over 500 km from the tagging location, with one (shark 24; 172014) dispersing approximately 650 km and one (shark 26; 220982) dispersing over 1,600 km, the longest maximum dispersal distance in this study. The activity space of this group included the western Gulf of Maine, Georges Bank, shelf waters near NJ, and extended into mesopelagic habitats, including a region southeast of Bermuda. Interestingly, the activity space of mature females of unknown reproductive state included habitats that were important to both gravid females (southeast of Cape Cod, MA) and non-gravid mature females (Stellwagen Bank) tagged in this study. It is possible that some of the mature females in this study that were not assessed for reproductive state were gravid while some were resting. Overall, this work demonstrates that assumptions about reproductive state should not be made when attempting to identify reproductive habitats for this taxon from telemetry data to prevent inaccurate assumptions being used as the basis for conservation and management decisions.

The current understanding of NW Atlantic porbeagle reproductive movements and pupping grounds is based on the tracking data of females of unknown reproductive states. While I recognize that the population was thought to reproduce annually (Jensen et al., 2002) and there was limited accessibility of non-lethal reproductive analyses (Sulikowski and Hammerschlag, 2011) at the time of the previous work, the conclusions provided in Campana et al. (2010) nevertheless require further evaluation given their relevance to conservation and management of the population. Although comparisons between studies are limited due to different tagging locations for mature females (northeastern US in this study, eastern Georges Bank and the Scotian Shelf in Campana et al. (2010)), movement patterns made by mature female porbeagles tagged in Campana et al. (2010) were more comparable to the patterns observed in the non-gravid mature females tagged in this study rather than the gravid females, even while considering data for non-gravid females were limited to a few months. First, the activity space of mature females in Campana et al. (2010) would be closer in size to the activity space of non-gravid mature females, rather than the activity space of gravid females. Moreover, several of the mature females tagged in Campana et al. (2010) visited Stellwagen Bank during the tag deployment, a documented female resting habitat (Natanson et al., 2019) that was also occupied by the non-gravid females in this study but not the gravid females. Finally, although none of the tagged females in this study migrated as far south as the Sargasso Sea, when considering raw, unfiltered fin-mount tag transmission data, one of the non-gravid mature females (shark 38; ID 221129) tagged in this study migrated south near Bermuda during the winter before suffering mortality. Moreover, given the lack of SSM location estimates in the winter for non-gravid females in this study, further tagging of this life stage is needed to assess their habitat use patterns during winter.

While the reason none of the tagged porbeagles in this study migrated to the Sargasso Sea remains unknown, it is possible that the mature females tagged by Campana et al. (2010) were not gravid and that the short tag durations for non-gravid females in this study limited my ability to document migrations as far south as the Sargasso Sea for this reproductive group. However, I also cannot rule out the possibility that there are different behavioral characteristics among gravid females, in which a portion of the population migrates for parturition, while another portion remains in cold-temperate waters to give birth (i.e., McMillan et al., 2019), especially considering mature female porbeagles were tagged in different locations in this study compared to Campana et al. (2010). For example, previous research has found evidence of partial migration for gravid female school sharks *Galeorhinus galeus* in Australia (McMillan et al., 2019) and blacktip reef sharks *C. melanopterus* in French Polynesia (Mourier and Planes, 2013), in which some females migrate to give birth while others remain near aggregation sites.

Limitations.

I discovered several limitations regarding the use of fin-mount satellite tags for porbeagles. First, the utility of these tags was particularly low for YOY porbeagles, as only one of the tagged YOY sharks had enough tag transmissions to include in habitat use analyses. I do not believe initial capture- and tagging-induced mortality was a principal factor in the lack of transmissions for tags deployed on YOY sharks in this study given post-release survival of immature porbeagles has been found to be high (100%) using rod-and-reel, including for YOY sharks (Anderson et al., 2021; Chapter 2). An unexpected finding was that at least one tagged YOY porbeagle appeared to be illegally harvested (shark31; ID 33098), which raises questions regarding the frequency of illegal harvest of the species and the possibility of more tagged YOY sharks being illegally harvested in this study that went undetected. Yet, we suspect that the fin-mount tag attachment style is more likely leading to reduced transmissions from tags on YOY sharks, as it is likely that the dorsal fins of YOY porbeagles are not large enough or dense enough to support the weight of the fin-mount tag for extended periods. Additionally, rapid growth during early life stages (i.e., Natanson et al., 2002) could cause the fin-mount tags to fall off the dorsal fin as it grows and potentially cause changes in fin morphology as seen in a sub-adult white shark (Jewell et al. 2011). In an attempt to mitigate these concerns, a prototype fin-mount tag design (Sirtrack Kiwisat K4) that is much smaller and lighter (and is designed to move on the fin as the shark grows) was deployed on two YOY porbeagles (shark 1; 221902 and shark 28; 221906) at the later stage of this study. One of these YOY sharks (shark 1; 221902) fitted with the prototype tag design provided enough transmissions to be used in habitat use analyses, although data from this individual was still limited.

Another limitation of the fin-mount tags in this study was the sparsity of transmissions received when porbeagles were in mesopelagic environments offshore of the continental shelf (Braun et al., 2023). Raw, unprocessed tag data indicated that several of our tagged porbeagles migrated to southern waters offshore of the continental shelf for several weeks during the winter and spring, but fin-mount transmissions were infrequent and had large gaps during these forays, thus some of these data could not be incorporated into habitat use analyses. Previous studies using PSATs have also found porbeagles to migrate south into mesopelagic waters and these sharks exhibited a submergence diving behavior in which they infrequently inhabited surface waters (Campana et al., 2010; Skomal et al., 2021; Braun et al., 2023; Chapter 3). It is likely that porbeagles in this study exhibited similar submergence behavior when in warm mesopelagic waters that caused the infrequent transmission from fin-mount satellite tags. Given this consideration, it is important to note that the KUDs calculated in this study are likely to be underestimated during the winter and spring and may be missing habitats used by porbeagles during some of these offshore excursions. Based on these findings, future studies deploying multiple tag types (fin-mount tags, PSATs) would best optimize the accuracy and amount of location estimates for this population. Considering the limited application of Lotek PSATFLEX for porbeagle geolocation discussed in Chapter 5, other PSAT models (e.g., Wildlife Computers) which can incorporate fin-mount tag data into SSMs for PSAT data may be the most appropriate approach for leveraging the strengths of both tag technologies.

Management implications.

Conservation and management of highly mobile sharks, such as porbeagles, requires a detailed understanding of spatial dynamics. Data on movement patterns can inform vulnerability to interactions with fisheries as well as provide support for the development of spatial management strategies (e.g., Cortés et al., 2010, Bowlby et al., 2020b). The vast majority of porbeagle location estimates in this study were within US waters (89.0%), with limited location estimates occurring in Canadian waters (10.3%), and even fewer in the high seas (<1%). This finding differs from previous research suggesting NW Atlantic porbeagles frequently cross national jurisdictions (i.e., Campana et al., 2010; Campana, 2016; Kohler and Turner, 2019; Skomal et al., 2021), although it is possible that the tagged sharks in this study represented a portion of the population that exhibits more restricted space use than is typical of the broader population. Essential fish habitat (EFH) is defined under the US Magnuson-Stevens Act as habitat required for spawning/breeding, feeding, and/or growth (NOAA, 1996). EFH is mandated to be identified and described for each life stage of a managed species, and adverse effects on such habitat is to be minimized to the extent practicable (NOAA, 1996). EFH was first described for porbeagles (of all life stages combined) in 1999 (NMFS, 2009) and was most recently updated in 2017 to include the Gulf of Maine (excluding Cape Cod Bay and Massachusetts Bay) and shelf-break habitats from Georges Bank to NJ (NMFS, 2017). The coastal waters north and south of Cape Cod, MA are not included in the current map of porbeagle EFH, yet these areas were important habitat year-round for porbeagles tagged in this study, as they were consistently identified as high occupancy areas. The coastal habitat south of Cape Cod, MA is particularly significant to at least a portion of this population given its apparent importance to gravid females tagged in this study. The data from this study support the future inclusion of the coastal waters north and south of Cape Cod, MA into the NW Atlantic porbeagle EFH.

In addition to consideration for designation of EFH, the relatively small high occupancy area surrounding Cape Cod, MA warrants further attention given its apparent importance to all life stages of porbeagles (including gravid females) across all seasons, as well as the concentration of fishing activity (rod-and-reel, trawl, gillnet; NOAA, 2023) that occurs year-round within this region. The overlap between porbeagle high occupancy area in this study and US fishing activity suggests vulnerability to capture is high (e.g., Queiroz et al., 2019). The most recent (2021) US catch statistics for the porbeagle indicate an estimated 1.2 metric tons (mt) were landed in the recreational rod-and-reel fishery while 25 individuals were discarded, and 1 mt were caught in pelagic longline fisheries (NOAA, 2023). While gillnet and trawl catch data are limited to a number of observed sets, porbeagle is the most frequently bycaught highly migratory shark in these fisheries in the Northeast region (NOAA, 2023). In 2021 for example, 202 individuals were discarded in 251 observed gillnet sets and 132 individuals were discarded in 208 observed bottom otter trawl trips (41% of which were dead at discard) (NOAA, 2023). Overall however, it’s predicted that catch statistics are substantially underestimated for this population due to underreporting (ICCAT, 2020). In fact, at least four (10.5%) of the porbeagles tagged in this study were confirmed or predicted to be recaptured in US fisheries within several months of tagging. Recaptured porbeagles included one YOY believed to be illegally harvested based on tag transmissions, one juvenile (above the legal harvest size limit) caught dead in a bottom trawl, one gravid female caught dead in a gillnet, and one non-gravid mature female believed to be harvested based on tag transmissions. Although 75% of the captured sharks were above the legal size limit, most of them were caught as bycatch and suffered at-vessel mortality. This finding highlights the need to quantify porbeagle mortality (including post-release mortality) in commercial fisheries in the region, and data is particularly lacking for gillnet and otter trawl fisheries.

Most work on porbeagle bycatch mortality has been done in pelagic longline fisheries and post-release mortality estimates vary, from approximately 14-27.2% (e.g., Gallagher et al., 2014; Campana et al., 2016; Bowlby et al., 2020a). Additionally, although sample size is limited, the tracking data observed here may also help justify the consideration of a spatial management strategy for the high occupancy area surrounding Cape Cod, MA to help promote timely population recovery, as high residency behavior and low movement rates are factors that have correlated to marine protected area effectiveness (Chapman et al., 2015; Escalle et al., 2015; Dwyer et al., 2020).

Table 4.1

Summary information for 38 porbeagles tagged in the Northwest Atlantic Ocean. FL = fork length; TL = total length; For life stage, Y = young-of-the-year, J = juvenile, M = mature (males), MU = mature (female) not assessed for pregnancy, MN = mature (female) non-gravid, MG = mature (female) gravid; DAL = days at liberty, SSM = state-space model. Sharks are separated first by those used in habitat use analyses and then organized by life stage and size. * indicates a shark removed from habitat use analyses due to mortality, short track duration, or nonconvergence of tracks. Italics indicated an estimated length measurement.

Shark ID	**PTT ID**	**Sex**	**FL (cm)**	**TL (cm)**	**Life Stage**	**Lat**	**Lon**	**Date Tagged**	**Last Transmission**	**DAL**	**SSM days**
1	221902	F	86	106	Y	41.38	-70.27	09/08/2021	10/02/2021	25	25
2	33140	M	113	123	J	43.65	-70.23	07/04/2017	01/13/2018	194	82
3	220986	F	167	174	J	41.39	-69.38	09/07/2021	01/17/2023	498	457
4	221131	M	170	200	J	41.44	-69.50	10/24/2022	11/23/2022	31	30
5	234530	F	175	195	J	41.37	-69.47	10/25/2022	08/21/2023	301	213
6	221130	F	180	204	J	42.55	-70.36	05/01/2022	06/01/2022	32	32
7	221136	F	196	209	J	41.35	-69.37	10/27/2022	01/19/2023	85	73
8	175793	F	198	223	J	41.34	-69.38	10/26/2022	06/26/2023	244	134
9	175792	F	209	224	J	42.90	-70.10	07/02/2019	10/17/2019	107	68
10	171617	F	210	240	J	41.62	-69.52	07/27/2018	08/04/2019	374	125
11	173110	M	198	NA	M	41.24	-69.39	11/30/2019	02/16/2021	445	378
12	175435	M	203	230	M	41.36	-69.39	09/11/2022	09/11/2023	366	194
13	175432	M	211	240	M	41.22	-69.29	11/03/2021	10/11/2023	708	416
14	234531	M	220	252	M	41.35	-69.37	10/27/2022	06/13/2023	230	223
15	207871	F	NA	256	MG	41.43	-69.42	10/27/2020	08/14/2021	292	60
16	175783	F	225	262	MG	41.34	-69.38	10/26/2022	05/24/2023	211	78
17	175782	F	225	262	MG	41.35	-69.36	10/27/2022	09/19/2023	328	159
18	175785	F	226	260	MG	41.41	-69.42	10/27/2020	09/03/2022	677	272
19	228332	F	233	272	MG	41.34	-69.37	10/27/2022	09/26/2023	335	78
20	175430	F	243	263	MG	41.43	-69.42	10/28/2020	06/17/2023	963	161
21	234532	F	244	NA	MG	41.44	-69.47	10/24/2022	08/09/2023	290	116
22	33131	F	220	230	MN	43.08	-70.04	05/14/2018	08/25/2018	104	29
23	33148	F	NA	*240*	MN	43.14	-70.06	06/26/2017	11/03/2017	131	67
24	172014	F	220	253	MU	41.62	-69.54	07/27/2018	07/31/2020	735	347
25	176753	F	221	NA	MU	41.24	-69.39	11/30/2019	09/06/2020	282	95
26	220982	F	231	264	MU	41.44	-69.40	09/07/2021	10/7/2023	761	311
27	33111*	M	81	93	Y	43.38	-70.30	07/22/2017	N/A	N/A	0
28	221906*	F	85	101	Y	43.38	-70.27	09/13/2021	09/26/2021	14	0
29	33069*	F	86	92	Y	43.73	-70.11	07/04/2017	07/20/2017	17	0
30	33070*	M	89	96	Y	43.44	-70.13	09/09/2017	09/20/2017	12	0
31	33098*	M	91	104	Y	43.41	-70.30	10/02/2017	N/A	N/A	0
32	33106*	F	106	122	Y	43.72	-70	07/04/2017	07/11/2017	8	0
33	33137*	M	107	117	J	43.44	-70.13	09/09/2017	09/12/2017	4	0
34	163579*	F	213	NA	J	41.42	-69.39	11/03/2017	02/10/2018	100	0
35	234533*	F	197	229	MG	41.30	-69.41	10/25/2022	03/19/2023	146	0
36	207870*	F	223	259	MG	41.43	-69.43	10/28/2020	11/12/2021	16	0
37	175434*	F	239	272	MG	41.34	-69.39	10/26/2022	N/A	N/A	0
38	221129*	F	224	262	MN	41.35	-69.38	10/27/2022	12/08/2022	43	0

Table 4.2

Seasonal activity space (95% kernel density estimate) and high occupancy area (50% kernel density estimate) size for tagged porbeagles.

Season	**Number of sharks**	**Activity space (km^2)**	**High occupancy area (km^2)**
Winter	16	347,616.78	54,528.12
Spring	18	315,312.11	53,543.57
Summer	22	173,287.34	37,055.16
Fall	18	123,320.68	19,930.61

Table 4.3

Life-stage-based activity space (95% kernel density estimate) and high occupancy area (50% kernel density estimate) size for tagged porbeagles.

Life Stage	**Number of sharks**	**Activity space (km^2)**	**High occupancy area (km^2)**
Juveniles	10	308,761.40	58,811.70
Mature males	4	143,801.45	35,151.46
Mature females of unknown reproductive state	3	377,728.33	48,074.52
Non-gravid mature females	2	234,617.35	28,190.46
Gravid females	7	106,117.13	17,834.81

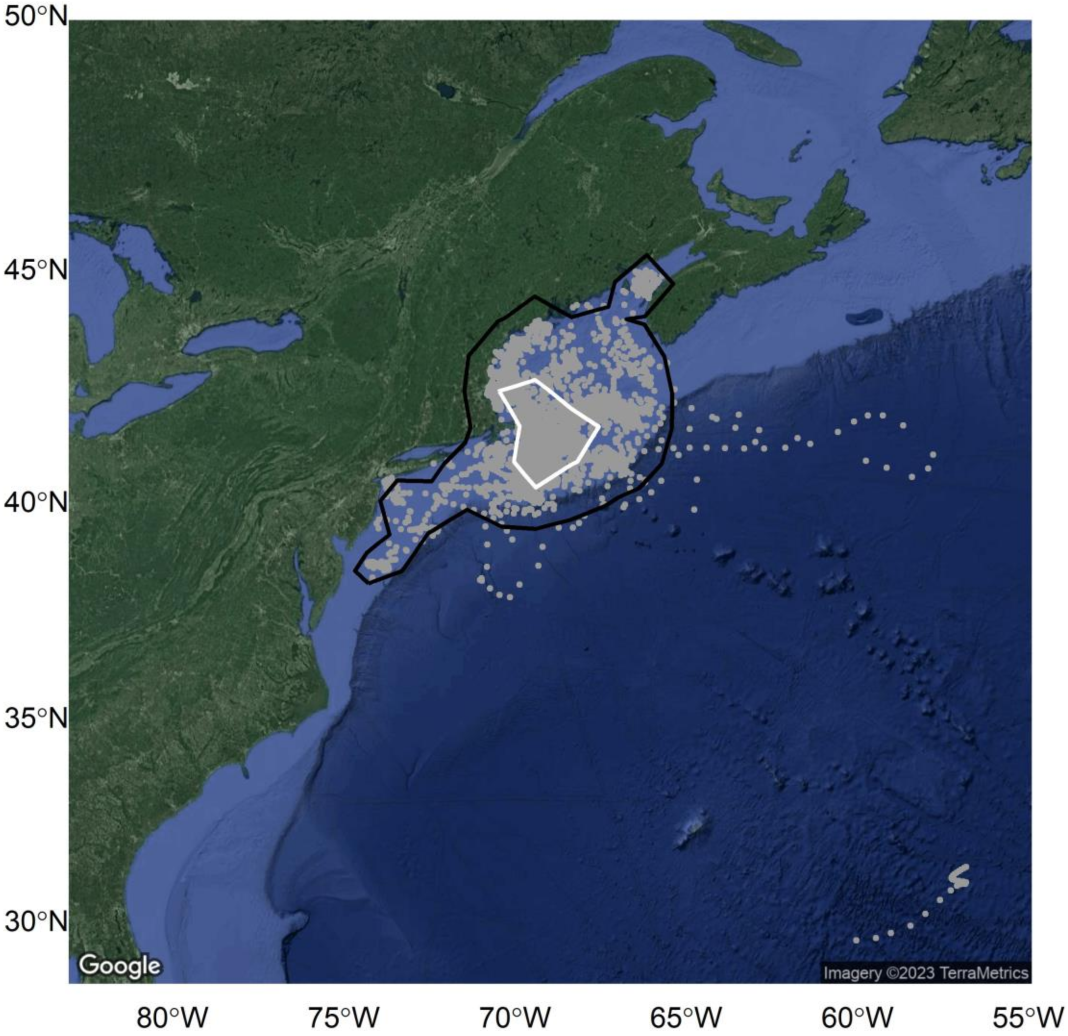


Figure 4.1. Map of the activity space (95% kernel density estimate; black outer polygon), high occupancy area (50% kernel density estimate; white inner polygon), and regularized state space model location estimates (grey points) for 26 porbeagles tagged in the Northwest Atlantic, including all life stages and seasons.

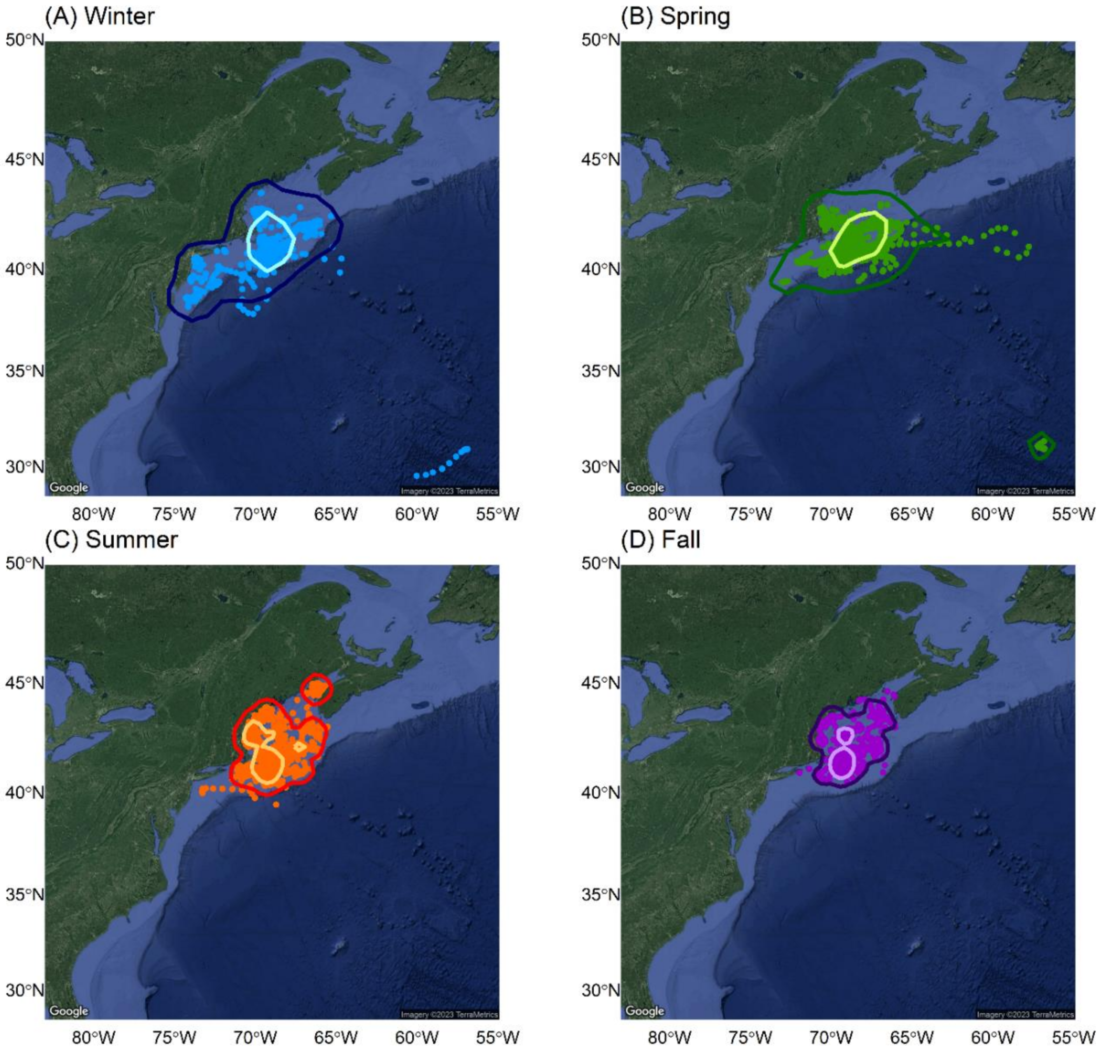


Figure 4.2. Maps of activity space (95% kernel density estimate; dark outer polygons), high occupancy area (50% kernel density estimate; light inner polygons), and regularized state space model location estimates (points) for porbeagles tagged in the Northwest Atlantic during the following seasons: winter (A; n = 16 sharks), spring (B; n = 18 sharks), summer (C; n = 22 sharks), and fall (D; n = 18 sharks).

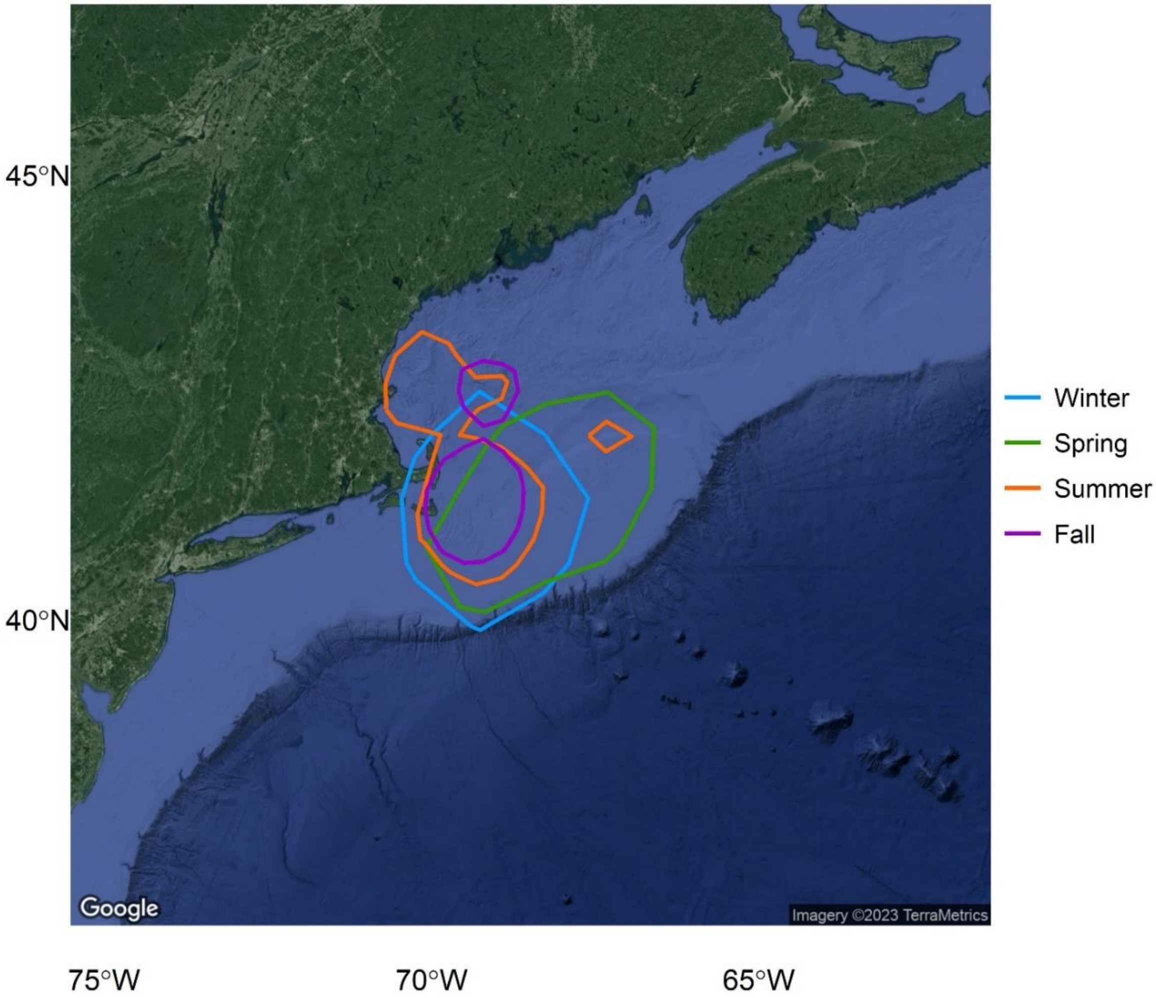


Figure 4.3. Map showing the seasonal overlap in high occupancy areas (50% kernel density estimates) for tagged porbeagles.

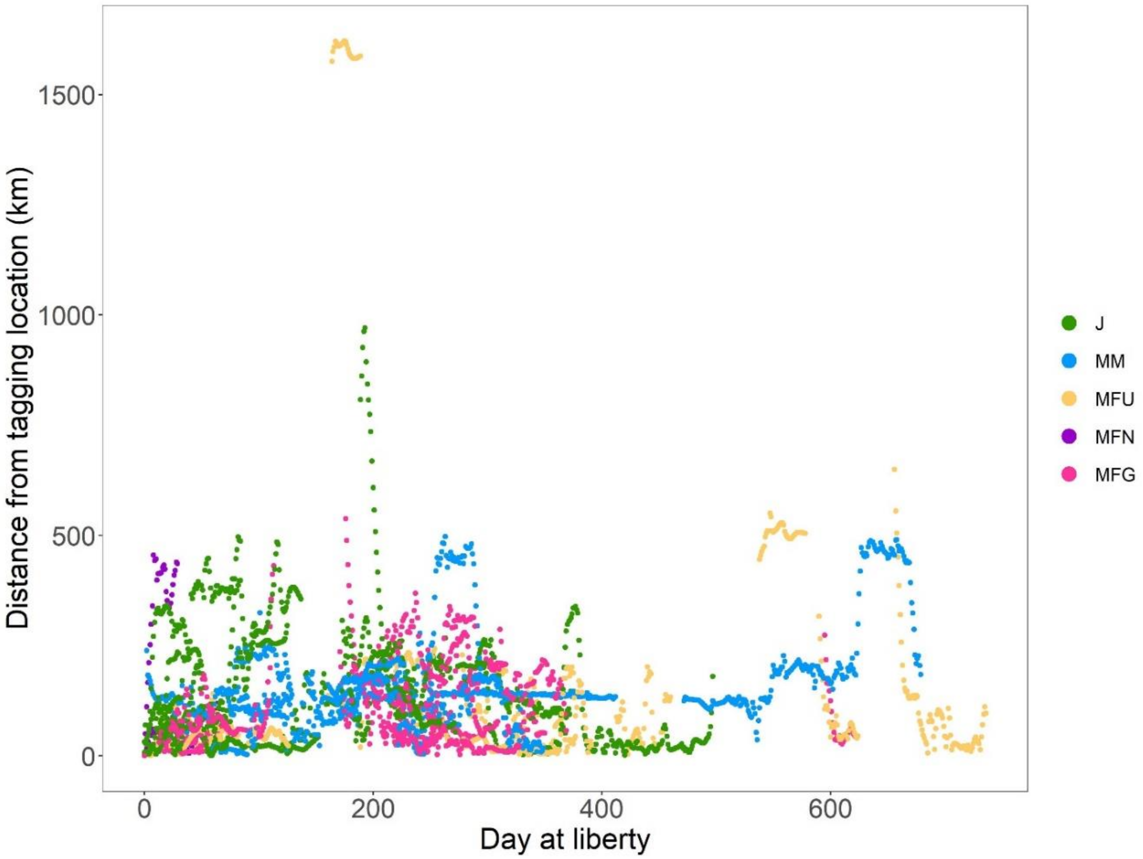


Figure 4.4. Distance (km) of daily location estimates from the tagging locations by day at liberty for 26 porbeagles tagged in the Northwest Atlantic, color-coded by life stage. For life stage, J = juvenile, MM = mature male, MFU = mature female of unknown reproductive state, MFN = non-gravid mature female, MFG = gravid female.

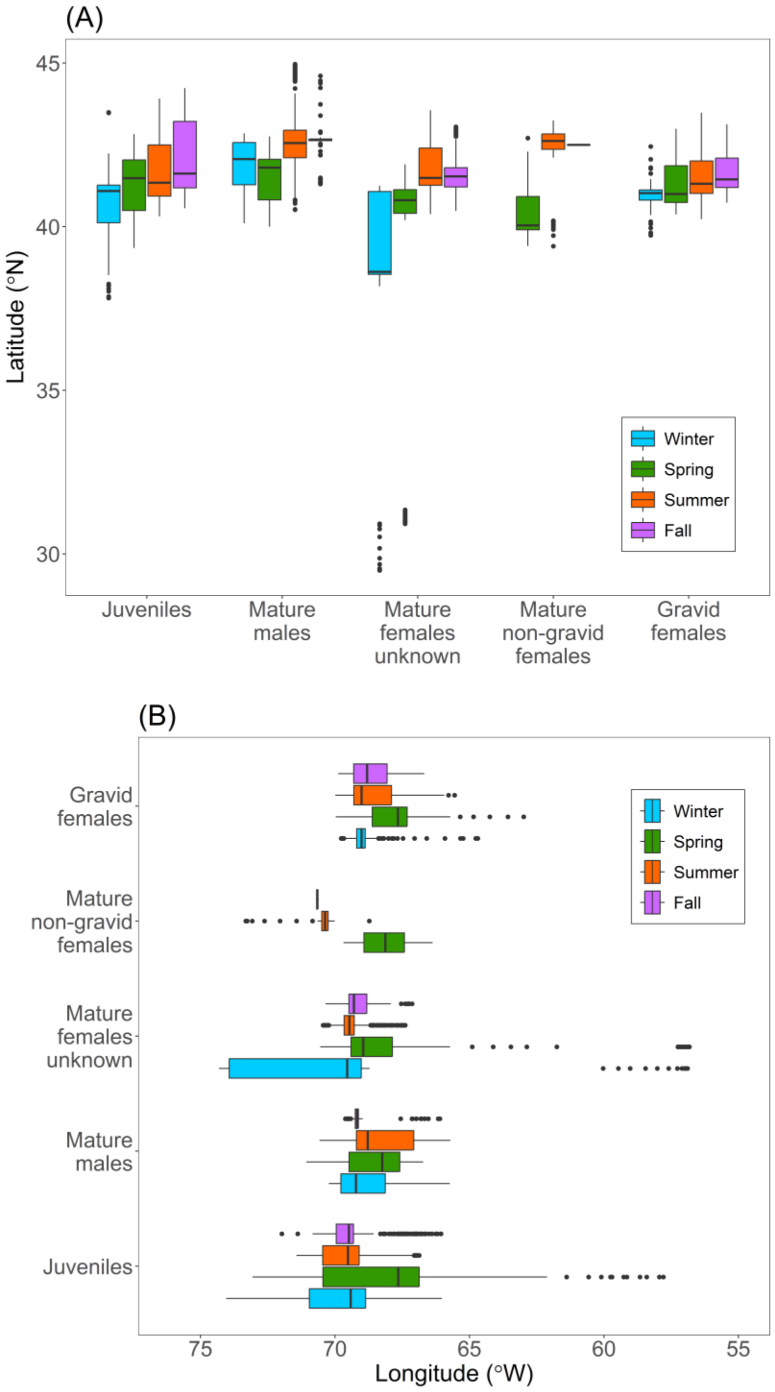


Figure 4.5. Seasonal latitudinal (A) and longitudinal (B) distribution for regularized state space model location estimates for tagged porbeagles, grouped by life stage. Circles represent outliers.

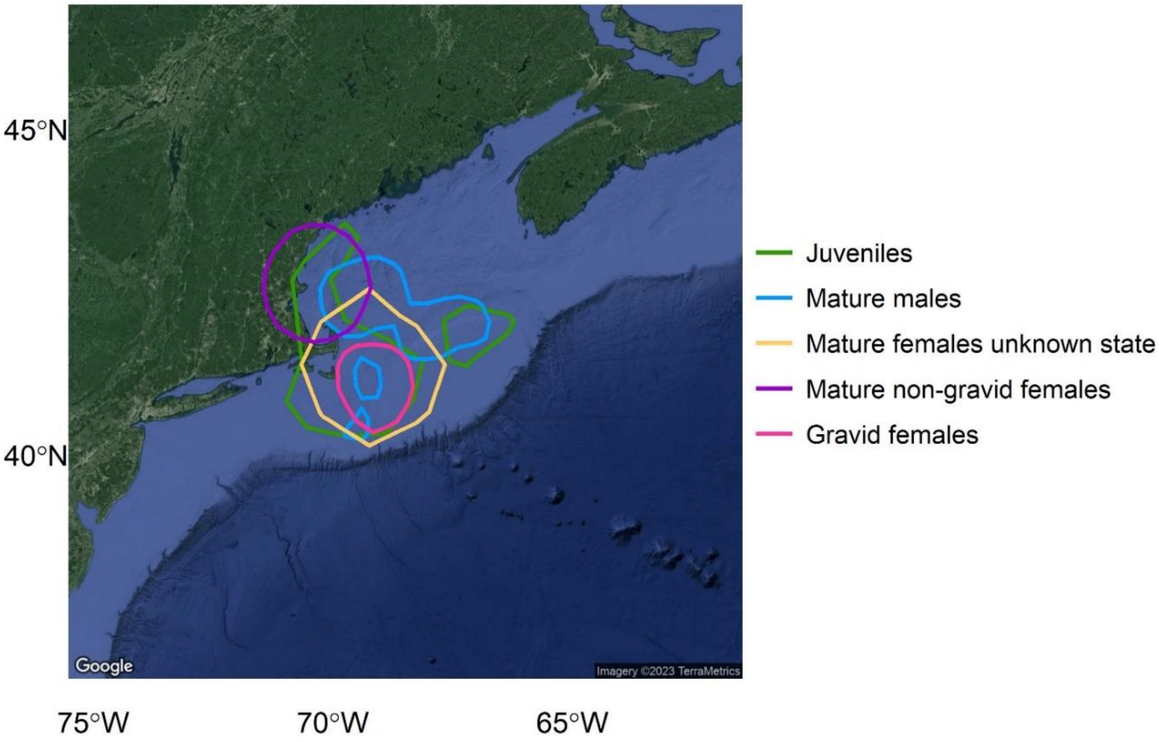


Figure 4.6. Map showing the overlap in high occupancy areas (50% kernel density estimates) across life stage for tagged porbeagles.

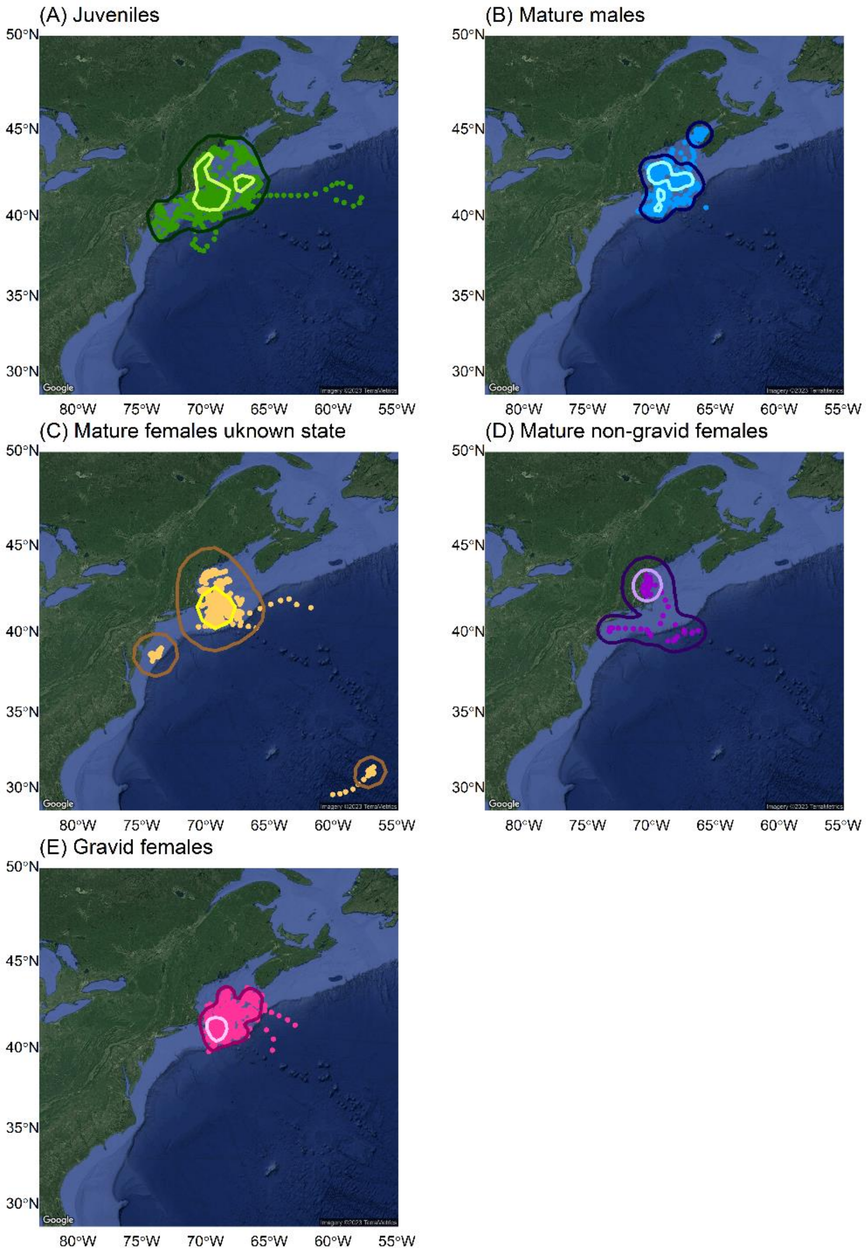


Figure 4.7. Maps of activity space (95% kernel density estimate; dark outer polygons), high occupancy area (50% kernel density estimate; light inner polygons), and regularized state space model location estimates (points) for tagged porbeagles in the Northwest Atlantic of the following life stages: juveniles (A; n = 10 sharks), mature males (B; n = 4 sharks), mature females of unknown reproductive state (C; n = 3 sharks), mature non-gravid females (D; n = 2 sharks), and gravid females (E; n = 7 sharks).

CHAPTER 5

HORIZONTAL AND VERTICAL MOVEMENTS OF GRAVID PORBEAGLES TAGGED IN THE NORTHWEST ATLANTIC

ABSTRACT

The historical lack of non-lethal techniques to study elasmobranch reproduction precluded the ability to link movement ecology to reproductive biology for this taxonomic group until recent decades. Direct evidence of movements during gestation and locations of pupping grounds are particularly lacking for pelagic species despite the importance of identifying and protecting these habitats for conservation and recovery of overfished populations. Recent advancements in non-lethal techniques to study elasmobranch reproduction offer a novel opportunity to directly connect movement ecology to reproduction, particularly in highly mobile species. In this study, I used *in-situ* ultrasonography and reproductive hormone analysis to confirm pregnancy in ten porbeagles *Lamna nasus* in the Northwest Atlantic. Gravid porbeagles were then tagged with both a fin-mount satellite-linked transmitter and a pop-off satellite archival tag to observe seasonal horizontal and vertical movements throughout gestation, respectively. Gravid porbeagles remained in continental shelf waters of the northeastern US during early gestation (fall). In mid- to late-gestation (winter to spring) sharks migrated south into deep, mesopelagic habitats. Before or during the expected pupping season (April through June), gravid porbeagles migrated back into continental shelf waters, mainly occupying habitats southeast of Cape Cod, MA and on Georges Bank. These gravid porbeagles exhibited seasonal and diel differences in depth use, occupying deeper waters in the winter and spring compared to summer and fall, and during the day compared to

night. This study adds to the limited body of work on the reproductive ecology of highly mobile shark species and may help inform conservation planning to protect the next generation of porbeagles in the NW Atlantic.

Elasmobranchs are currently recognized as one of the most threatened taxonomic groups on a global scale (Dulvy et al., 2021; Pacoureau et al., 2021). Principle external threats facing this group include overfishing, habitat loss or degradation, and climate change (Dulvy et al., 2021; Pacoureau et al., 2021). However, it is also important to consider that slow life history characteristics (i.e., late maturity, low reproductive output) make this group inherently vulnerable to extinction and can hinder a populations capacity to recover from anthropogenic threats (i.e., Walker, 2005; Dulvy et al., 2008; Pardo et al., 2016). Given the connection between life history characteristics and extinction risk, having information on reproduction is necessary for developing accurate stock assessments and determining sustainable harvesting limits (i.e., Walker, 2005; Awruch, 2013). Moreover, understanding the habitats (mating, gestation, pupping, and nursery grounds) used by elasmobranchs during important reproductive events can inform conservation planning and aid in the protection of the next generation of individuals entering the population (i.e., Sulikowski et al., 2016; Sulikowski and Hammerschlag, 2023). Most knowledge regarding the reproductive habitats of elasmobranchs focuses on coastal species (i.e., Castro, 1993; Feldheim et al., 2002; Carrier et al., 2003; Mourier and Planes, 2013), and is often based on the sampling of the youngest life stages in proposed nursery grounds (i.e., Carlson, 1998; Merson and Pratt, 2001; Parsons and Hoffmayer, 2007). However, the identification of gestation and parturition grounds are absent or speculative for most species (Sulikowski and Hammerschlag, 2023), as these reproductive events may occur in separate locations and evidence suggests some young-of-the-year (YOY) sharks have the capacity to disperse widely after birth (Nosal et al., 2019). For example, based on pop-off satellite archival tag (PSAT) data, YOY blue

Prionace glauca, shortfin mako *Isurus oxyrinchus*, and porbeagle *Lamna nasus* sharks have been observed to travel minimum distances of approximately 224-667 km, 135-298 km, and 74-962 km, respectively, over 8-86 days at liberty (Nosal et al., 2019; Chapter 3).

Formal data regarding habitats used for gestation and parturition are particularly limited for highly migratory elasmobranch species (Sulikowski et al., 2016; Fujinami et al., 2021; Sulikowski and Hammerschlag, 2023). In some cases, reproductive status of tagged females was assumed based on size and used to interpret observed movement patterns for highly migratory elasmobranchs (e.g., Campana et al., 2010; Domeier and Nasby-Lucas, 2013; Franks et al., 2021), leading to a potentially biased view of a populations' reproductive ecology and inappropriate conservation decision-making. This largely resulted from technological limitations that prevented assessment of reproductive status (e.g., mature, gravid, post-parturition) when interpreting movement studies, as the historical approach to studying this groups' reproduction relied on lethal sampling techniques (e.g., Hisaw and Albert, 1947; Zeiner and Wolf, 1993; Heupel and Simpfendorfer, 2010). However, given the conservation concern for an increasing number of elasmobranch species (Dulvy et al., 2021; Pacoureau et al., 2021), alternative non-lethal approaches have been developed in the last few decades to gather data on reproductive biology and to support management and conservation needs for this group (Hammerschlag and Sulikowski, 2011; Penfold and Wyffels, 2019; Sulikowski and Hammerschlag, 2023). For example, concentrations of reproductive hormones in plasma or muscle have been found to correlate to maturity and reproductive state (i.e., gravid or non-gravid, gestational stage) in many species (e.g., Awruch, 2013; Penfold and Wyffels, 2019). In general for female elasmobranchs, 17β-estradiol (E_2) has been related to vitellogenesis, progesterone (P_4) has been related to ovulation and early gestation, and T has been related to vitellogenesis as a precursor to E_2 production (e.g. Awruch, 2013). Additionally, ultrasonography offers an immediate determination of reproductive state (gravid or non-gravid) and can be combined with telemetry techniques to formally monitor the movements of confirmed gravid elasmobranchs through gestation (Anderson et al., In Press). To date, a handful of studies have directly monitored the movements of gravid elasmobranchs by combining ultrasound and telemetry, including studies on school sharks *Galeorhinus galeus* (McMillan et al., 2019), blue sharks (Fujinami et al., 2021), tiger sharks *Galeocerdo cuvier* (Smukal et al., 2022; Sulikowski and Hammerschlag, 2023), and a scalloped hammerhead *Sphyrna lewini* (Sulikowski and Hammerschlag, 2023).

The porbeagle is a large, pelagic, and endothermic shark species inhabiting cold-temperate waters of the Atlantic, south Pacific, and southern Indian Oceans (Francis et al., 2008). Once the target of a commercial pelagic longline fishery (Aesen, 1963; Campana et al., 2002), the Northwest (NW) Atlantic population is overfished and is captured as bycatch in numerous fisheries (rod-and-reel, trawl, gillnet, pelagic longline) within the region (i.e., Curtis et al., 2016). Population declines have led to the species being designated as Endangered in Canada (COSEWIC, 2004; COSEWIC, 2014) as well as the implementation of fishing regulations, including a live retention ban in Canada (Campana et al., 2015) and catch and minimum size limits in the United States (US) (NMFS, 2007; ICCAT, 2015). Due to their life history traits, population recovery is estimated to take 100 years (NOAA, 2023). In particular, NW Atlantic porbeagles have late ages at sexual maturity (8 and 13 years for males and females, respectively), long lifespans (up to 45 years in an unfished population), and low fecundity (Jensen et al. 2002; Natanson et al., 2002). Porbeagle reproduction is characterized by oophagy, mating is predicted to occur in September through November, and pupping of approximately 4 pups is predicted to occur in April through June after 8-9 months of gestation (Jensen et al., 2002). The population was originally thought to have an annual reproductive cycle (Jensen et al., 2002) but more recent data provided evidence of a biennial cycle (Natanson et al., 2019), which impacts the populations' productivity and predicted rate of recovery (Natanson et al., 2019). Given the conservation concern for the population and its' low reproductive output, identifying habitats used for reproduction could inform future conservation strategies to support population recovery.

The movement patterns and habitats used by gravid females as well as the potential use of discrete pupping grounds have yet to be formally assessed for the NW Atlantic porbeagle population. One previous study (Campana et al., 2010) deployed PSATs on 21 porbeagles in the NW Atlantic, including 11 mature females. Data from that work suggested mature females migrated south during the winter and early spring to the Sargasso Sea (Campana et al., 2010). At the time of that initial work, the NW Atlantic porbeagle population was believed to exhibit an annual reproductive cycle (Jensen et al., 2002). Thus, based on the timing and the disparity in movements between mature females and other life stages, Campana et al. (2010) suggested that the Sargasso Sea served as a pupping ground for this population. However, reproductive state (gravid, non-gravid) was not formally assessed for sharks tagged by Campana et al. (2010), and more recent data indicate that at least a portion of NW Atlantic porbeagles reproduce biennially (Natanson et al., 2019). Given these considerations, it is possible that migrations to the Sargasso Sea were not linked to parturition. To add clarity to the understanding of the reproductive ecology of NW Atlantic porbeagles, I used *in-situ* ultrasonography and reproductive hormone analysis to confirm pregnancy in porbeagles for the first time and then used a combination of satellite tagging technologies to observe the horizontal and vertical movements of gravid porbeagles throughout gestation. The specific objectives were to 1) preliminarily assess the use of reproductive hormone concentrations to predict pregnancy in porbeagles, 2) assess seasonal horizontal movement patterns of gravid porbeagles, 3) identify high use areas of gravid porbeagles during the expected pupping season, and 4) assess seasonal and diel vertical movement patterns of gravid porbeagles.

METHODS

Capture techniques.

Gravid porbeagles were targeted via rod-and-reel (following Anderson et al., 2021) southeast of Cape Cod, Massachusetts (MA), US in late October to early November in 2020 through 2022. Once captured, porbeagles were brought onboard the fishing vessel and a saltwater pump was immediately inserted into the shark's mouth to facilitate respiration. Sex, fork length (FL; cm) and/or total length (TL; cm), and capture location were recorded.

Reproductive assessments.

Female porbeagles near or above the size at maturity (210-230 cm FL; Jensen et al., 2002) were opportunistically examined for mating scars, characterized by teeth marks on pectoral fins or fresh lacerations on the body (Sulikowski et al., 2016). Ultrasonography was performed to determine the reproductive state of captured female porbeagles following Sulikowski and Hammerschlag (2023). An Ibex EVO II portable ultrasound (E.I Medical Imaging) with a 60 mm curved linear array 5-2.5 MHz transducer (model 290470) capable of a 24 cm scan depth was used to obtain images of the reproductive tract. Scanning was performed on the ventral surface from the pectoral to the pelvic fin in both a transverse and longitudinal orientation to obtain cross-sectional and lengthwise images of the uterus and ovary, respectively. Blood was also collected from a subset of individuals for reproductive hormone analysis (see Appendix C for details).

Tagging.

Gravid porbeagles were tagged with both a fin-mount satellite-linked transmitter (hereafter "fin-mount tag") and a pop-off satellite archival tag (PSAT). The fin-mount tag was either a Sirtrack K2F transmitter (Lotek Wireless; n = 4), Sirtrack F6F FastGPS Argos transmitter (Lotek Wireless; n = 2), Sirtrack K2F 176D dive transmitter (Lotek Wireless; n = 2), or SPOT 6 transmitter (Wildlife Computers; n = 2). The fin-mount tag was attached to the sharks' first dorsal fin following established protocols (Hammerschlag et al., 2012; Gibson et al., 2021). Additionally, a 365 d PSATFLEX (Lotek Wireless) was looped through a hole in the first dorsal fin of each shark following Anderson et al. (2021). PSATs were programmed to collect pressure (i.e., depth, hereafter referred to as depth) and ambient water temperature (°C) at 20 s intervals for the pre-programmed 365 d deployment period, after which the tag was designed to float to the sea surface and transmit archived data. Due to battery life and satellite throughput limitations, the full depth and temperature time-series at 20 s intervals are not transmitted by the tags following pop-off. Instead, a subset of the recorded time-series, in 2 h rather than 20 s intervals, is sent to the satellites. Daily light-based geolocation estimates were determined onboard the tag by manufacturer proprietary software and were based on the time of sunrise and sunset and noon and midnight (Ekstrom, 2004). PSATs were programmed to release prematurely if pressure remained constant (± 5 m) for 3 days, indicating a mortality or a shed tag floating at the sea surface or washed ashore.

Data processing & analyses.

For horizontal movement analyses, only data from fin-mount tags were used due to their higher location accuracy compared to PSATs. There were few reliable position estimates from light-based PSAT data, especially during the winter and spring, as many of the geolocation estimates during this time were in the southern hemisphere. In particular, PSAT-estimated latitudes ranged from 90.11°S to 89.41°N and longitudes ranged from 179.94°W to 179.61°E. Moreover, PSAT-estimated latitudinal error ranged from 0 to 67.04 degrees (mean ± SD = 12.08 ± 13.93 degrees) and longitudinal error ranged from 0 to 51.57 degrees (mean ± SD = 4.29 ± 5.52 degrees), making these data unsuitable for horizontal movement analyses. While the unusually high level of error in PSAT location estimates seems to be largely due to insufficient proprietary software, the deep diving behavior of porbeagles while in mesopelagic habitats likely contributed to a proportion of inaccurate and erroneous positions in each PSAT track (Campana et al., 2010; Heard et al., 2017). Fin-mount tag position estimates for up to one year after capture and release were used for horizontal movement analyses. This timeframe was used in order to (1) match fin-mount deployment lengths with programmed PSAT deployment lengths (2) assess one gestation period of movement, and (3) have relatively similar amounts of data among sharks, as only two fin-mount tags transmitted beyond one year after capture and release (shark 2 and 3).

Porbeagle position estimates from fin-mount tags were downloaded from Argos satellites (CLS America, Inc.). Argos provides location accuracy using the following location classes (LC): 3, 2, 1, 0, A, B, and Z (in decreasing accuracy; Figure C.1). These LCs are associated with the following error estimates: LC3 < 250 m, 250 m < LC2 < 500 m, 500 m < LC1 < 1500 m, and LC0 > 1500 m. Argos does not provide error estimates for LC A or B, but LC A and LC B have been found to be accurate to > 1 km and > 5 km radius, respectively (Tougaard et al., 2008). The lowest accuracy category transmissions (LC Z) are poor, unreliable location estimates and were removed from the dataset (<1% of transmissions). Due to irregular surfacing of sharks (and thus irregular transmission rates) and variation in satellite coverage at any given time, satellite tracking data often have large data gaps, and may also be subject to autocorrelation and spatial biases. Therefore, all fin-mount tag positional data were regularized and interpolated following an approach comparable to Hammerschlag et al. (2022). Specifically, using the R package ‘aniMotum’ (Jonsen et al., 2023), a continuous-time correlated random walk (CTCRW) state-space model (SSM), with a 2 m/s speed filter (per Skomal et al., 2021), was used to interpolate and regularize positional data along an estimated movement path of each shark. Data were regularized to daily position estimates. Since interpolating track sections with large temporal gaps increases uncertainty in the location estimates (Jonsen et al., 2023), I did not interpolate gaps in the data that exceeded 14 days (Figure C.2). Instead, full tracks with gaps exceeding 14 days were segmented into multiple sub-tracks prior to model fitting and interpolation was completed separately for each sub-track. This

14 d interval was chosen in an attempt to increase the number of location estimates in offshore habitats during winter and spring, as many data gaps >10 days were from offshore excursions during these seasons. Regularized and interpolated tracks were plotted using the R package ‘ggmap’ (Kahle and Wickham, 2013).

To further examine the habitat used by gravid porbeagles during the expected pupping season (April through June; Jensen et al., 2002), a kernel utilization distribution (KUD) was calculated from the interpolated positions during April through June using the ‘adehabitatHR’ R package with the “href” bandwidth estimator (Calenge, 2015). Kernel density estimates (KDEs) were used to quantify areas of higher and lower shark use within the KUD (Worton, 1989). Specifically, we calculated 95% and 50% density volume contours from the KDEs, with the 95% KDE volume contour representing low use areas and the 50% KDE volume contour representing high use areas.

To assess vertical movements from PSAT data, temperature-integrated diving tracks were plotted across the tag deployment period for each shark. Post-release recovery periods (e.g., Chapter 1; Chapter 2) were not assessed and removed in this chapter for two reasons. First, the two h interval depth data is not at a high enough resolution to assess recovery behavior, as porbeagles may make substantial dives in under two hours that would not be represented in the time-series. Second, daily maximum depth provided by the tags indicated that the shallowest maximum dive depth during the day of tagging and release was 42.5 m (shark 10), suggesting all sharks made relatively deep dives giving consideration for the bathymetry of the tagging locations. Taking into account the SSM-estimated location and the date, the R package ‘suncalc’ was used to determine the times of sunrise and sunset for daily positions and subsequently categorize

PSAT data into diel periods (day or night) (Thieurmel and Elmarhraoui, 2022). For days without a SSM position estimate, the most recent available position estimate was used to categorize the diel period. Data were also categorized into seasons as follows: winter: December-February, spring: March-May, summer: June-August, and fall: September-November. To assess seasonal and diel differences in the depth distribution of gravid porbeagles, PSAT time-series depth data were split into the following bins: 0-25 m, 25-50 m, 50-100 m, 100-200 m, 200-500 m, 500-1,000 m, 1,000-1,500 m, and 1,500-2,000 m. The proportions of time spent within each depth bin during the day and night and during each season were calculated for each shark. These proportional data were subsequently averaged across all sharks within each category (diel period, season) for plotting. Similarly, PSAT time-series temperature data were split into the following bins: 3-6°C, 6-9°C, 9-12°C, 12-15°C, 15-18°C, 18-21°C, 21-24°C, and 24-27°C. The proportions of time spent within each temperature bin during the day and night and during each season were calculated for each shark. These proportional data were subsequently averaged across all sharks within each category (diel period, season) for plotting.

Statistical analyses.

Linear mixed models (LMMs) with gaussian distributions were used to investigate the influence of diel period and season and their interaction on the depth use of gravid porbeagles. The response variable was either the log-transformed average depth (an indicator of overall depth preference) or the log-transformed standard deviation (SD) of depth (an indicator of vertical activity levels), where the raw depth data was used for calculating averages and standard deviations over each diel period (i.e., 2 averages and

SDs of depth per day per shark). Both response variables were log-transformed prior to model fitting to meet the assumption of normality. Additionally, the corAR1 function was used to account for temporal autocorrelation. Models were fitted using the R package ‘nmle’ (Pinheiro et al., 2022). Akaike information criterion (AIC) and backward selection were used to determine the most parsimonious model (Akaike, 1973).

RESULTS

Tag reporting & fate of tagged sharks.

Ten gravid porbeagles ranging in size from 229-272 cm TL were tagged southeast of Cape Cod, MA, US in late October of 2020 (n = 4) and 2022 (n = 6) during early gestation (Table 5.1). No gravid porbeagles were captured during 2021. Three gravid porbeagles did not survive the duration of the tag deployment. Tag ingestion or predation of shark 4 was suggested 148 days after tagging based on the depth and temperature data from the PSAT, which transmitted southwest of Bermuda on 03/29/2021 (Figure 5.1). Approximately 4 days before the tag floated to the sea surface, depth data showed continual ascending and descending in the water column while temperature increased by approximately 8°C above ambient and remained elevated at several hundred m depth, indicating tag ingestion, likely by another shark based on internal temperature (Figure 5.1; Kerstetter et al., 2004; Beguer-Pon et al., 2012; Cosgrove et al., 2015). However, the fin-mount tag for this shark failed to transmit messages after 40 days at liberty (12/05/2020), confounding our ability to infer whether the PSAT tag was ingested or the animal was predated upon. Based on fisherman reporting, shark 6 was caught in a monkfish gillnet set at approximately 113 m depth south of Cape Cod, MA on 03/27/2023, 154 days after tagging. Depth data suggested the shark was in the gillnet for approximately 48 hours before removal. Lastly, shark 7 died immediately upon release, as indicated by the tag sinking to the seafloor, remaining at depth for 15 days, the mortality release being triggered, and the fin-mount tag failing to transmit. This shark was foul hooked in the ventral surface and thus endured an extended fight time (47 min) on rod-and-reel. Data from this shark was not incorporated into movement analyses.

Fin-mount tags reported a total of 2,050 Argos locations, with most locations assigned a LC of B (28.9%), followed by 3 (17.9%), 2 (17.0%), and 0 (11.4%) (Figure C.1). Less than 1% of fin-mount tag locations were assigned a LC of Z (n = 4) and were removed from the dataset (Figure C.1). Overall, the number of days between successive fin-mount tag transmissions mostly ranged between 0-5 days (Figure C.2). However, all sharks had a large gap (>14 days; Figure C.2) in their fin-mount tag transmissions in late winter or early spring. The fin-mount tag attached to shark 4 transmitted too few locations (n = 1) before it was predated upon, and this shark was not included in horizontal movement analyses. Following the removal of the immediate mortality and the fin-mount tag with limited transmissions, track segments of varying durations were available for the 8 other gravid porbeagles for data regularization and interpolation with the SSM. The SSM produced a total of 1,115 position estimates for horizontal movement analyses. It is important to note that position estimates were not evenly distributed throughout the year; a large proportion of position estimates were during the summer (June-August; 44.8%) and relatively few were from February through April (7.4%) (Figure C.3).

Five of the PSATs transmitted after completing the entire programmed deployment period (365-days), while 4 others shed and transmitted prematurely, with these deployments ranging from 45 to 185 days in duration, and one PSAT failed to transmit altogether (shark 3). Premature tag transmissions were either due to mortality (sharks 4, 6, 7; described above) or tag shedding (shark 8). For unknown reasons, the PSAT data transmitted for shark 9 was limited to the first 19 days following capture and release, and the time-series of depth and temperature data was in 5 min intervals rather than the programmed 2 h intervals. Except for visualizations of the diving track time-series, data from this tag was not included in depth and temperature analyses in order to maintain relatively consistent data resolution and sample size across individuals.

Horizontal movements.

Tracks generated from regularized daily position estimates were concentrated on the northeastern US continental shelf (Figure 5.2) near Cape Cod, MA and on Georges Bank. Overall, based on SSM location estimates, gravid porbeagles occupied a latitudinal range of 38.7° to 43.6°N and a longitudinal range of 56.7° to 71.0°W (Figure 5.3). Based on these SSM location estimates, gravid porbeagles generally occupied lower latitudes in winter months (December-February) and higher latitudes in July through October (Figure 5.3A). While there were no clear seasonal shifts in occupied longitudes, the longitudinal range was greatest from February through June (Figure 5.3B).

The SSM position estimates identified instances of five of the gravid porbeagles (sharks 2, 5, 6, 8, and 10) entering and/or exiting mesopelagic habitats offshore of the continental shelf (Figure 5.2A). However, when combined with long-term PSAT depth data, it was apparent that at least seven of the gravid porbeagles (sharks 1, 2, 4, 5, 6, 8, and 10) migrated to mesopelagic habitats at some point during the winter and/or spring, as indicated by swimming depths >200 m (Figure 5.2B; Figure 5.4). Overall, these forays in mesopelagic habitat occurred in December through May (Figure 5.2B). Based on a combination of fin-mount tag and PSAT depth data, gravid porbeagles appeared to enter mesopelagic habitats between approximately December 16 (shark 6) and March 3 (shark 10) (Figure 5.2B; Figure 5.4) and return to continental shelf waters between March 6 (shark 6) and May 22 (shark 5) (Figure 5.2B; Figure 5.4). Time spent offshore in mesopelagic habitat ranged from approximately 71 (shark 2) to 98 days (shark 5).

Seven of the gravid porbeagles had regularized SSM location estimates (n = 309) during the expected pupping season (April through June; Jensen et al., 2002). Location estimates during the pupping season were also concentrated on the continental shelf of the northeastern US (Figure 5.5). In particular, most location estimates during the pupping season were in coastal waters southeast of Cape Cod, MA or on the western edge of Georges Bank, as indicated by the high use area (50% KDE volume contour; white polygon; Figure 5.5). However, a few tracks during the pupping season included return migrations from mesopelagic habitats into continental shelf waters during April (shark 2) or May (sharks 5 and 10), indicating these sharks spent at least of portion of the pupping season in mesopelagic habitats, as indicated by the low use area (95% KDE volume contour; black polygon; Figure 5.5).

Vertical & thermal habitat use.

Following the removal of data after mortalities or tag shedding, time-series of depths and ambient water temperatures were available from PSATs for periods ranging from 19 to 365 days. Collectively, gravid porbeagles exhibited a wide range of dive depths (Figure 5.4) from the sea surface to a maximum of 1,599 m by shark 2 (Table 5.2). Associated water temperatures ranged from a minimum of 3.6 (shark 5) to 25.0°C (shark

5; Table 5.2). Excluding shark 9, gravid porbeagles reached an average maximum depth of 1,136 ± 284 m (range = 912-1,599 m) during the tag deployments (Table 5.2). Collectively, tagged sharks spent approximately 73.1% of time in the epipelagic zone (0-200 m), 26.9% in the mesopelagic zone (200-1,000 m), and less than 1% of time deeper than 1,000 m.

There were clear shifts in depth distributions and diving patterns across seasons for gravid porbeagles. Gravid porbeagles exhibited a more restricted depth distribution during the summer and fall months when on the continental shelf (Figure 5.6) and displayed oscillatory ("yo-yo") diving between surface waters and approximately 100-200 m (Figure 5.4; Figure 5.7A). In comparison, when gravid porbeagles spent time in mesopelagic habitats during the winter and spring, they occupied deeper depths and exhibited diel vertical migration (Figure 5.4; Figure 5.6; Figure 5.7B). Accordingly, the maximum depth was shallower from June through November (46-338 m) and deeper from December through May (77-1599 m). When the time-series depth data were binned, gravid porbeagles spent the majority of time between 0-49.9 m during the summer (65.0% of time) and fall (77.1% of time). In comparison, they spent the majority of time between 25-99.9 m during the winter (56.0% of the time), and between 200-999.9 m during the spring (70.0% of time).

Diel differences in depth distributions were most apparent during the spring and winter (Figure 5.8). During the spring, gravid porbeagles spent the majority of the day at 500-999.9 m (57.3% of daytime), while the majority of the night was spent at 200-499.9 m (51.0% of nighttime) (Figure 5.8B). During the winter, most of the day was spent at either 50-99.9 m (40.4% of daytime) or 500-999.9 m (31.4% of daytime), while most of the night was spent at 25-100 m (59.3% of nighttime) (Figure 5.8A). The bimodal distribution of depths occupied in each diel period during the winter (Figure 5.8A) coincided with the transition from continental shelf waters to mesopelagic habitats during the winter for six (85.7%) out of seven sharks that had PSAT data during that time period (Figure 5.4). In comparison, while gravid porbeagles did spend more time at shallower depths during the night in the summer (Figure 5.8C) and fall (Figure 5.8D), diel patterns in depth distributions were not as clear as those for the spring and winter.

In terms of seasonal temperature distributions, gravid porbeagles overall spent more time at colder temperatures during the summer and winter and at warmer temperatures during the spring and fall (Figure 5.9). Gravid porbeagles spent the majority of time (i.e., > 50%) at temperatures between 6-11.9°C during the summer (64.9% of time) and winter (57.9% of time). During the fall, gravid porbeagles spent the majority of their time in water temperatures ranging from 12-14.9°C (52% of time). Gravid porbeagles exhibited less of a temperature preference during the spring, as they spent most of this season at temperatures between 6-20.9°C (60.8% of time), but also spent 23.8% of time at temperatures between 18-20.9°C. When split into early (March 1-April 15) and late (April 15-May 31) spring, most of the time spent at warmer temperatures was in the early spring (i.e., 30.8% of early spring was spent at 18-20.9°C whereas only 13.1% of late spring was spent in this temperature range). Conversely, most of the time at colder temperatures was in late spring (i.e., 27.9% of late spring was spent at 6-8.9°C whereas only 5.9% of early spring was spent in this temperature range). Diel differences in occupied water temperatures were most apparent during spring, followed by summer and winter (Figure 5.8). During these seasons, gravid porbeagles spent more time at warmer temperatures during the night and more time at colder temperatures during the day (Figure 5.8). In comparison, there were minimal diel differences in occupied water temperatures during the fall, with gravid porbeagles displaying approximately equal affinity for 12-14.9°C during both day (53.1% of daytime) and night (53.9% of nighttime; Figure 5.8D).

The gravid porbeagles tagged in this study were expected to give birth during the previously reported pupping season (April through June; Jensen et al., 2002) based on ultrasonography at the time of tagging. PSAT depth and temperature data were available during the pupping season (April through June; Jensen et al., 2002) for 5 of the gravid porbeagles. At the start of the pupping season, these porbeagles were occupying mesopelagic habitats and were diving between approximately 100-200 m during the night and 500-1,000 m during the day (Figure 5.10). However, all of these gravid porbeagles appeared to return to continental shelf waters and transitioned to shelf-restricted oscillatory ("yo-yo") diving between the surface and approximately 100-200 m at some point in the pupping season (Figure 5.10). Based on the PSAT depth data, the transition to shallow oscillatory diving occurred between mid-April to mid-May for these sharks (Figure 5.10).

Linear mixed models.

The most parsimonious model of log average depth for gravid porbeagles included the fixed effects of both diel period and season, as well as their interaction (Table 5.3). Average depth was deeper during the day than night for each season. Additionally, average depth was deeper during the winter and spring than during the summer and fall. For the response variable of log SD of depth, the most parsimonious model also included the fixed effects of both diel period and season, as well as their interaction (Table 5.3). SD of depth was greater during the night than day in the winter and spring but not in the summer and fall. Additionally, daily SD of depth was overall greater during the winter and spring than during the summer and fall for both diel periods.

DISCUSSION

Movement patterns of tagged gravid porbeagles.

This study presents the first observations of horizontal and vertical movements of confirmed gravid porbeagles during the gestation and presumed pupping seasons. Although horizontal tracking data were limited, all gravid porbeagles appeared to exhibit seasonal patterns in their movements, occupying deeper mesopelagic habitats during late winter and early spring and returning to shallower continental shelf waters thereafter. While on continental shelf waters, gravid porbeagles vertical movements were characterized as oscillatory “yo-yo” diving between the surface and 100-200 m. Alternatively, while in mesopelagic habitats, gravid porbeagles exhibited diel vertical migration, preferring to remain at approximately 100-200 m during the night and 500-1,000 m during the day.

Collectively, during early gestation (October through December), gravid porbeagles appeared to remain near the tagging site in continental shelf waters surrounding Cape Cod, MA. Diving behavior during early gestation was characterized by oscillatory “yo-yo” diving between surface waters and approximately 100-200 m, with relatively minimal diel differences in depth or ambient water temperatures occupied. During mid- to late-gestation (January through March), gravid porbeagles migrated offshore to mesopelagic habitats and transitioned their diving patterns to diel vertical migration. In particular, gravid porbeagles spent their nights at shallower depths (approximately 100-200 m) and warmer temperatures (approximately 15-21°C) and their days at deeper depths (approximately 500-1,000 m) and colder temperatures (approximately 6-15°C). While one gravid porbeagle (shark 6) had already migrated back to the continental shelf during early March before it was caught in a gillnet and died, all other gravid porbeagles appeared to return to shelf waters in April through May, during the expected pupping season (April through June; Jensen et al., 2002), providing support for the hypothesis that pupping occurs on the continental shelf for this population. Accordingly, diving behavior during the pupping season was split between diel vertical migration in the mesopelagic zone and shallow oscillatory diving when they returned to shelf waters.

Overall, the seasonal movement patterns observed here are not unique to the gravid life stage in the NW Atlantic. Seasonal southward migrations have been documented in YOY (Chapter 3), larger juvenile (Skomal et al., 2021; Chapter 3 and 4), and to a lesser extent mature male (Campana et al., 2010; Chapter 4) life stages during late fall or winter in the NW Atlantic. Moreover, similar to the gravid porbeagles tagged in this study, YOY (Chapter 3) and larger juvenile (Skomal et al., 2021) porbeagles exhibited transitions in diving when occupying mesopelagic environments, in which they initiated submergence behavior and occupied deeper depths overall. While tag durations limited the ability to observe movements of YOY (Chapter 3) and mature males (Campana et al., 2010) year-round, larger juveniles moved back into continental shelf waters in the summer (Skomal et al., 2021).

Potential ecological factors related to movement patterns.

Foraging (and the distribution of prey) is considered one of the primary drivers of shark movement patterns (e.g., Hammerschlag et al., 2012; Andrzejaczek et al., 2019; Braun et al., 2023), and has been suggested as a factor influencing the seasonal horizontal and vertical movements of other life stages of porbeagles in previous work (Saunders et al., 2011; Francis et al., 2015; Skomal et al., 2021; Chapter 3). The migrations of gravid porbeagles into mesopelagic habitat and transitions to diel vertical migration during late winter and/or early spring could have similarly been related to foraging. For example, oophagy is likely associated with relatively high maternal energetic demands (Gilmore et al., 2005; Chapman et al., 2013) that would require a large quantity of food resources to meet. During the time when gravid porbeagles migrated offshore in this study, the proportion of cephalopods and pelagic teleosts in the diet of large (>200 cm) NW Atlantic porbeagles has been shown to increase (Joyce et al., 2002). Species within these pelagic prey groups are known to migrate to and/or overwinter in offshore habitats within the NW Atlantic (e.g., Hendrickson, 2004; Van Beveren et al., 2023). Gravid porbeagles tagged in this study may therefore have migrated offshore and exhibited diel vertical migration in order to follow the seasonal horizontal and vertical movement patterns of pelagic prey (e.g., Atlantic herring *Clupea harengus*, Atlantic mackerel *Somber scombrus*, and cephalopods; Joyce et al., 2002), as has been suggested for porbeagles of other life history stages in previous work (Saunders et al., 2011; Francis et al., 2015; Skomal et al., 2021; Chapter 3).

Thermal requirements may also have influenced the migration of gravid porbeagles. Although porbeagles are regionally endothermic and thus can maintain warmer internal temperatures relative to ambient water (Carey et al., 1985), they still have a thermal tolerance range. For several of the tagged gravid porbeagles, the ambient water temperatures in the weeks prior to migrating offshore fell within the lower limits of the thermal range observed in this study and were similar to the lower range of occupied water temperatures in previous studies on this species (Carey et al., 1985; Campana et al., 2010; Skomal et al., 2021). Therefore, gravid porbeagles tagged in this study may have been seeking warmer habitats. If this is indeed the case, one possible reason for this observed behavior would be to use these warmer waters during pregnancy to accelerate embryonic development and gestation (e.g., Nosal et al., 2014; Sulikowski et al., 2016; Nosal et al., 2021). However, gravid porbeagles also exhibited submergence behavior in which they no longer frequented the sea surface while offshore. Previous studies on porbeagles have found similar submergence behavior in juveniles and mature females of unknown reproductive states and suggested this was likely related to the avoidance of excessively warm surface waters (Campana et al., 2010; Skomal et al., 2021; Chapter 2). Given these considerations, gravid porbeagles may have been seeking more optimal thermal conditions for gestation while migrating offshore, preferring to remain within warmer waters than those on the continental shelf during the winter and spring, but at the same time avoiding excessively warm surface waters. While direct comparisons between gravid sharks is limited, gravid blue sharks have been shown to initiate deep diel vertical migration in locations with warm surface waters, a strategy suggested to preserve energy for embryonic development and seasonal migrations (Fujinami et al., 2021). However, further work is needed to understand the potential thermal influence on this behavior in gravid porbeagles, as this is the first study to observe movements of endothermic, oophagous sharks that were confirmed to be gravid.

Pupping location hypothesis.

Campana et al. (2010) deployed 11 PSATs on mature female porbeagles in the NW Atlantic and PSATs popped off these sharks in the Sargasso Sea between February 28 and May 6. Based on the timing and location of PSAT pop-offs, Campana et al. (2010) suggested NW Atlantic porbeagles give birth in the Sargasso Sea. However, unlike in this study, these sharks were not formally assessed to confirm pregnancy and the tag deployments did not encompass the entire expected pupping season. Pupping in the Sargasso Sea would require gravid porbeagles to migrate approximately 2,000 km to give birth (i.e., mature females porbeagles tagged by Campana et al. (2010) migrated approximately 1,500-2,400 km between tagging and pop-off locations in the Sargasso Sea), and then both the YOY and post-partum females would need to migrate back to the continental shelf within days to months after parturition, as both groups are known to be inhabiting this region by spring to early summer (Jensen et al., 2002; Anderson et al., 2021; Chapter 3; the current study; NMFS, unpublished data provided by L. Natanson and N. Kohler). The energetic costs that would be associated with such a long-distance dispersal would be high for neonate sharks (McMillan et al., 2021), and the metabolic and evolutionary benefit of pupping in the Sargasso Sea has always been unclear (Campana et al., 2010). The confirmed gravid porbeagles tagged in this study did not appear to migrate as far south in the Sargasso Sea, although it's important to note that fin-mount tag data was limited during late February through April and thus could have overlooked such movements.

Gravid porbeagles migrated back into continental shelf waters before or during the expected pupping season in this study. In fact, the majority of the location estimates during the pupping season were in waters southeast of Cape Cod, MA and on the western edges of Georges Bank, corresponding with the high use area (50% KDE) identified by the KUD. During this time, gravid porbeagles transitioned to relatively shallow oscillatory diving between the sea surface and approximately 100-200 m depth. However, it’s important to consider that there were not distinct indications of parturition events in the tag data and the horizontal and vertical movement behaviors of these gravid females have been observed in other life stages in the region (i.e., Skomal et al., 2021; Chapter 3; Chapter 4). These considerations challenge the applicability of movement data from tagging to refine the understanding of when and where pupping occurs during the pupping season. Although the exact locations of parturition cannot be determined with data from this study (Sulikowski and Hammerschlag, 2023), I hypothesize that these porbeagles likely gave birth in continental shelf waters around Cape Cod, MA. This hypothesis is supported by the occurrence of young-of-the-year (YOY) porbeagles in nearshore waters of the northeastern US by mid-June (Anderson et al., 2021; Chapter 3; NMFS, unpublished data provided by L. Natanson and N. Kohler). Moreover, YOY porbeagles that were tagged in the NW Atlantic spent 62.2% of their time in the top 10 m of the water column and spent less than 2% of their time deeper than 100 m during the summer (Chapter 3). This further supports the hypothesis that NW Atlantic porbeagles are more likely to give birth in shallower continental shelf waters that would provide the most suitable environmental conditions for their neonates. Gravid blue sharks have also been found to transition from mesopelagic to epipelagic diving during the pupping season

(Fujinami et al., 2019) and were predicted to do so in order to give birth in physiologically optimal temperatures for their neonates (Nosal et al., 2019).

The reason for the differences in horizontal movement patterns between the gravid porbeagles tagged in this study and the mature females tagged by Campana et al. (2010) is uncertain, but could indicate the sharks tagged by Campana et al. (2010) were migrating to the southern Sargasso Sea for purposes unrelated to reproduction (e.g., foraging). Similar offshore movements observed in juvenile life stages further support the notion that southward migrations may not be related to parturition in NW Atlantic porbeagles (Skomal et al., 2021; Chapter 3), although it's important to note that similar movement patterns may be linked to multiple ecological functions. However, it is also possible that there are behavioral differences between the two tagging groups, as gravid sharks were tagged southeast of Cape Cod, MA in this study while sharks were tagged on Georges Bank and the Scotian Shelf in Campana et al. (2010). Partial migration, in which some females migrate to give birth while others remain near aggregation sites, has been documented in school sharks (McMillan et al., 2019) and blacktip reef sharks *Carcharhinus melanopterus* (Mourier and Planes, 2012) and needs to be further evaluated for porbeagles. Moreover, recent work suggests that a related lamnid, the shortfin mako, likely pups along the entire eastern coast of North America (Natanson et al. 2020), and thus it is possible that this family of sharks may not give birth in discrete pupping grounds.

Despite the differences in horizontal movements, general diving patterns were similar between the gravid porbeagles tagged in this study and the mature females tagged by Campana et al. (2010). Additionally, temperature ranges occupied by mature female porbeagles were also similar between this study and Campana et al. (2010). In particular, sharks tagged by Campana et al. (2010) also occupied relatively shallow depths (<250 m) and had weakly diurnal diving patterns during the fall yet transitioned to deeper depths and exhibited diel vertical migration in the winter and early spring. While the gravid females tagged in the current study transitioned back to shallow depths of the continental shelf during the early to mid-pupping season, the mature females tagged by Campana et al. (2010) were still occupying deeper mesopelagic depths in the Sargasso Sea in mid-February through early May.

Limitations.

The biggest limitation of this study was the sparsity of usable horizontal movement data during a critical period of the reproductive cycle (mid- to late-gestation). Fin-mount tags failed to transmit on a regular basis and PSAT light-based geolocation data were highly erroneous during this timeframe, with the available estimation model from Lotek putting gravid females in the southern hemisphere and having positional errors of tens of degrees latitude. Based on PSAT depth data and fin-mount tag data before and after this period, it is clear that gravid porbeagles were offshore in mesopelagic habitats during most of this timeframe. The lack of usable horizontal data during offshore migrations appears to be partially due to submergence behavior of gravid porbeagles, in which they did not regularly occupy surface waters. Similar submergence behavior was documented by mature females (Campana et al., 2010) as well as juveniles (Skomal et al., 2021; Chapter 3) while in mesopelagic environments. This submergence behavior would prevent fin-mount tags from transmitting altogether (Winship et al.,

2012) and would reduce the accuracy of light-level-based estimates of sunrise and sunrise needed to approximate PSAT geolocation (Braun et al., 2018).

Given these data limitations, the extent of gravid porbeagles' migrations within mesopelagic habitats is currently unknown from the analyses completed in this study. This represents a major challenge to understanding movement patterns during the entire pupping season, as these offshore movements overlapped with the beginning of the pupping season for many of these tagged sharks. A future direction to overcome this data limitation would be to use depth and temperature profiles recorded by the tags to improve the light-based estimates of geolocation (Braun et al., 2018). For example, Braun et al. (2018) developed a hidden Markov model approach for PSATs deployed on animals which exhibit diving behaviors comparable to the gravid porbeagles tagged in this study. This hidden Markov model uses depth and temperature data collected from the PSAT in comparison to open-source oceanographic data in order to improve the accuracy of light-based geolocation estimates six-fold (Braun et al., 2018). While public use of the model's R package is currently limited due to further development, this approach could be used in the near future to model the existing gravid porbeagle PSAT geolocation data and subsequently improve the understanding of their offshore migrations during mid- to late-gestation.

Conservation & management implications.

This study provides the first formal data on the habitat use of gravid porbeagles in the NW Atlantic that can be used to support conservation and management decisions for the population. Although the sample size was limited to a small number of individuals tagged in a small geographic portion of the populations range, this work has implications for the management of porbeagles in the US. For example, gravid porbeagle location estimates in this study were concentrated in continental shelf waters of the northeastern US, particularly around Cape Cod, MA and Georges Bank, for the majority of the gestation and pupping periods, implying increased protection from fisheries for porbeagle in these areas would protect gravid females as well as the next generation of individuals entering the population. The documented gillnet mortality that occurred south of Cape Cod, MA for one of the gravid porbeagles tagged in this study just before the pupping season further highlights the need for conservation measures for this important life stage.

CONCLUSION

Ecology and physiology have historically been seen as distinct fields of study for elasmobranchs, yet reproduction lies at the intersection of these disciplines (Lyons et al., 2019) and protecting reproductive habitats is important for conservation and management purposes (Sulikowski et al., 2016; Sulikowski and Hammerschlag, 2023; Anderson et al., In Press). A limited number of studies have directly assessed the reproductive ecology of elasmobranchs; particularly limited are assessments of the habitats used for gestation and/or parturition (e.g., Sulikowski et al., 2016; McMillan et al., 2019; Fujinami et al., 2021; Sulikowski and Hammerschlag, 2023), largely due to the very recent development of non-lethal methodologies to study elasmobranch reproduction (Hammerschlag and Sulikowski, 2011; Anderson et al., In Press). This study adds to the limited body of research identifying the movement patterns of elasmobranchs that were formally assessed for reproductive state and confirmed to be gravid, and is the first to do so for a lamnid shark species. Gravid porbeagles exhibited a seasonal southward migration during mid- to late-gestation and returned to shallow continental shelf waters before or during the expected pupping season (April through June). These findings challenge the previous assumptions regarding porbeagle pupping grounds in the NW Atlantic (Campana et al., 2010) and suggest that at least some individuals within this population likely give birth in continental shelf waters of the northeastern US. However, it is important to note that the precise identification of pupping sites was not possible in this study. Newly developed intrauterine satellite-linked transmitters would need to be deployed to identify the exact timing and location of parturition for individuals (Sulikowski and Hammerschlag, 2023), and to help determine if there are specific movement characteristics (e.g. diving behavior patterns) that are associated with pupping events. This would be a natural next step for future work. Nevertheless, the observed importance of continental shelf waters around Cape Cod, MA and Georges Bank to the gravid porbeagles in this study support a shift in conservations directions away from the Sargasso Sea (Campana et al., 2010) and toward coastal habitats in order to protect gravid and neonate porbeagles in the NW Atlantic.

Table 5.1

Summary information for 10 gravid porbeagles tagged in the NW Atlantic. PSAT = pop-off satellite archival tag, FL = fork length, TL = total length, SSM = state space model. * indicates a shark that died during the tag deployment. [a] indicates a tag that did not transmit.

Shark	**Fin-mount ID**	**PSAT ID**	**FL (cm)**	**TL (cm)**	**Tag Lat**	**Tag Lon**	**Date Tagged**	**Days of PSAT Data**	**SSM Days**
1	207871	203524	-	256	41.43	-69.42	10/27/2020	333	87
2	175785	203525	226	260	41.41	-69.42	10/27/2020	339	267
3	175430	206992[a]	243	263	41.43	-69.42	10/28/2020	0	199
4*	207870	206996	223	259	41.43	-69.43	10/28/2020	153	0
5	234532	203527	-	244	41.44	-69.47	10/24/2022	359	168
6*	234533	203520	196.6	229	41.30	-69.41	10/25/2022	147	16
7*	175434[a]	203518	239	272	41.34	-69.39	10/26/2022	15	0
8	175783	198749	225	262	41.34	-69.38	10/26/2022	181	97
9	228332	33352	233	272	41.34	-69.37	10/27/2022	19	104
10	175782	228318	225	262	41.35	-69.36	10/27/2022	343	177

Table 5.2

Summary results of the depth and ambient water temperature data recorded by the pop-off satellite archival tags deployed on gravid porbeagles. Maximum depth was rounded to the nearest m and minimum and maximum temperature and temperature range to the nearest 0.1°C. * indicates a shark that died immediately after release. [a] indicates a shark whose PSAT failed to transmit data. [b] indicates a tag that transmitted a 19-day, 5-min interval time-series.

Shark	**Max depth (m)**	**Mean ± SD depth (m)**	**Min temp (°C)**	**Max temp (°C)**	**Temp range (°C)**
1	912	147 ± 220	5.7	22.7	17.0
2	1,599	147 ± 226	4.4	19.9	15.5
3[a]	-	-	-	-	-
4	1,116	252 ± 230	6.2	22.9	16.7
5	931	174 ± 249	3.6	25.0	21.4
6	1,471	273 ± 266	4.9	21.4	16.5
7*	-	-	-	-	-
8	1,004	267 ± 289	4.6	23.4	18.8
9[b]	110	38 ± 18	8.5	15.8	7.3
10	917	141 ± 230	4.9	22.2	17.3

Table 5.3

Comparisons of models of the influence of diel period and season and their interaction on the depth use of gravid porbeagles (n = 7) using Akaike's Information Criterion (AIC). ∆AIC indicates difference between AIC scores and top-ranked model. All models are \linear mixed models with shark identity as a random variable and incorporate temporal autocorrelation. Mean depth (m) and standard deviation (SD) of depth (m) were both log-transformed prior to analysis to meet assumptions of normality. The top ranked model is shown in bold.

Model	**DF**	**AIC**	**∆AIC**
1. Mean depth ~ diel period*season	3559	7978.018	
Mean depth ~ diel period + season	3562	8379.428	401.41
Mean depth ~ diel period	3565	8704.559	726.541
Mean depth ~ season	3563	9586.833	1608.815
Mean depth ~ 1	3566	10086.56	2108.542
2. SD of depth ~ diel period*season	3559	9187.967	
SD of depth ~ diel period + season	3562	9327.172	139.205
SD of depth ~ season	3563	9373.467	185.5
SD of depth ~ diel period	3565	9753.556	565.589
SD of depth ~ 1	3566	9808.147	620.18

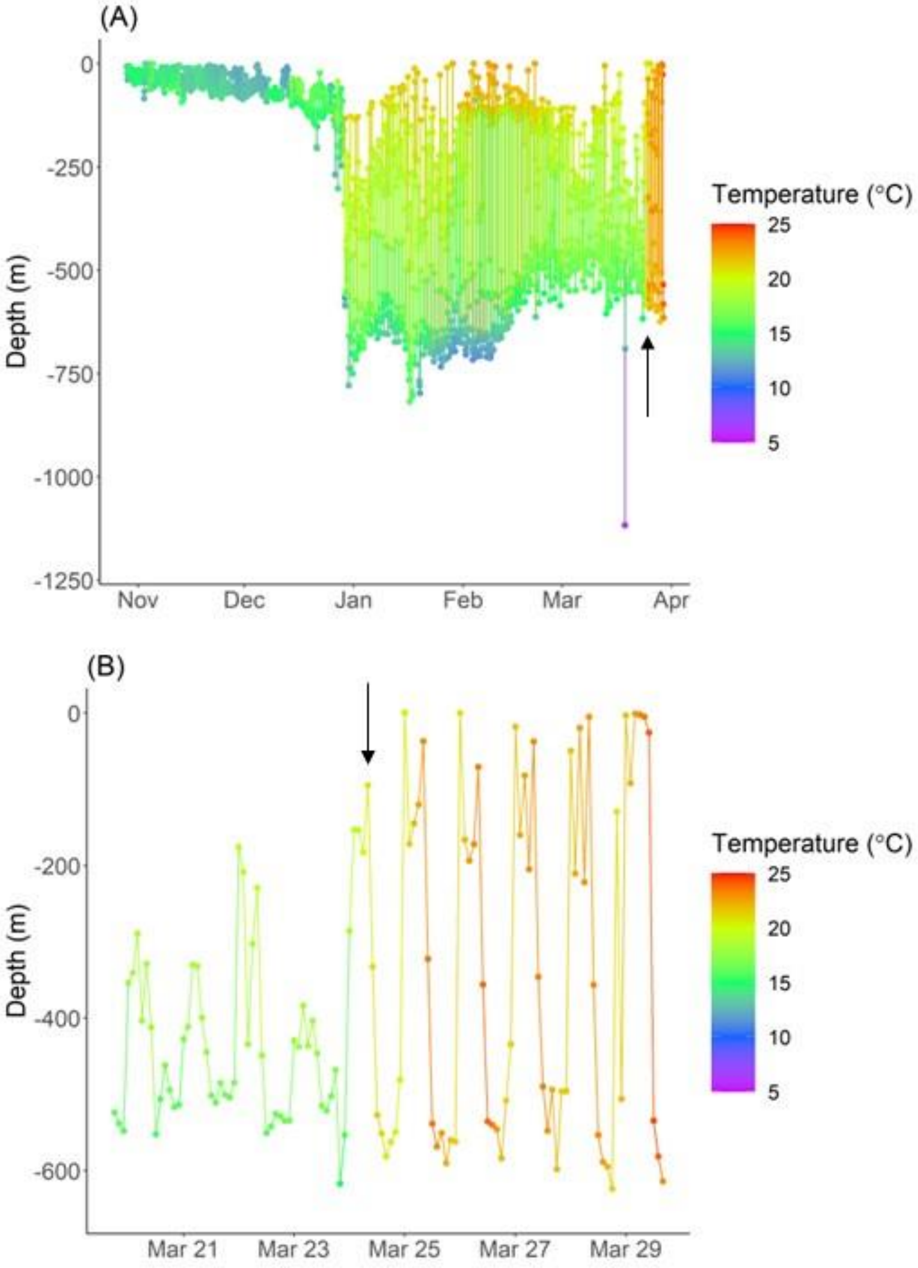


Figure 5.1. Pop-off satellite archival tag time-series plots of temperature-integrated dive profiles for shark 4. Plot (A) shows the entire time-series and plot (B) shows the final week of the time-series where predation was evident on March 24. Black arrows point to estimated time of the predation event.

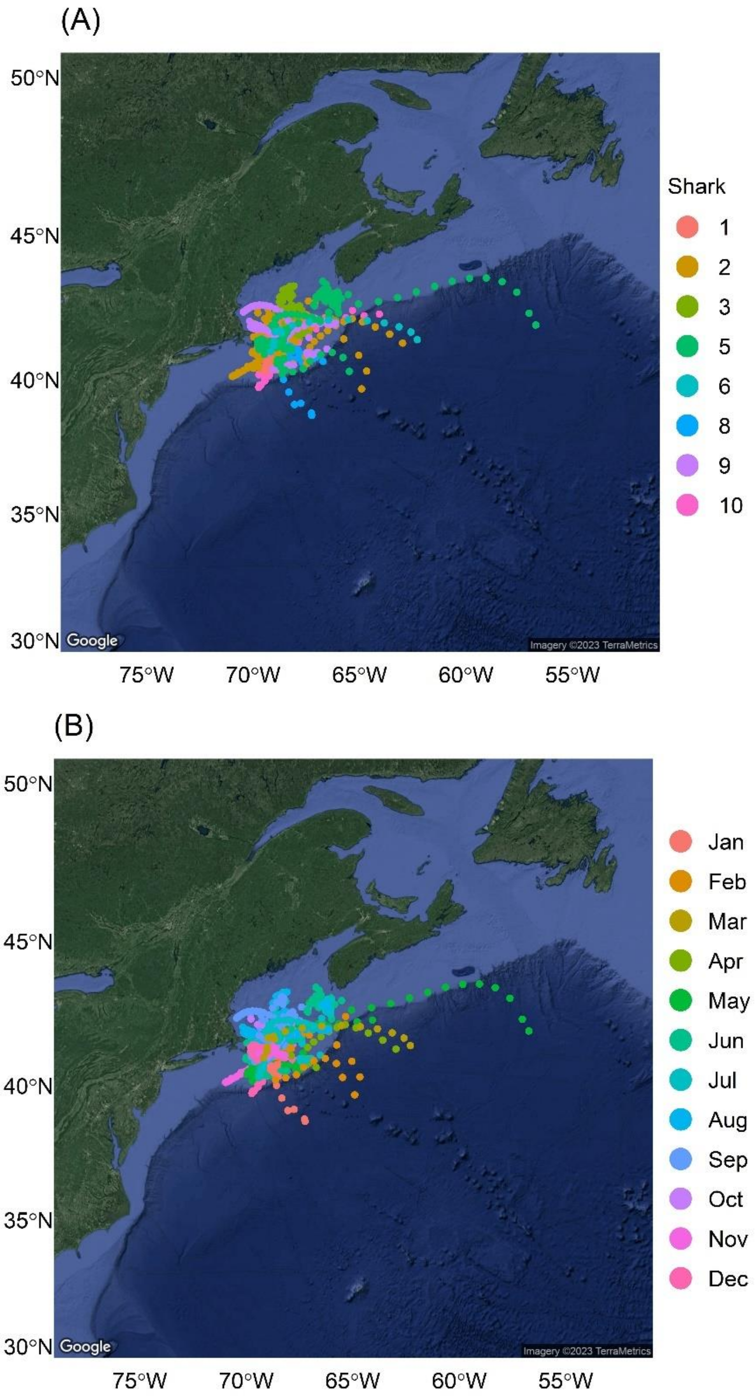


Figure 5.2. Maps of regularized state space model location estimates (R package ‘aniMotum’; Jonsen et al., 2023) from fin-mount tags deployed on gravid porbeagles (n = 8) in the Northwest Atlantic, color coded by (A) shark ID or (B) month of the year.

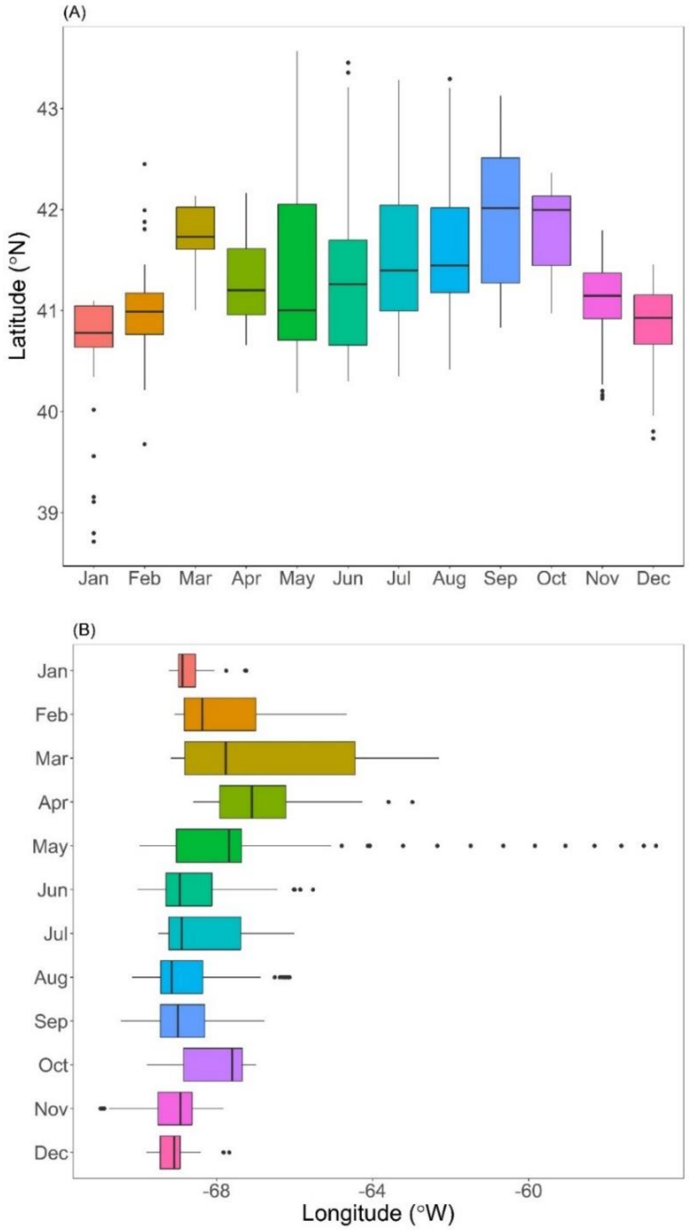


Figure 5.3. Monthly latitudinal (A) and longitudinal (B) distribution for regularized state space model location estimates (R package 'aniMotum'; Jonsen et al. 2023) from fin-mount tags deployed on gravid porbeagles (n = 8) in the Northwest Atlantic. Circles represent outliers (values more extreme than 1.5*interquartile range on either end of the box). Colors represent month of the year and correspond with monthly colors from Figure 2B.

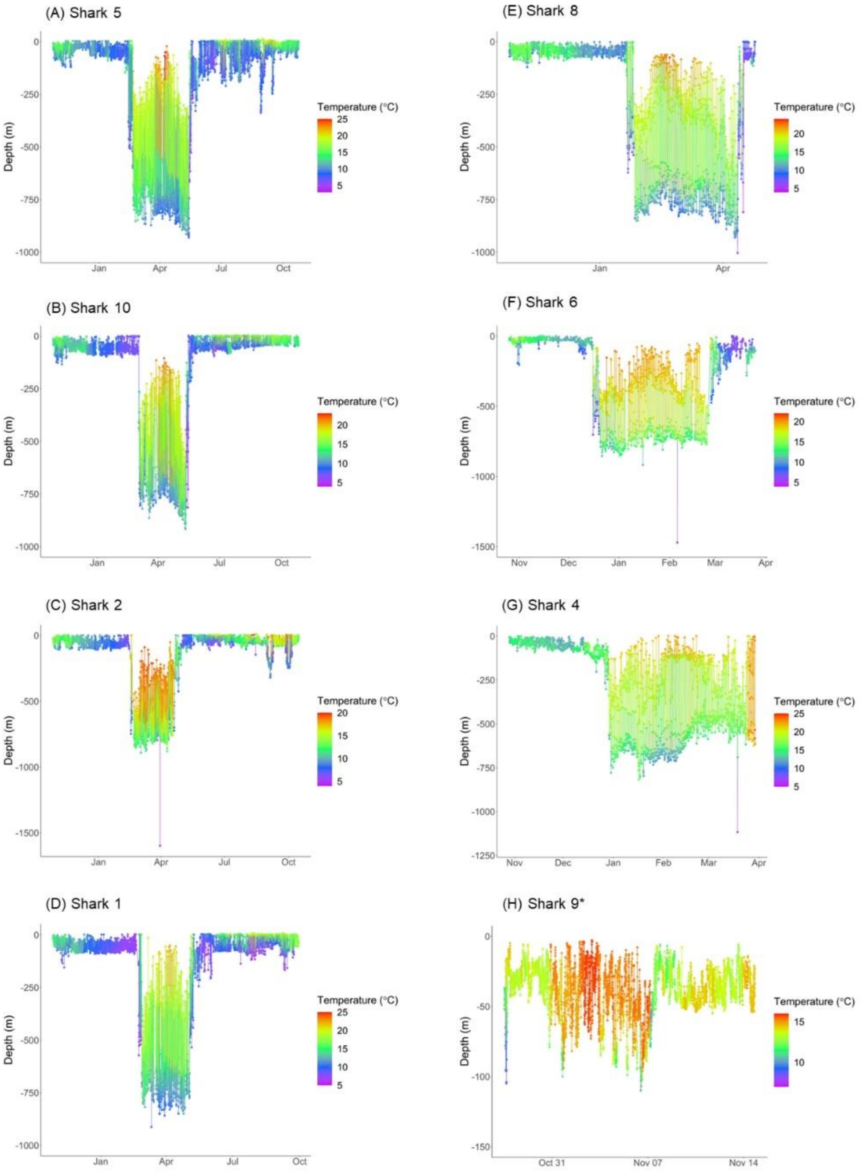


Figure 5.4. Temperature-integrated diving time-series from pop-off satellite archival tags deployed on gravid porbeagles (n = 8) in the Northwest Atlantic. Note the plots have different axis and legend scales to reflect the range in available deployment dates and depths and temperatures occupied by each individual. Plots are ordered by deployment durations, from longest to shortest. * indicates the tag that transmitted in 5-min intervals for 19 days (shark 9 (H)) rather than the programmed 2-h intervals for 365 days.

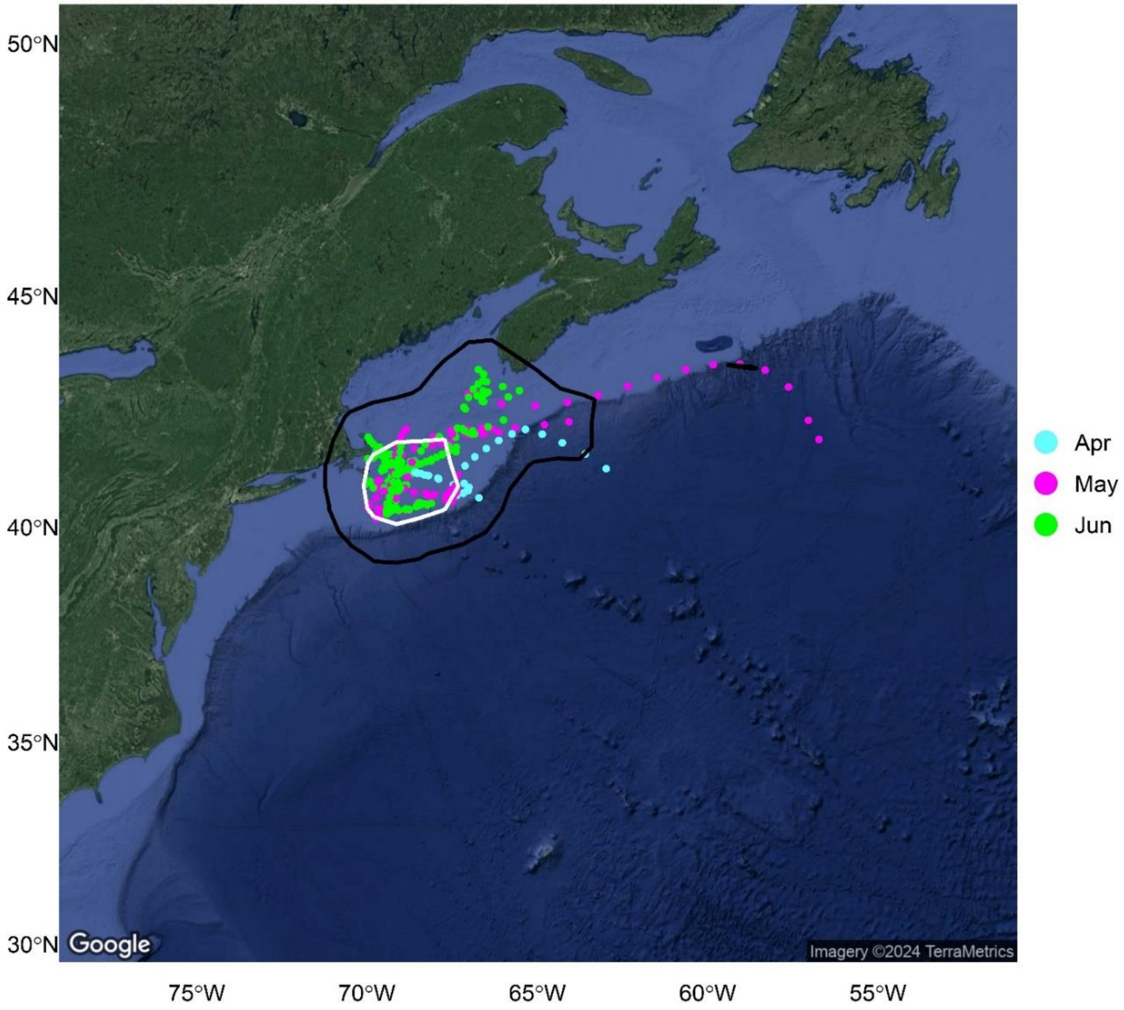


Figure 5.5. Map of the 95% (black outer polygon) and 50% (white inner polygon) kernel density estimates and regularized state space model location estimates (points; R package 'aniMotum'; Jonsen et al., 2023) from fin-mount tags deployed on gravid porbeagles (n = 7) in the Northwest Atlantic during the expected pupping season (April through June; Jensen et al. 2002). Position estimate points are color coded by month.

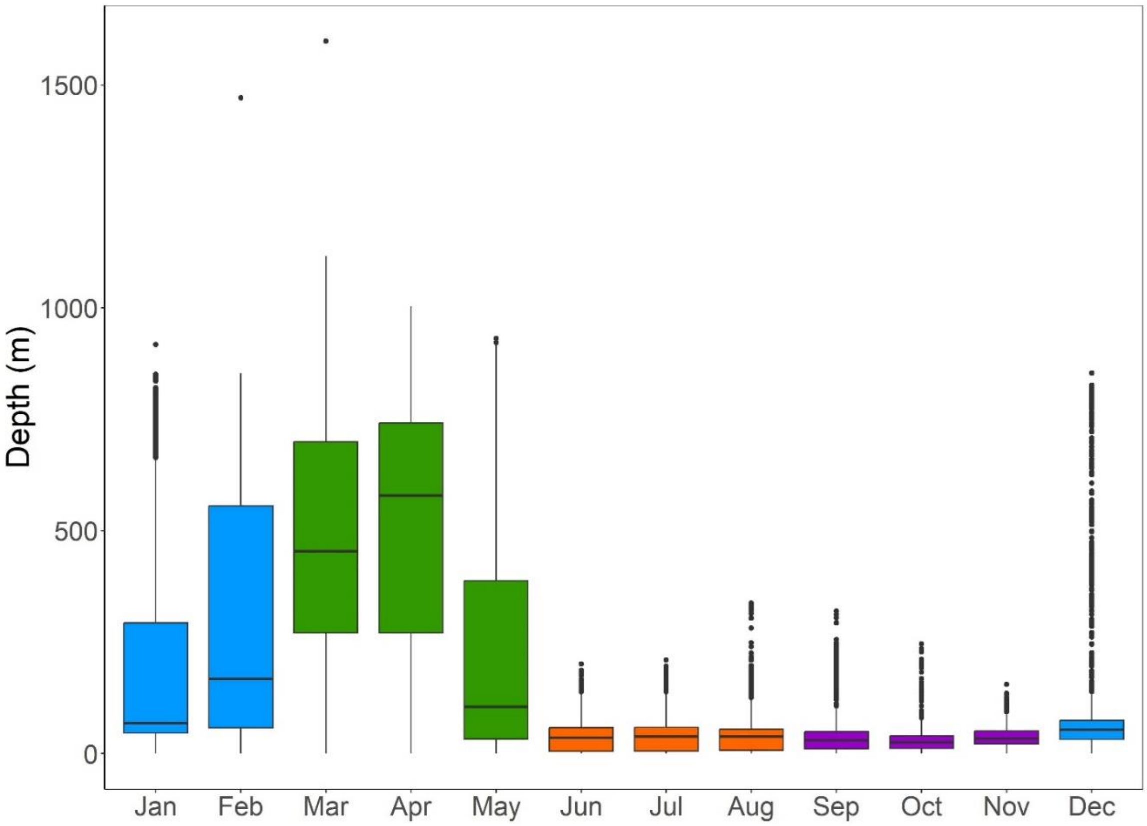


Figure 5.6. Boxplots of depths (m) occupied by gravid porbeagles (n = 7) during each month based on data from pop-off satellite archival tags. The circles represent outliers (values more extreme than 1.5*interquartile range on either end of the box). The color of the box represents the season, where winter is blue, spring is green, summer is orange, and fall is purple.

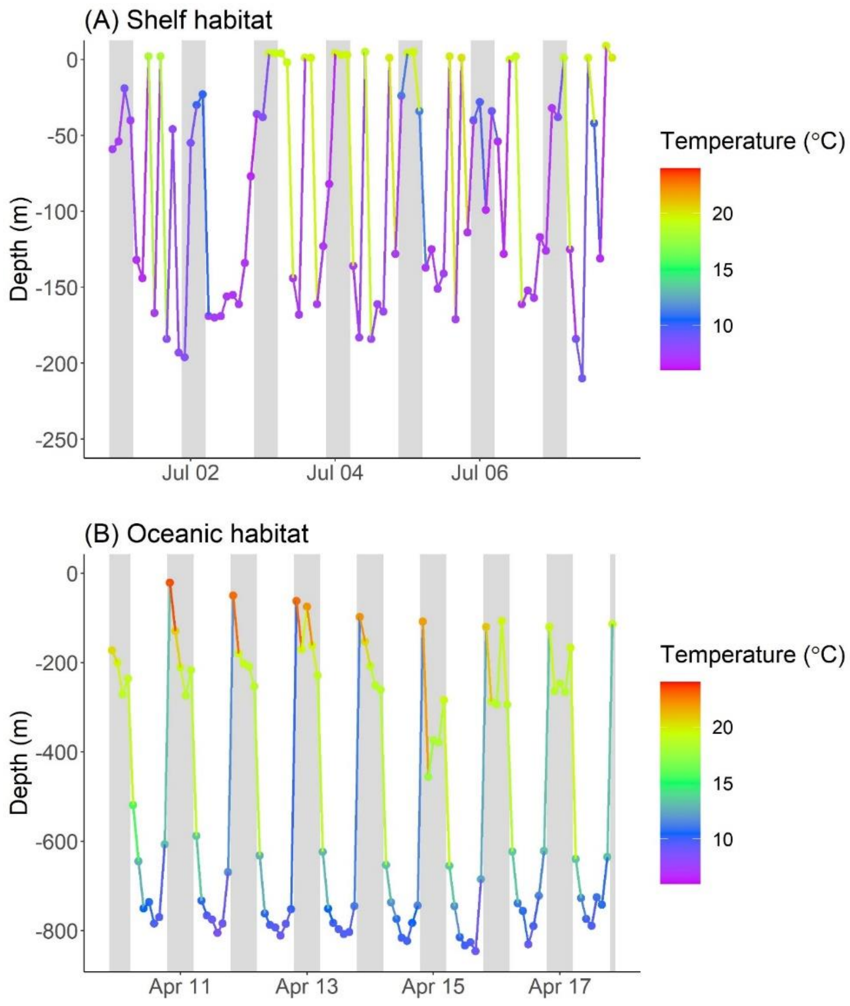
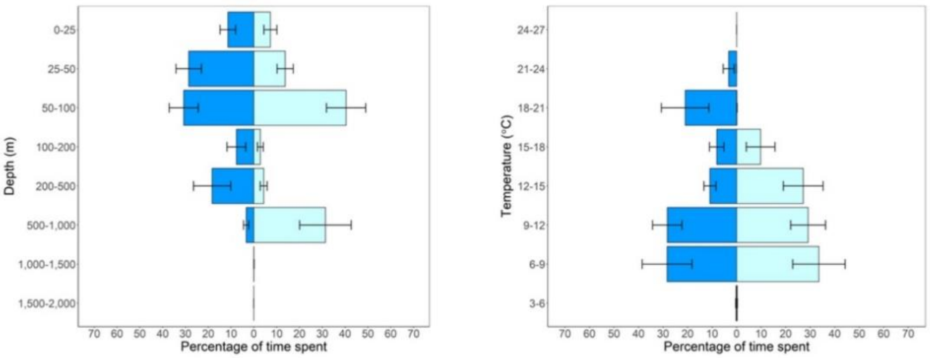
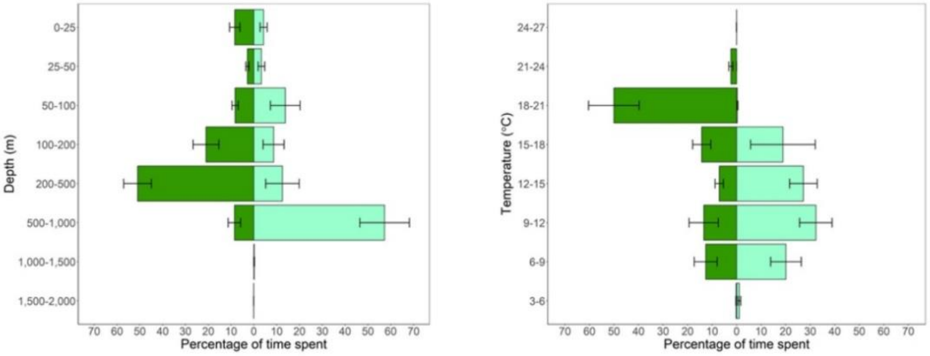


Figure 5.7. Example week-long time-series plots of depth and ambient water temperature data from the pop-off satellite archival tag deployed on shark 5 showing representative differences in the diving behavior of gravid porbeagles based on habitat. (A) shows shallow oscillatory “yo-yo” diving in continental shelf habitat and (B) shows deep diel vertical migration in oceanic habitat. Note the differences in the scales of axes (dates and depth ranges) between the two plots, with (A) showing diving between approximately 0 and 250 m in early July and (B) showing diving between approximately 0 and 825 m in mid-April.

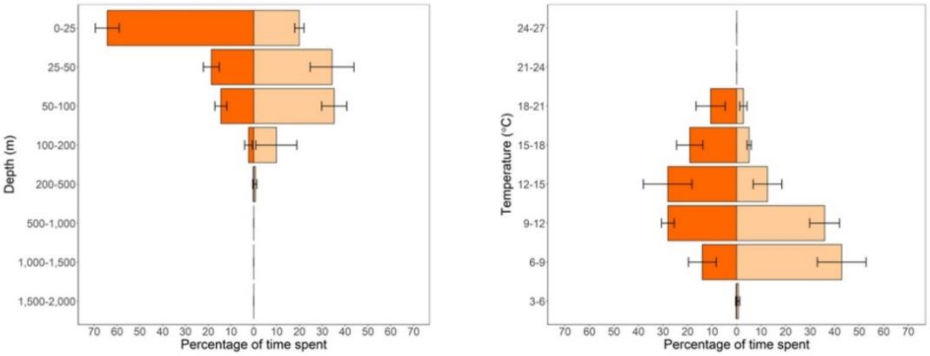
(A) Winter



(B) Spring



(C) Summer



(D) Fall

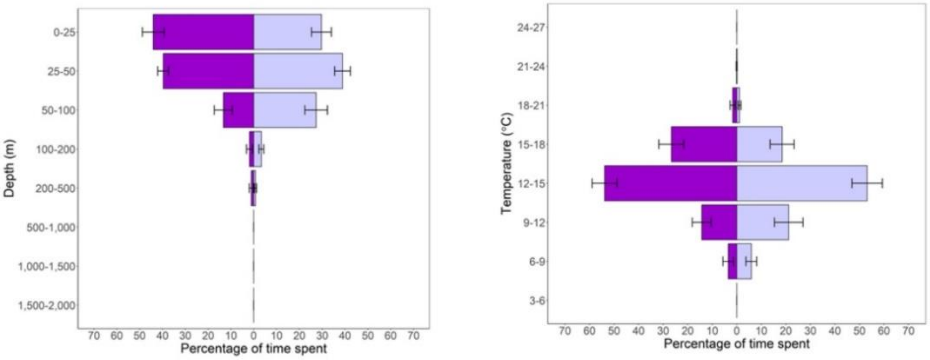


Figure 5.8. The average percentage of time gravid porbeagles (n = 7) spent at depth (m; left plots) and ambient water temperatures (°C; right plots) during the night (dark colored bars on left) and day (light colored bars on right) during (A) winter, (B) spring, (C) summer, and (D) fall based on data from pop-off satellite archival tags. To calculate the average percentage of time at depth and temperature, the proportion of depth (or temperature) data points in each depth (or temperature) bin during the day and night for each season were calculated for each individual and then averaged across individuals. The error bars represent standard error.

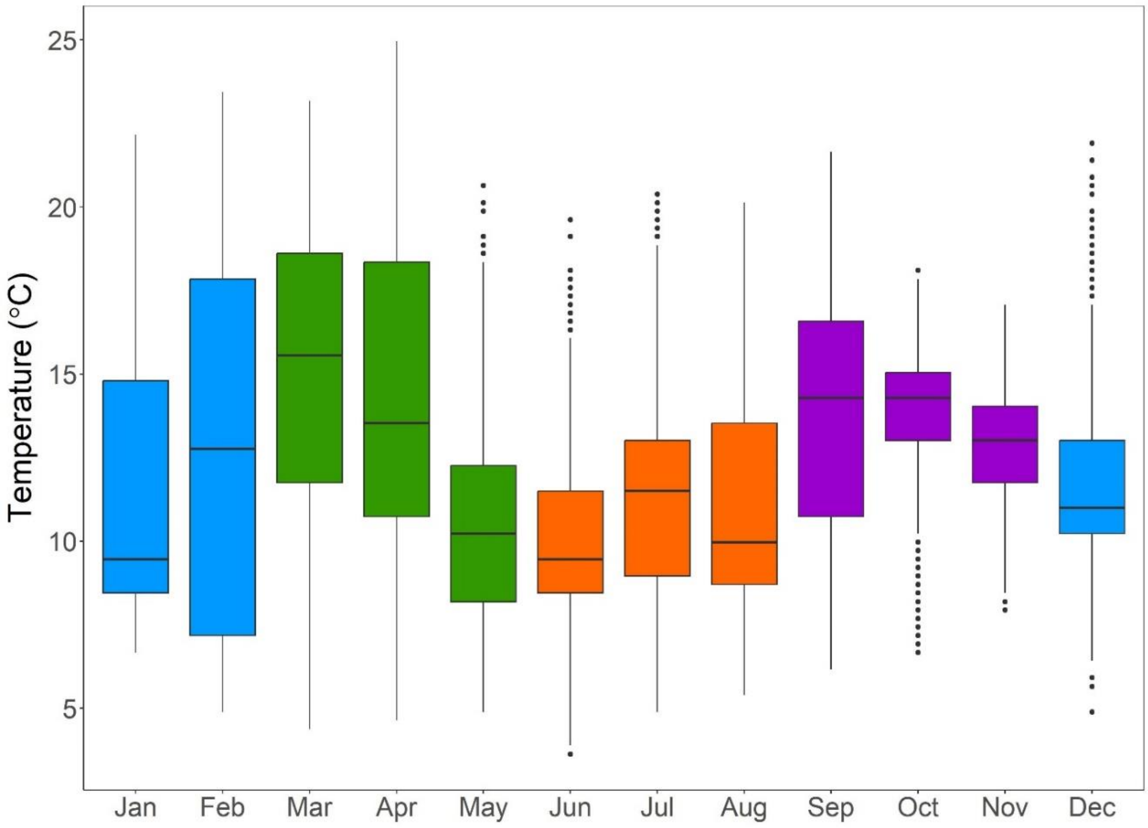


Figure 5.9. Boxplots of ambient water temperatures (°C) occupied by gravid porbeagles (n = 7) during each month based on data from pop-off satellite archival tags. The circles represent outliers (values more extreme than 1.5*interquartile range on either end of the box). The color of the box represents the season, where winter is blue, spring is green, summer is orange, and fall is purple.

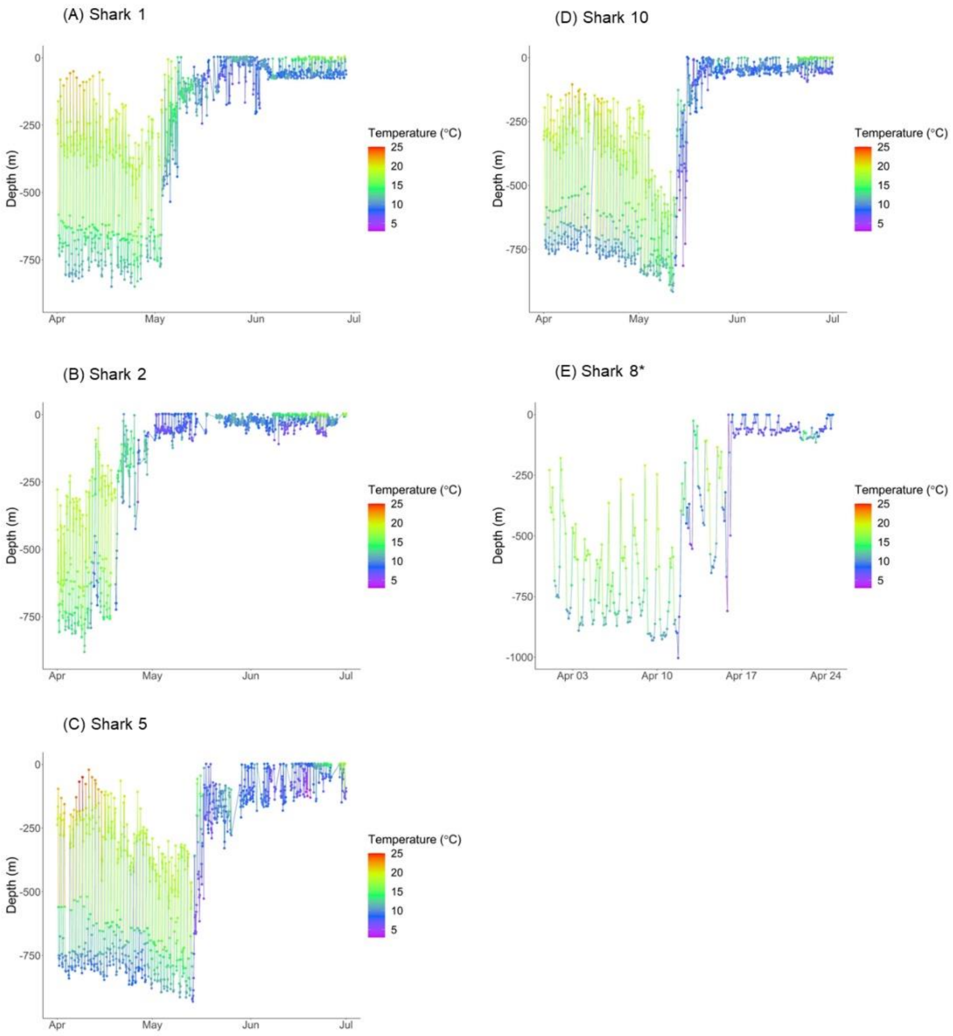


Figure 5.10. Temperature-integrated diving time-series from pop-off satellite archival tags deployed on gravid porbeagles (n = 5) during the pupping season (April through June; Jensen et al. 2002). Note the plots have different axis scales to reflect the range in available deployment dates and depths occupied among individuals. Plots are ordered first by deployment duration, from longest to shortest, then by shark ID. * indicates a porbeagle (shark 8 (D)) whose tag popped off prematurely during the pupping season and thus depth data during the pupping season is limited to April 1-24 for this individual.

FINAL REMARKS

This collection of work has provided several novel insights into the movement ecology of NW Atlantic porbeagles that can help inform conservation and management directions for this overfished population. For example, I collected the first data on movement patterns of this population during the earliest years of life and during gestation, two life history stages for which movement data were lacking yet are critical for population persistence and recovery (e.g., Kinney and Simpfendorfer, 2009; Carlisle et al., 2015; Anderson et al., In Press). Additionally, I sampled from a relatively understudied portion of the populations' geographic range, which can begin to provide insights into potential regional variability in behavior and region-specific management needs, especially if sample size is increased with future work.

Collectively, the horizontal habitat use of NW Atlantic porbeagles tagged in this work were found to be relatively conserved across life history stages as demonstrated by high spatial overlap in KUDs. Additionally, seasonal horizontal movement patterns were found to be similar among several life stages, with juveniles and mature females (including gravid females) migrating southward into mesopelagic habitat during colder seasons. Interestingly, mature male porbeagles were the only group that appeared to remain in continental shelf waters year-round, as they made very limited use of mesopelagic habitats. While the reason for the disparity in movements between mature males and other life stages cannot be determined with certainty, I hypothesize that it is at least partially related to energetics (e.g., Tamburello et al., 2015; Lawson et al., 2019; Shaw, 2020). For example, growth and reproduction are associated with high energetic demands on top of basal requirements (e.g., Brown et al., 2004; Lawson et al., 2019).

Growth is generally accelerated during the juvenile life stage (e.g., Natanson et al., 2002) and females likely have higher reproductive energetic requirements than males, especially given female porbeagles exhibit oophagy (e.g., Gilmore et al. 2005). It is possible that the metabolic benefits of migrating offshore, where they would have access to warmer environments (which may accelerate gestation; e.g., Nosal et al., 2014; Sulikowski et al., 2016; Nosal et al., 2021) and/or seasonal concentrations of prey (e.g. Hendrickson, 2004; Van Beveren et al., 2023) to meet the demands of growth and reproduction, exceed the costs of movement (e.g., Bowler and Benton, 2005; Chapman et al., 2012; Lawson et al., 2019) for juveniles and mature females. On the other hand, given they are likely allocating less energy toward growth and reproduction compared to their younger and mature female counterparts, the energetic requirements of mature males may be sufficiently met by remaining in cooler continental shelf waters.

Ontogenetic change in habitat use is prevalent in the ecology of many taxa, including elasmobranchs, and has been associated with factors such as size-related energetics, competition/predation, abiotic needs, and/or foraging efficiency (e.g., Speed et al., 2010; Bansemer and Bennet, 2011; Afonso and Hazin, 2015; Ajemian et al., 2020; Frank et al., 2021; Kock et al., 2022). While there was high spatial overlap in habitat use across life stages in NW Atlantic porbeagles tagged in this work, young porbeagles migrated southward into mesopelagic habitat earlier in the year compared to both larger juveniles (Skomal et al., 2017) and gravid females (Chapter 5). I also discovered potential evidence of ontogenetic changes in depth use. In the case of NW Atlantic porbeagles, it appears that young porbeagles are more surface-oriented and may not dive as deep as larger life stages including larger juveniles and adults (Campana et al., 2010; Chapter 3;

Chapter 5; B. Anderson and J. Sulikowski, unpublished data). I predict that these ontogenetic differences in habitat use are driven by a combination of competitive release and physiological tolerance (Chapman et al., 2012). While the diet of porbeagles overlaps across life stages, there is a shift from greater importance of pelagic prey during early life stages to greater importance of groundfish during later life stages (Joyce et al. 2002). The higher proportion of pelagic species in the diet of young porbeagles, and in turn the greater affinity for surface waters during the summer and fall, may be a mechanism to reduce foraging competition between life stages, although it's important to note that mouth gape size is also likely influencing porbeagle diet across ontogeny (e.g., Dulvy and Trebilco, 2018). The earlier southward migration by young porbeagles may also allow these individuals to take advantage of concentrations of pelagic prey while competition from larger conspecifics is minimized. On the other hand, the earlier southward migration and greater use of surface waters may also be an indication of an ontogenetic change in thermal tolerance, in which young porbeagles have a narrower thermal tolerance range and prefer warmer waters compared to larger conspecifics (e.g., Carlisle et al., 2015; Shaw et al., 2021). Overall however, more research is needed to discern the underlying mechanisms involved in the life-stage based habitat use of NW Atlantic porbeagles.

In terms of conservation and management, this work suggests that fishing activities (i.e., rod-and-reel, gillnet, trawl) occurring in US waters may significantly impact the NW Atlantic porbeagle population (Chapter 4; Chapter 5) and this should be given further research attention (i.e., studies of at-vessel and post-release mortality of all life stages), especially given the documented at-vessel mortality of a gravid female. The high spatial overlap among life stages can have both benefits and concerns for conservation and management of NW Atlantic porbeagles. On one hand, the relatively small high occupancy area for this tagging population that includes all life stages, and the overlap of this area with a high concentration of fishing activity, indicates that all life stages of the population would likely be vulnerable to fishing capture within their important habitat. On the other hand, a benefit of the high spatial overlap among life stages is that any spatial management strategies would likely protect multiple components of the population. These considerations highlight the apparent importance of the study region to conservation and management of NW Atlantic porbeagles and that this should be a geographic area of continued research. For example, while the development of a large protected area or shark sanctuary may be unrealistic in this economically and culturally important fishing region, future work could test the development of bycatch reduction devices or gear modifications that could effectively reduce captures of porbeagles within their high occupancy area.

Limitations & future directions.

There are two major limitations that impact the ecological conclusions that can be made from this body of work. First, the number of individuals tagged was relatively low for each chapter. Overall, sample size was limited due to two factors: (1) the cost of satellite tags, which can range from several hundred to several thousand US dollars each (Sequeira et al., 2019) and (2) the inherent challenge of catching a large number of individuals for an overfished (US; Curtis et al., 2016) and endangered (Canada; COSEWIC, 2014) population over a limited number of study years. Increasing sample size, such as through meta-analysis (e.g., Andrzejaczek et al., 2022b) or future collaborative tagging efforts across the region, would broaden the scale and scope of questions that could be addressed for this population (Sequeira et al., 2019) and this is an area potential for future research efforts. For example, by tagging porbeagles across a broader geographical range, regional variability in movement patterns could be explored (Sequeira et al., 2019). Moreover, by increasing the number of porbeagles tagged in each life stage to tens of individuals, ecological conclusions could be made with increasing confidence.

Additionally, while this body of work provides substantial new insights into the movement ecology of the NW Atlantic porbeagle, especially as related to life stage differences in habitat use, additional work is needed to support hypotheses regarding underlying ecological and/or evolutionary motivations behind movement patterns. In particular, it would be beneficial to study the energetics of NW Atlantic porbeagles, including for different life stages and reproductive stages, to provide more metabolic context to movement patterns. For example, quantifying the energetic requirements of mature females during vitellogenesis, during each phase of gestation, and during the resting year, could help to better understand the decisions to migrate south and could be correlated to the extent of their migrations. Additionally, quantifying the energetics of neonate sharks could help predict the likelihood of NW Atlantic porbeagles pupping in distant mesopelagic habitat (Campana et al., 2010) vs. continental shelf habitat (Chapter 5) based on the earliest life stages' potential for long-distance dispersal (e.g., McMillan et al., 2019). In addition to energetics, complimentary studies on prey distributions could help provide more support for the hypothesis that the seasonal horizontal movements and vertical movements of NW Atlantic porbeagles are related to the distributions of prey (Andrzejaczek et al., 2019). Finally, given the limited trans-national movements observed in this work, future genetic analysis (e.g., Testerman, 2014; Klein et al., 2021) of tagged individuals across the populations geographic range may provide insight into population dynamics for the NW Atlantic porbeagle. For example, a combined genetic and tagging study across a broad geographic region could help discover how often and where components of the population are mixing.

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APPENDIX A

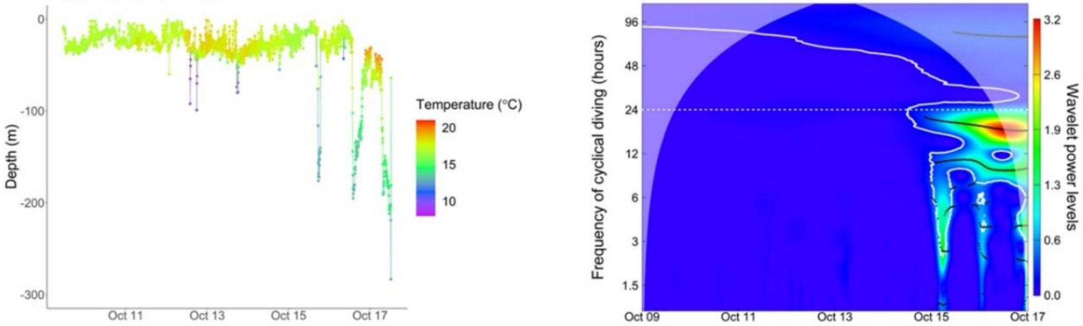
CHAPTER 3 SUPPLEMENTAL MATERIALS

Table A.1

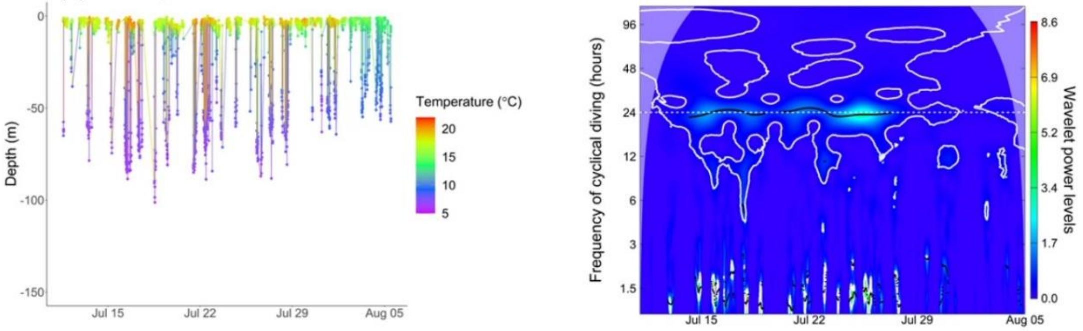
Results of the optimal linear mixed models. Models were run with shark identity as a random variable and temporal autocorrelation. Mean depth (m) and standard deviation (SD) of depth (m) were both log-transformed prior to analysis to meet assumptions of normality.

Response	**Fixed effect**	**Coefficient**	***SE***	***t***	***p***
Mean depth	Intercept	3.669662	0.17704638	20.727124	<0.001
	Diel period	-0.599450	0.04603658	-13.021158	<0.001
	Season	-0.487178	0.20431647	-2.384428	0.0174
	Diel period:Season	-0.237339	0.07381186	-3.215454	0.0014
SD of depth	Intercept	2.8490358	0.1681703	16.94137	<0.001
	Diel period	-0.5483173	0.0476886	-11.49787	<0.001

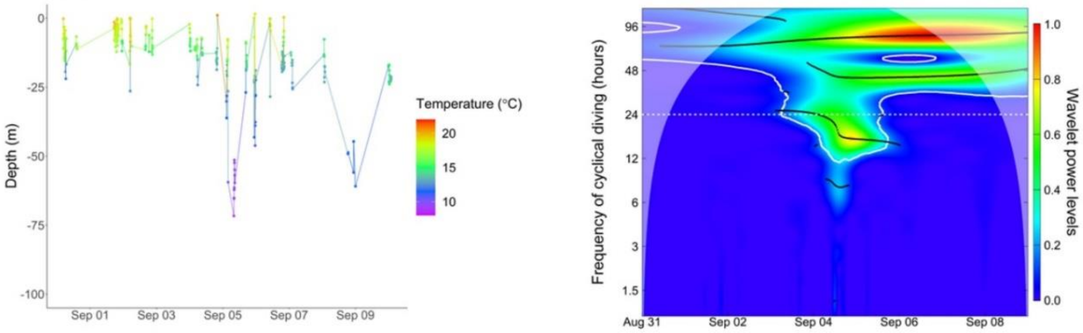
(A) Shark 1, 80 cm



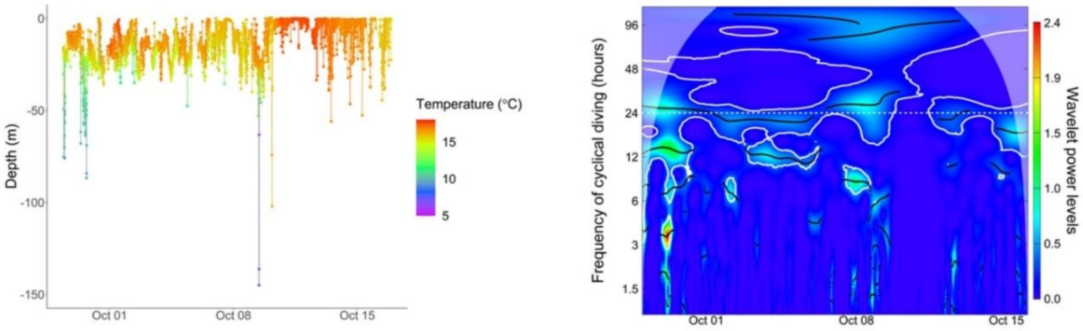
(B) Shark 2, 88 cm



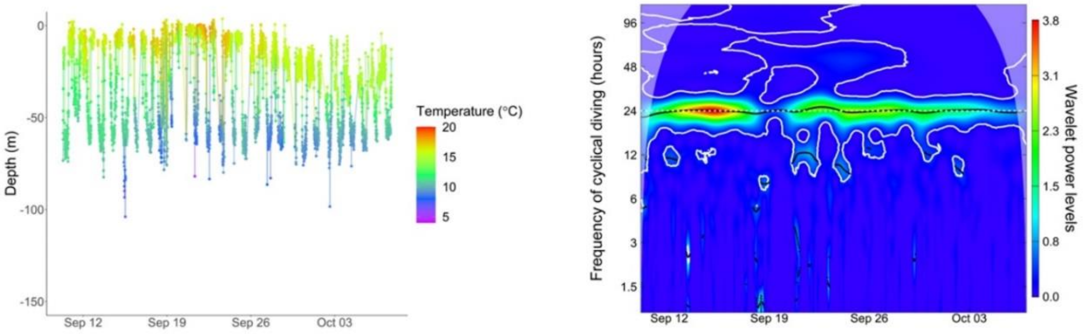
(C) Shark 3, 90 cm



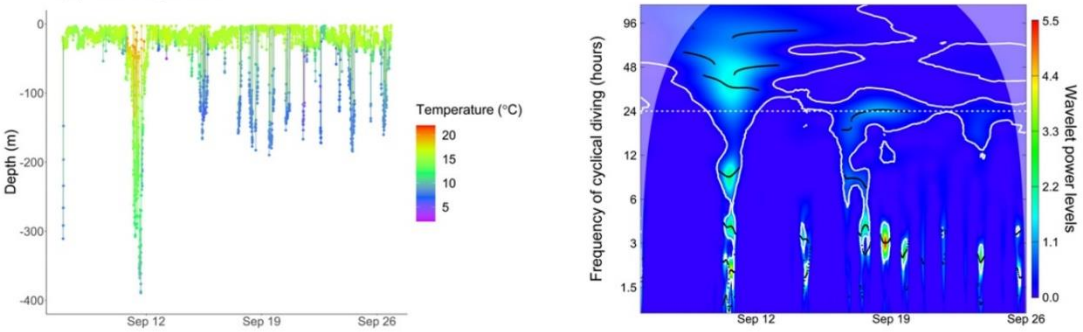
(D) Shark 4, 90 cm



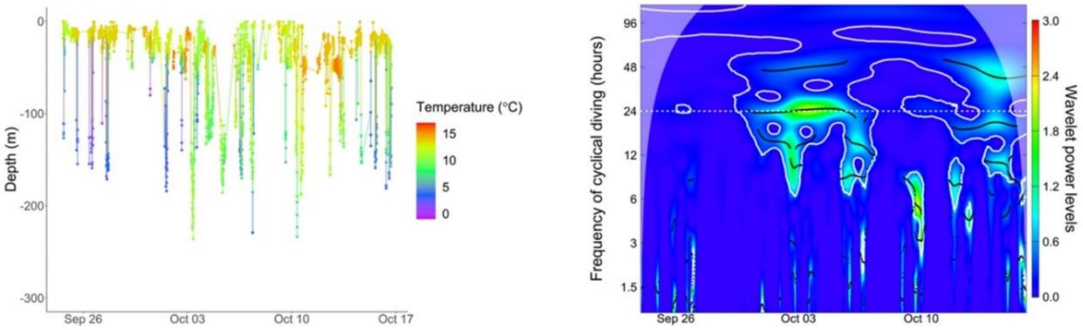
(E) Shark 5, 94 cm



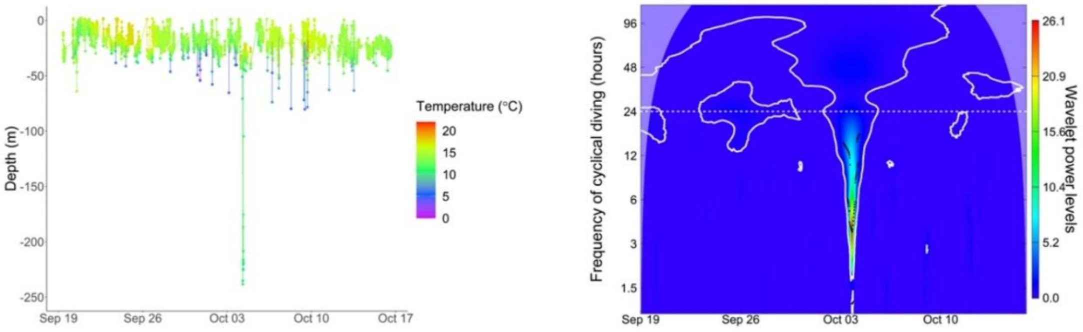
(F) Shark 6, 95 cm



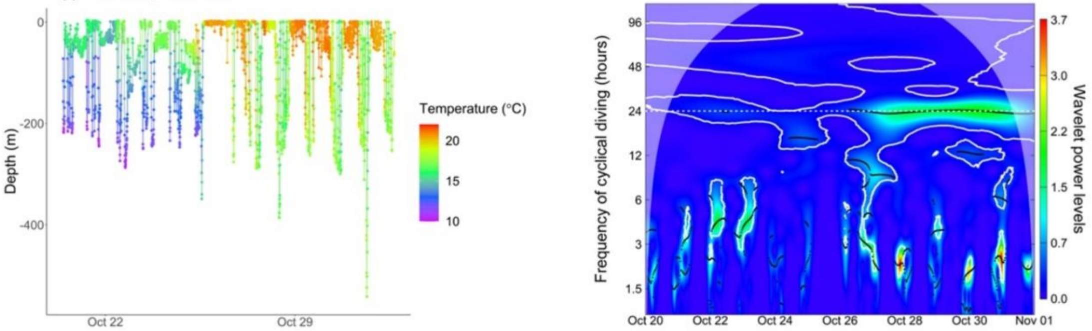
(G) Shark 7, 95 cm



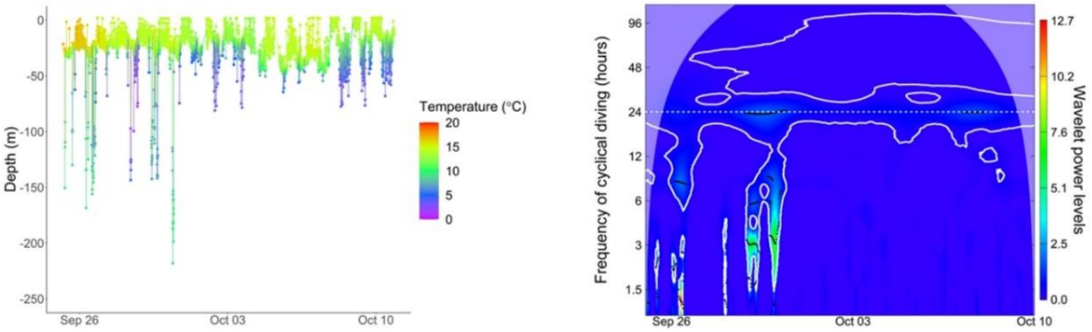
(H) Shark 8, 96 cm



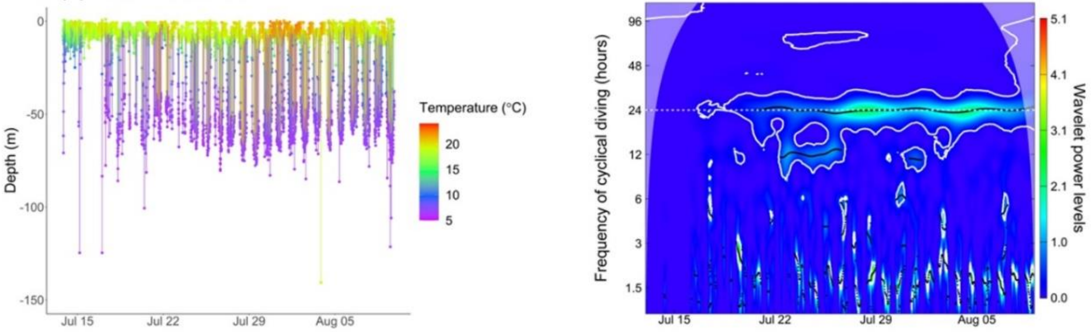
(I) Shark 9, 100 cm



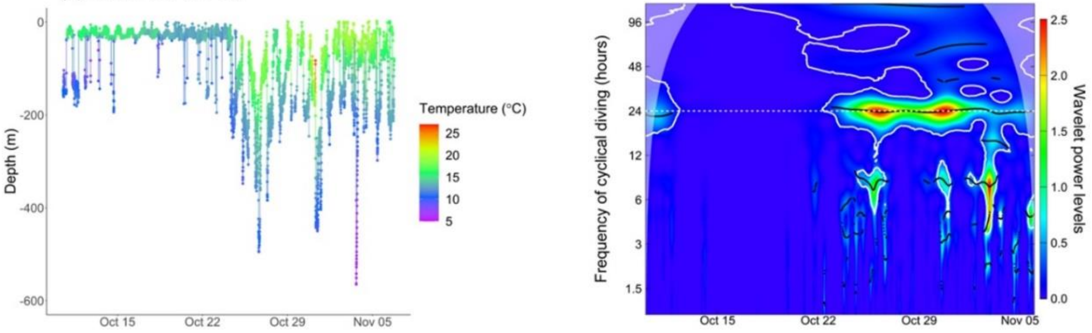
(J) Shark 10, 102 cm



(K) Shark 11, 103 cm



(L) Shark 12, 110 cm



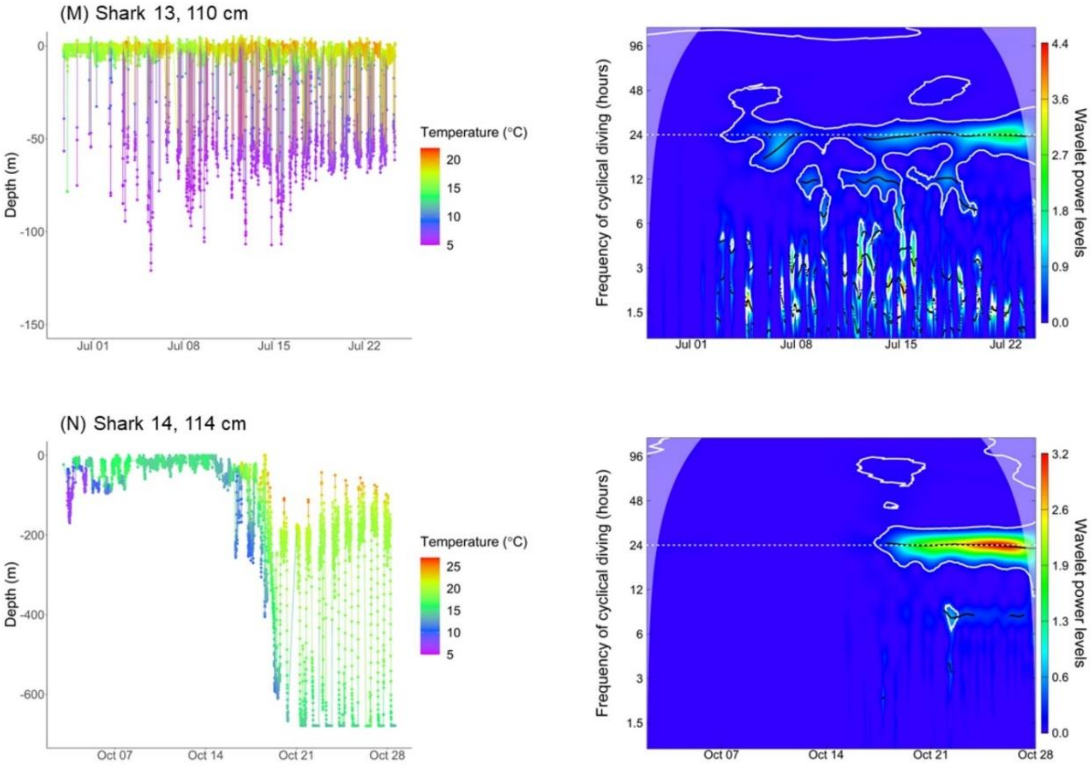
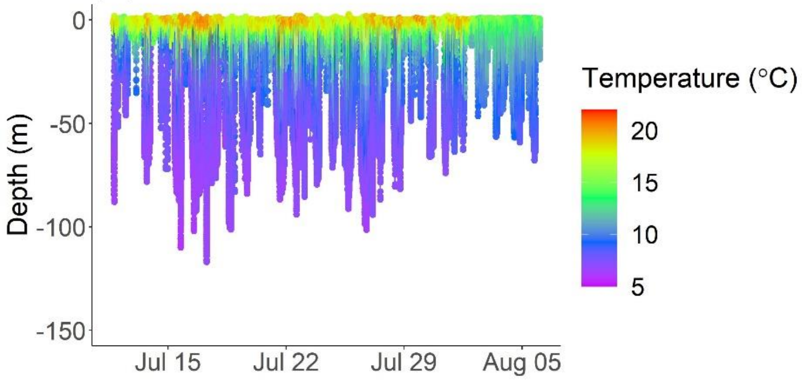
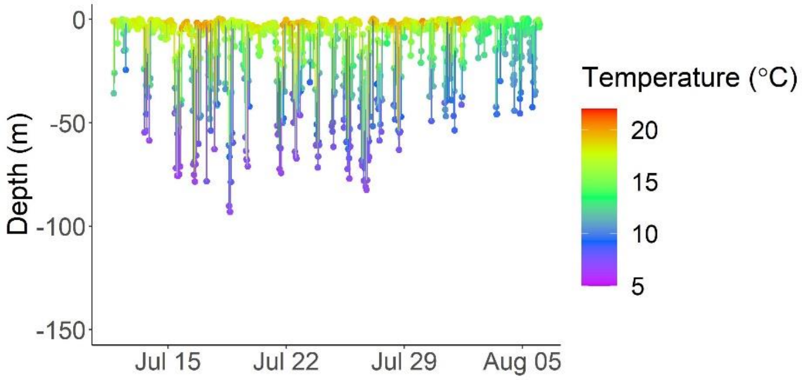


Figure A.1. Time series of temperature-integrated dive profiles (left) and corresponding continuous wavelet power spectra (right) over the duration of tag deployment for each young-of-the-year (YOY) and one-year-old porbeagle in this study. For the wavelet power spectra, areas encircled in white represent time periods with significant cyclical patterns ($p < 0.05$). Within the white encircled areas, the wavelet power level (color) reflects the strength of the cyclical pattern detected, with red representing the strongest cyclical pattern. The black lines represent wavelet power ridges, or the local maxima of wavelet power. In general, significant wavelet power indicates a pattern of diving and ascending over a common temporal interval. The periods (y-axis) reflect the time interval over which the cyclical diving pattern is detected. The white dashed reference line identifies the periodicity of 24-h. Shaded areas outside of the cone of influence should not be interpreted. Note the differences in scales of axes and legends among individual plots.

(A) Full archival record



(B) Archival record binned into 30 min bins



(C) Transmitted record binned into 30 min bins

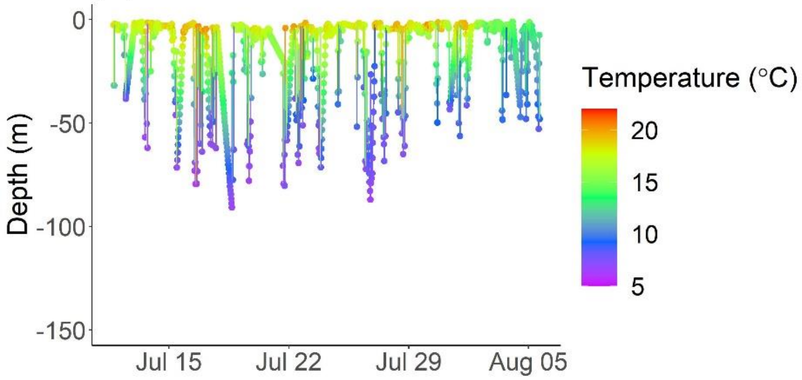


Figure A.2. Time-series of temperature-integrated dive profiles for the full downloaded archival record (10-s intervals; A), the downloaded archival record binned into 30-min windows (B), and the transmitted record (5-min intervals) binned and interpolated into 30-min windows (C) for Shark 2 (ID 175805).

APPENDIX B

CHAPTER 4 SUPPLEMENTAL MATERIALS

Section 1. Move persistence index

The SSM applied also associated each estimated location with a behavioral mode using a move persistence model based on speed and direction. The resulting move persistence behavioral index estimates range from 0 (“resident” behavior, relatively slow and meandering movement path) to 1 (“transient” behavior, relatively fast and directional movement path) for each position. This was used to classify behavioral modes, with values >0.75 classified as “transient” behavior and values <0.25 classified as “resident” behaviors. Behavioral state was classified as “intermediate” if values were between 0.25 and 0.75.

Based on the move persistence SSM that included 26 of the tagged porbeagles, the majority (n = 2528; 60.8%) of location estimates were classified as “intermediate”, followed by “transient” (n = 1302; 31.3%). Very few of the location estimates were classified as “resident” behavior (n = 329; 7.9%). In regard to national boundaries, “resident” behavior occurred at the highest proportion in the US EEZ, with 8.3% of U.S. location estimates classified at “resident” behavior. In comparison, 4.7% of Canadian location estimates were classified as “resident” behavior and no high seas location estimates were classified as “resident” behavior. “Transient” behavior occurred at the highest proportion in the high seas, with 83.9% of high seas location estimates classified as “transient”. In comparison, 36.5% of Canadian locations and 30.3% of US locations were classified as “transient”. “Intermediate” behavior occurred at similar proportions within US waters (61.4%) and Canadian waters (58.8%). However, only 16.1% of high seas location estimates were classified as “intermediate”. Accordingly, the SSM’s behavioral state estimation identified “resident” behavior exclusively in continental shelf regions, mainly in the Gulf of Maine, Georges Bank, and the Bay of Fundy (Figure B.4). In comparison, “transient” behavior was identified throughout the activity space identified by the KUD (Figure B.4). All of the location estimates occurring offshore of the continental shelf were identified as “transient” or “unknown” behavior (Figure B.4). In relation to seasonal patterns, “resident” and “transient” behavior occurred at similar frequencies throughout the year (Table B.1). When considering life stage, most of the “resident” behavior was observed in mature males (72%; Table B.1). All the location estimates for mature non-gravid females were classified as “intermediate” (Table B.1).

Unfortunately, I found relatively limited application for the move persistence behavioral index in this study. The majority of the behavioral index estimates were “intermediate”. The high proportion of “intermediate” behavioral estimates could have been related to the need to separate individual animal tracks into multiple segments due to gaps in fin-mount transmissions, or could have been related to the prediction interval (24 hour) being too long to be able to identify real variability in movement patterns (Jorgensen et al., 2023). However, although limited, I did find that the estimates that were able to be classified as “resident” and “transient” generally fit the understanding of shark behavior. For example, “resident” behavior was classified exclusively in continental shelf waters where I expect porbeagles to exhibit more area-restricted movements (i.e., Skomal et al., 2021). In comparison, most of the location estimates in mesopelagic environments of the high seas, where porbeagles have made more extensive, directed movements (Campana et al., 2010), were classified as “transient” behavior.

Table B.1

Percentage and frequency of behavioral state index estimates (γ_t) within seasons and life stages of tagged porbeagles.

	Resident (<0.25)	**Transient (>0.75)**	**Intermediate (0.25-0.5)**
Winter	6.67% (n = 57)	40.75% (n = 348)	52.58% (n = 449)
Spring	10.14% (n = 93)	26.83% (n = 246)	63.03% (n = 578)
Summer	5.11% (n = 81)	17.78% (n = 282)	77.11% (n = 1223)
Fall	12.22% (n = 98)	53.12% (n = 426)	34.66% (n = 278)
Juveniles	6.30% (n = 78)	54.00% (n = 669)	39.71% (n = 492)
Mature males	20.75% (n = 238)	2.09% (n = 24)	77.16% (n = 885)
Females of unknown reproductive state	0.93% (n = 7)	35.33% (n = 266)	63.75% (n = 480)
Non-gravid females	0.00% (n = 0)	0.00% (n = 0)	100.00% (n = 96)
Gravid females	0.65% (n = 6)	37.12% (n = 343)	62.23% (n = 575)

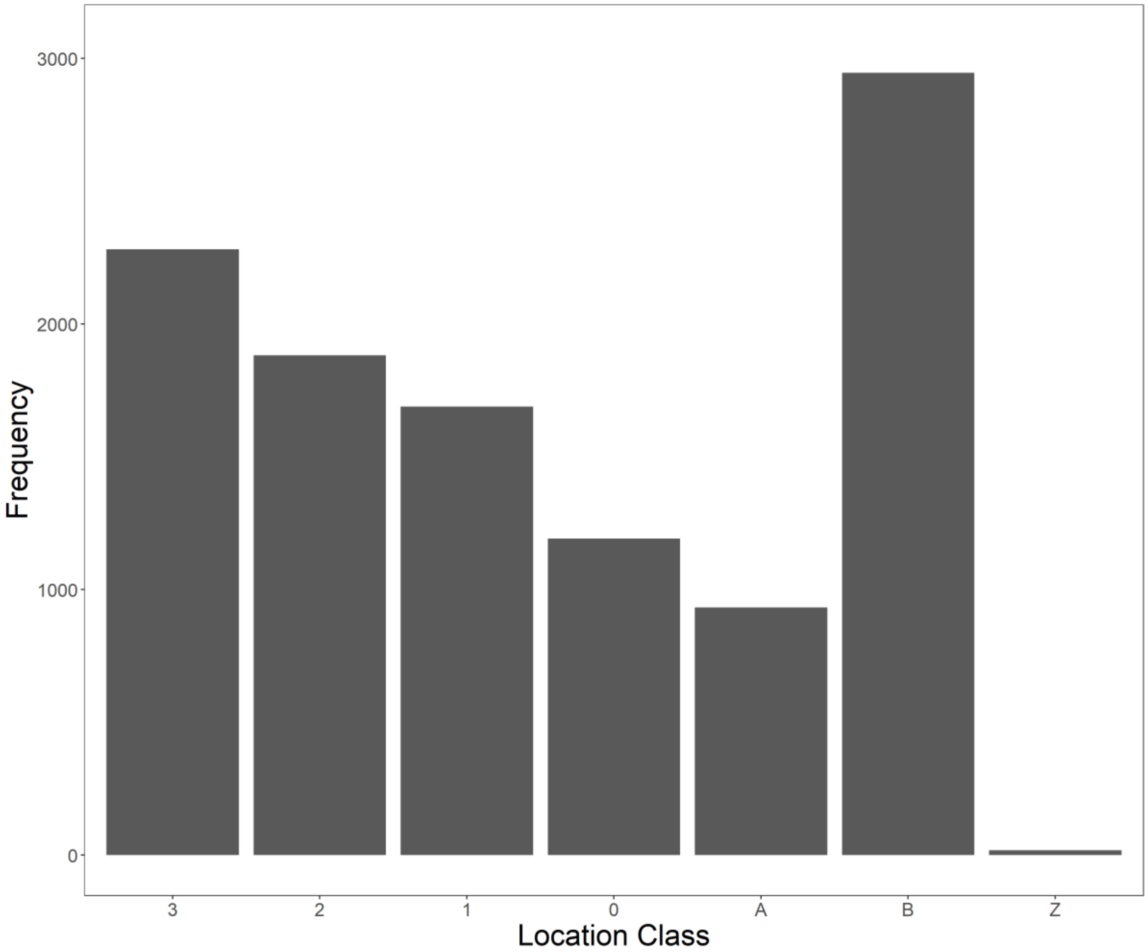


Figure B.1. Frequency distribution of the location classes (LC) associated with all satellite tag transmissions. These LCs are associated with the following error estimates: LC3 < 250 m, 250 m < LC2 < 500 m, 500 m < LC1 < 1500 m, and LC0 > 1500 m. Argos does not provide error estimates for LC A or B, but LC A and LC B have been found to be accurate to > 1 km and > 5 km radius, respectively (Tougaard et al., 2008). The lowest accuracy category transmissions (LC Z) are poor, unreliable location estimates and were removed from the dataset (n = 18).

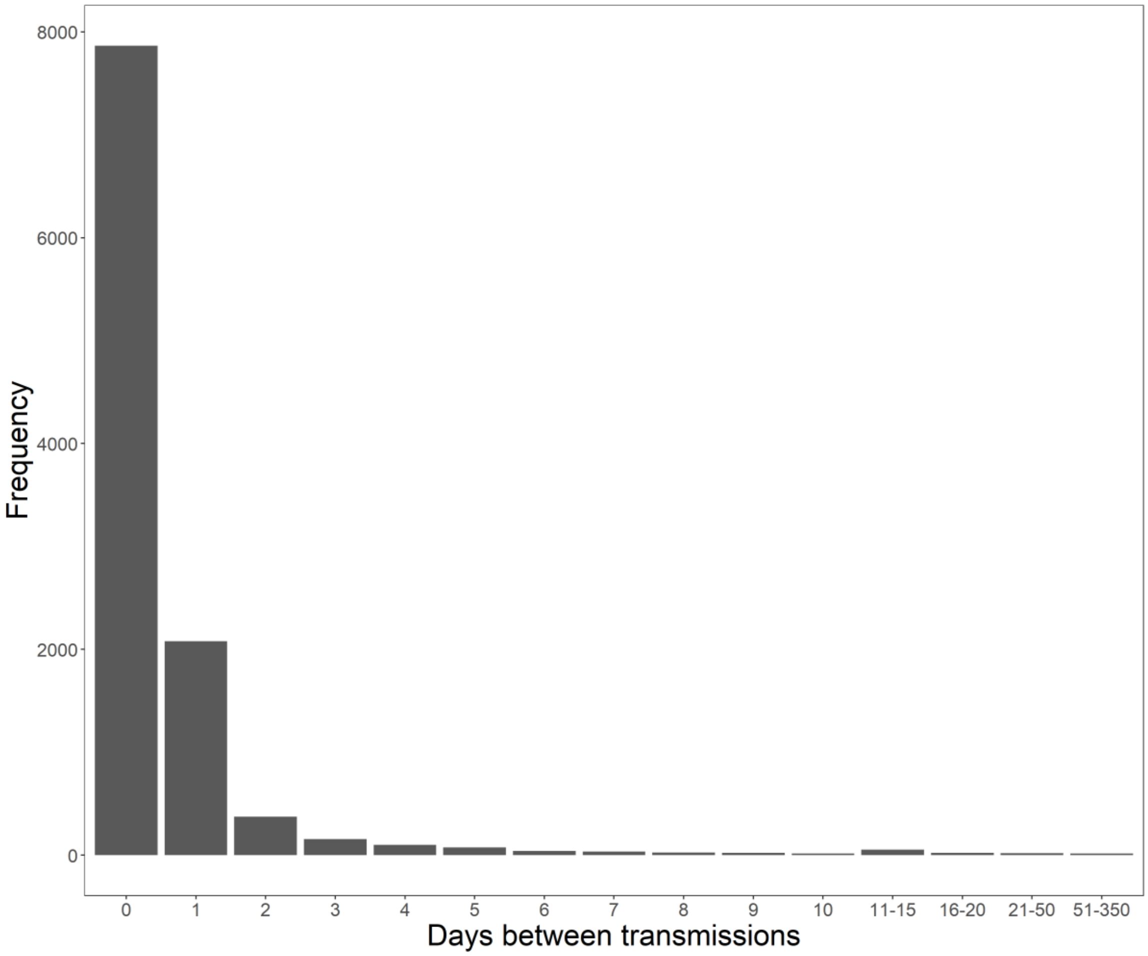


Figure B.2. Frequency distribution of the time interval (in days) between subsequent satellite tag transmissions for tagged porbeagles. When the time interval between subsequent transmissions was > 10 days, the track was split into sub-tracks.

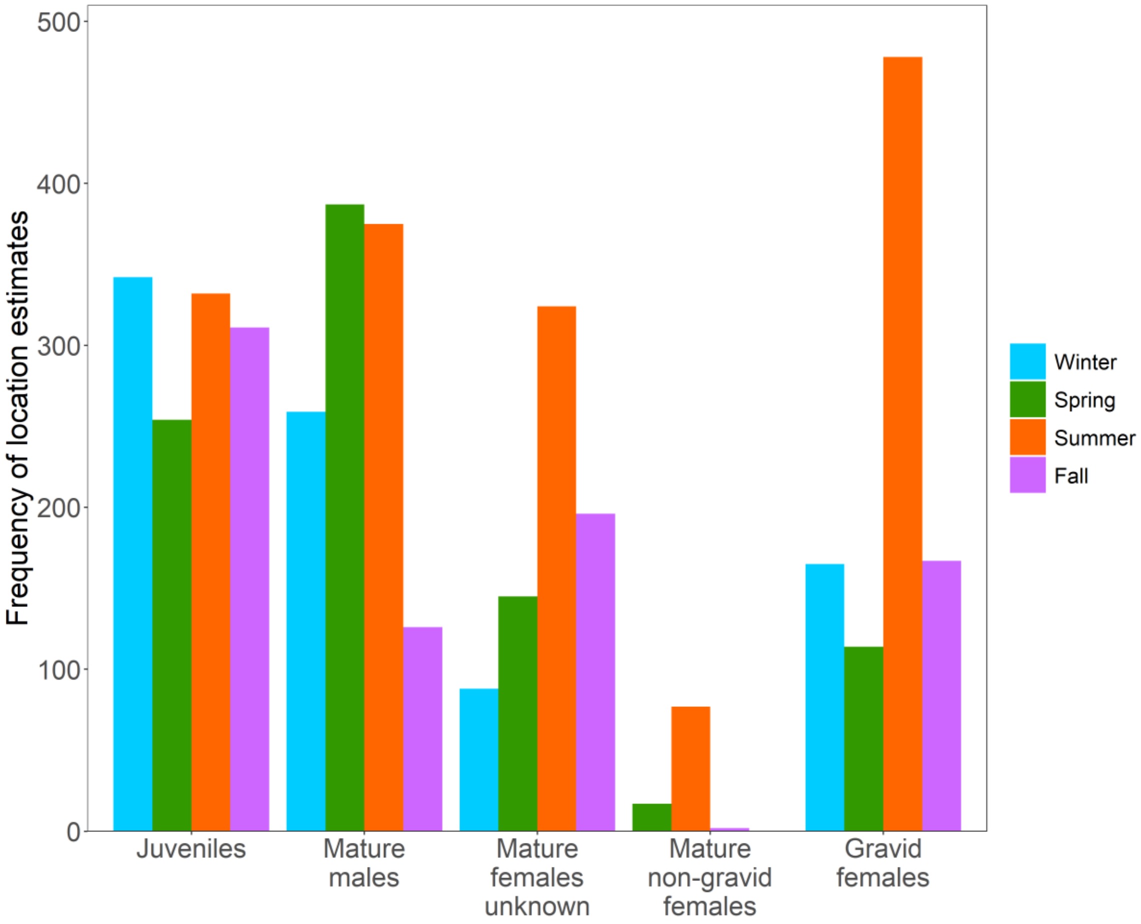


Figure B.3. Frequency distribution of state-space model (SSM) location estimates used in habitat use analyses by season and life stage.

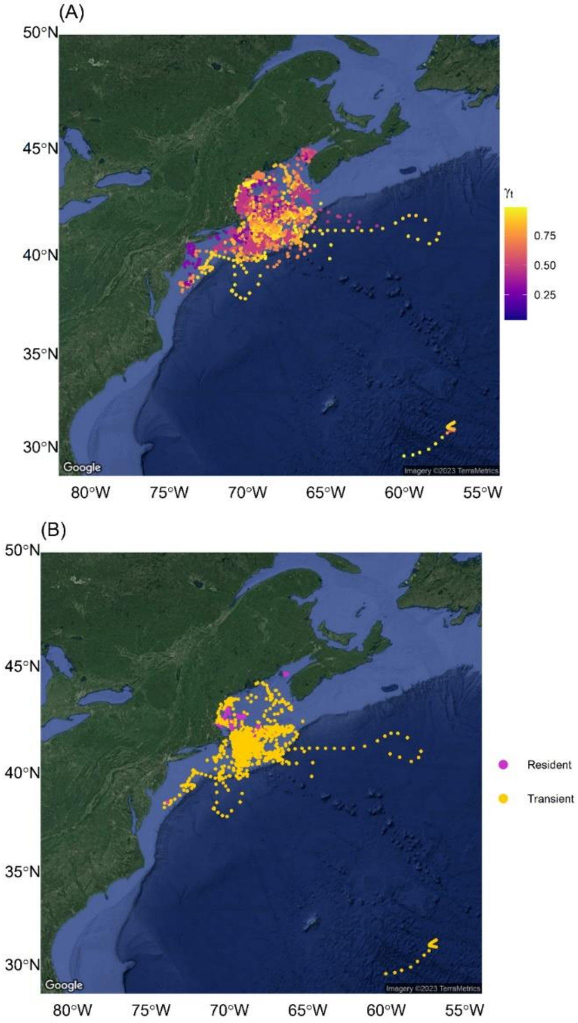


Figure B.4. Map of regularized state space model location estimates for porbeagles tagged in the Northwest Atlantic. For (A), the color of the point represents the specific value of the behavioral state index estimate (γ_t) for that location estimate, with values < 0.25 representing "resident" behavior and values > 0.75 representing "transient" behavior. Values between 0.25-0.75 are considered "intermediate". For (B), only location estimates that were classified as "resident" or "transient" behavior are plotted, and the color of the location estimate represents the behavioral classification.

APPENDIX C

CHAPTER 5 SUPPLEMENTAL MATERIALS

Section 1. Reproductive hormone analysis

Approximately 5-10 mL of blood was collected from the caudal vein from a subset of individuals (n = 7) using a heparinized syringe and 18-gauge needle. Blood samples were kept at 4°C overnight to allow the separation of plasma from red blood cells. Separated plasma samples were frozen, shipped on ice to Arizona State University (Glendale, AZ), and then kept frozen at -20°C until processing for reproductive hormones. Thawed plasma samples were spiked with approximately 1,000 counts per min of tritiated T, E_2, or P_4 (Perkin Elmer, Waltham, Massachusetts) to calculate the percent recovery of hormone during the extraction process. Samples were extracted for T, E_2 and/or P_4 following protocols from Sulikowski et al. (2004). In brief, each plasma sample was extracted twice for each hormone with 10X volumes of diethyl ether (ACS grade) and snap frozen in a dry ice and acetone (ACS grade) bath. The liquid phase was decanted into a second borosilicate tube and evaporated at 37°C under a stream of nitrogen. Dried hormone extracts were reconstituted in phosphate buffered saline with 0.1% gelatin (PBSG) and stored at 4°C. The recovery of hormone during the extraction process was calculated separately for each sample and hormone. There was insufficient plasma to quantify all three hormones for all individuals. When plasma was limited for an individual, hormone analysis was prioritized for E_2, then P_4, and finally T.

Hormone concentrations from plasma extracts were quantified following a radioimmunoassay procedure described in Prohaska et al. (2013). Antibodies (provided by Colorado State, Fort Collins, CO) used to bind hormones for quantification were diluted in PBSG to final concentrations of 1:27,600, 1:30,600, and 1:5,000, for T, E_2, and P_4, respectively. Radioactivity was calculated using a Tri-Carb 4910 TR liquid scintillation counter (Perkin Elmer Life Sciences, Waltham, MA). Final concentrations were corrected for procedural loss during the extraction using individual sample hormone extraction recoveries. The inter-assay coefficients of variation were 9.0%, 13.2%, and 13.6%, and the average intra-assay coefficients of variation were 9.5%, 5.4%, and 7.2%, for T, E_2, and P_4, respectively.

Average hormone recoveries from plasma during the extraction process were 81.8%, 70.2%, and 65.4% for T, E_2, and P_4, respectively. Reproductive hormone concentrations ranged from below the minimum detection limit (6.25 pg/mL; shark 6) to 2,472 pg/mL (shark 10) for T, below the minimum detection limit (5 pg/mL; shark 6) to 3,586 pg/mL (shark 4) for E_2, and below the minimum detection limit (6.25 pg/mL; shark 6) to 3,204 pg/mL (shark 1) for P_4 (Table C.1).

In general for female elasmobranchs, E_2 concentrations have been found to be elevated during the follicular phase prior to ovulation, P_4 concentrations have been found to be elevated during ovulation and early pregnancy, and T concentrations have been found to be elevated during vitellogenesis as a precursor to E_2 production (Awruch, 2013). In this study, the concentrations of reproductive hormones in the plasma of gravid porbeagles ranged widely, from below the detection limits of the assays to several thousand pg/mL for T, E_2, and P_4. While these wide-ranging concentrations may suggest that reproductive hormones may not be a sufficient stand-alone predictor of pregnancy on an individual basis in this population, it’s important to consider the limited sample sizes in this study ($n = 5$, 7, and 6 for T, E_2, and P_4, respectively), and the previously documented individual-level variability in reproductive hormone concentrations of elasmobranchs (e.g., Verkamp et al., 2022; Anderson et al., 2023). For example, while the muscle E_2 concentrations of gravid NW Atlantic porbeagles also ranged from below the minimum detection limit to approximately 1,000 pg/g during early gestation, muscle E_2 concentrations were collectively higher in gravid females compared to non-gravid females, likely due to the continued follicular development and ovulation throughout gestation in oophagous sharks (Anderson et al., 2023). Given this consideration, it is still possible that general trends in plasma hormone concentrations are related to reproductive state in this population. Increasing the sample size of plasma hormone concentrations for gravid females, as well as sampling from other life stages, is needed to clarify the ability of these hormones to serve as a potential indicator of reproductive state in the NW Atlantic porbeagle.

Section 2. Move persistence index

The SSM applied also associated each estimated location with a behavioral mode using a move persistence model based on autocorrelation in speed and direction and considering the magnitude of variability in movement for the individual (Jonsen et al., 2019). The resulting move persistence behavioral index estimates ranged from 0 (“resident” behavior, relatively slow and meandering movement path) to 1 (“transient” behavior, relatively fast and directional movement path) for each position. This was used to classify behavioral modes, with values >0.75 classified as “transient” behavior and values <0.25 classified as “resident” behavior. Behavioral state was classified as “intermediate” if values were between 0.25 and 0.75.

Based on the move persistence SSM, the majority of location estimates were classified as “intermediate” (n = 619; 55.5%), followed by “transient” (n = 486; 43.6%). Very few of the location estimates were classified as “resident” (n = 10; <1%). The

SSM’s behavior state index identified “resident” behavior exclusively on the northwestern point of Georges Bank in late January and early February. In comparison, “transient” and “intermediate” behavior were identified throughout the geographical range occupied by gravid porbeagles.

The move persistence behavior state index estimates should be interpreted with caution. Most location estimates were classified as “intermediate” behavior and very few were classified as “resident” behavior. The gaps in fin-mount transmissions and need to separate individual tracks into multiple segments likely resulted in limited magnitudes of movement variability within each sub-track and may therefore have prevented the move persistence model from classifying differences in behaviors that may be more apparent when considering longer track durations. Moreover, the move persistence model is sensitive to the time interval used to regularize location data, in which long intervals may overly smooth real variability in movements (Jonsen et al., 2023). This may have been the case in the current study given data were regularized over 24-hour intervals and the move persistence model was tested over much shorter intervals (0.5-16-min). It is possible that greater variability in move persistence behavior classification may have occurred if location data could have been regularized over shorter intervals.

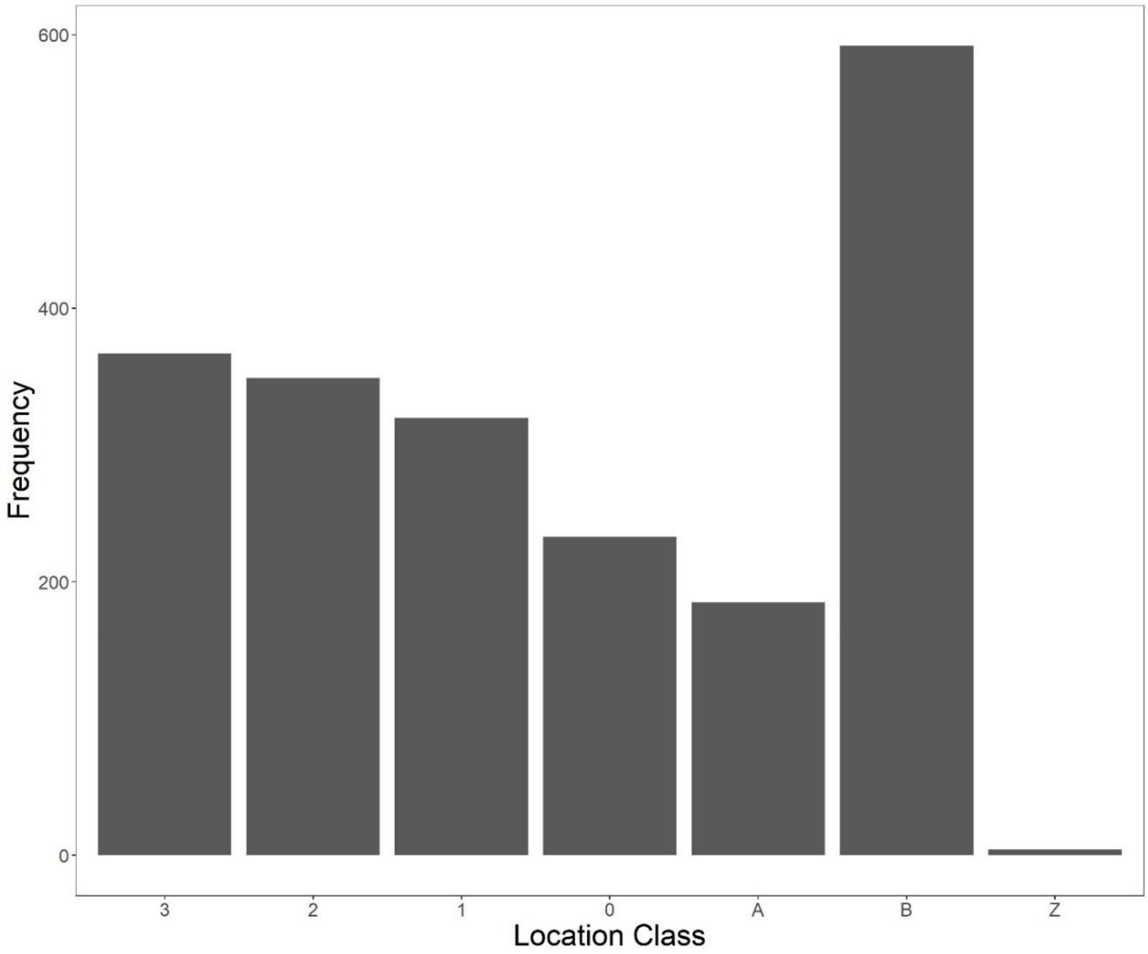


Figure C.1. Frequency distribution of the location classes (LC) associated with all finmount satellite tag transmissions. These LCs are associated with the following error estimates: LC3 < 250 m, 250 m < LC2 < 500 m, 500 m < LC1 < 1500 m, and LC0 > 1500 m. Argos does not provide error estimates for LC A or B, but LC A and LC B have been found to be accurate to > 1 km and > 5 km radius, respectively (Tougaard et al., 2008). The lowest accuracy category transmissions (LC Z) are poor, unreliable location estimates and were removed from the dataset (n = 4). 200

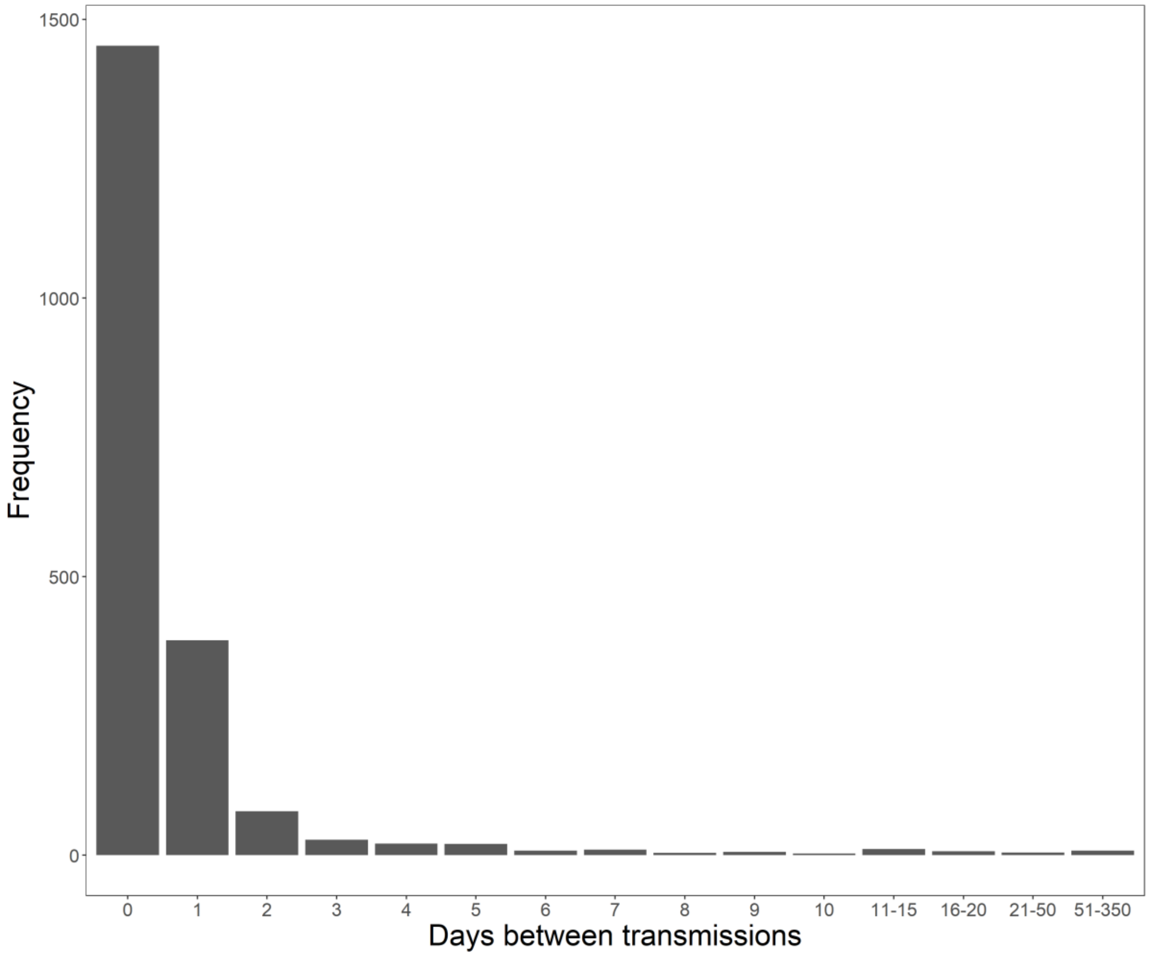


Figure C.2. Frequency distribution of the time interval (in days) between subsequent finmount satellite tag transmissions for tagged porbeagles. When the time interval between subsequent transmissions was > 14 days, the track was split into sub-tracks.

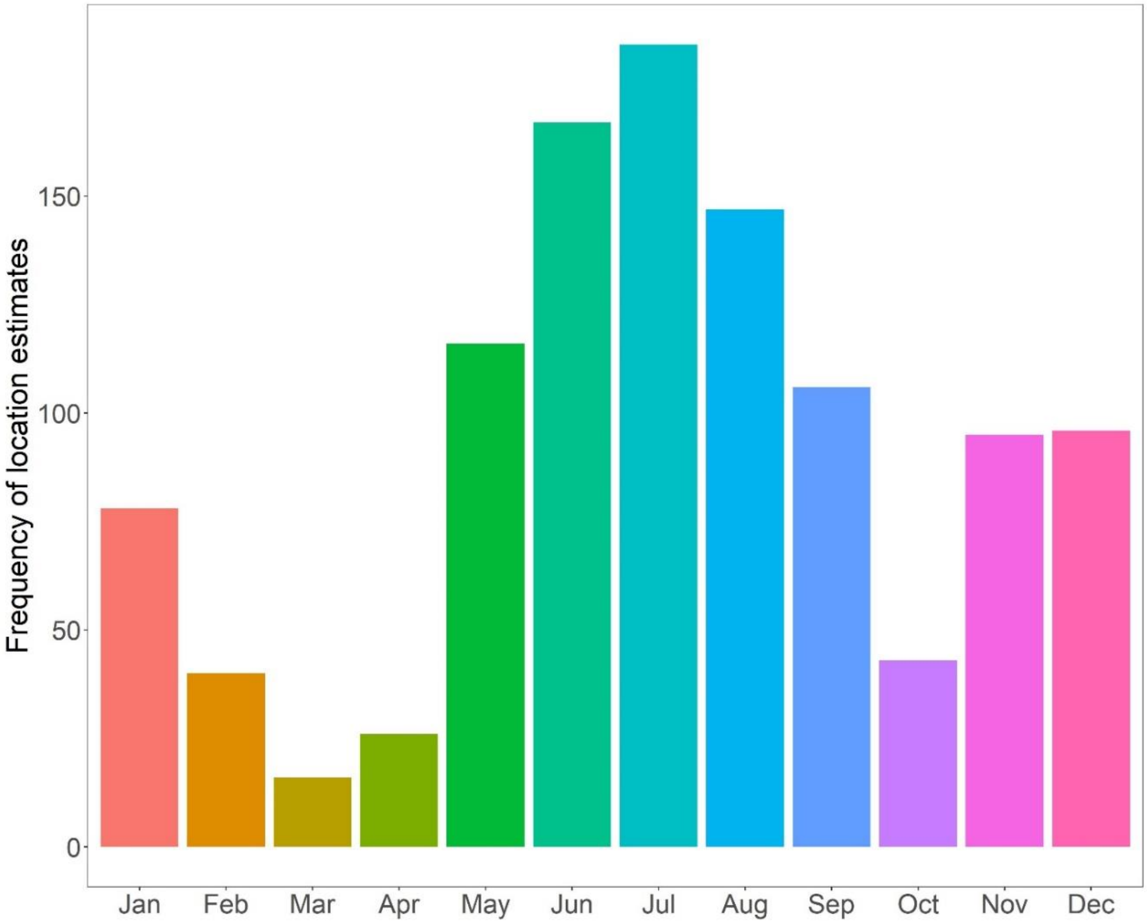


Figure C.3. Frequency distribution of state space model location estimates by month of the year from finmount satellite tags.

Table C.1

Plasma T, E_2, and P_4 concentrations (pg/mL) for gravid porbeagles. T = testosterone, E_2 = 17β-estradiol, P_4 = progesterone. Min indicates the hormone concentration was below the minimum detection limit of the assay (6.25 pg/ml for T and P_4, 5 pg/mL for E_2). – indicates that there was not enough plasma available from an individual shark to run the analysis on the hormone.

Shark ID	**T (pg/mL)**	**E_2 (pg/mL)**	**P_4 (pg/mL)**
1	-	498	3,204
2	2,001	1,642	1,068
3	-	-	-
4	1,776	3,586	1,986
5	-	-	-
6	Min	Min	Min
7	2,215	1,804	587
8	-	1,204	-
9	-	-	-
10	2,472	3,065	1,687

APPENDIX D

CO-AUTHOR APPROVAL

Co-authors have given their permission for the following published work to be included as a dissertation chapter for Brooke Anderson:

Anderson, B.N., Bowlby, H.D., Natanson, L.J., Coelho, R., Cortés, E., Domingo, A., and Sulikowski, J.A. (2021). Preliminary estimate of post-release survival of immature porbeagles caught with rod-and-reel in the Northwest Atlantic Ocean. *Marine Ecology Progress Series, 660*, 153-159.

Co-authors have given their permission for works that have not yet been accepted for publication in a peer-reviewed journal to be listed as dissertation chapters.