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Movement and foraging behavior of short-finned pilot whales in the Mid-Atlantic Bight: importance of bathymetric features and implications for management

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ABSTRACT: Shelf break systems are ecologically important regions of the ocean, and are often characterized by enhanced productivity and high densities of species from lower to upper trophic levels. Along with associated submarine canyons, shelf break regions provide important foraging habitat for deep-diving odontocetes such as pilot whales. Short-finned pilot whales *Globicephala macrorhynchus* are found throughout tropical and subtropical waters, but there is little information on the habitat use of this species in the northwest Atlantic. We examined the movements and foraging behavior of short-finned pilot whales using data from satellite tags (n = 33) deployed off Cape Hatteras, North Carolina, USA in 2014 and 2015. Pilot whale tracks ranged from Cape Lookout, North Carolina north to Georges Bank, with movements and habitat use primarily focused north of Cape Hatteras. We observed 2 distinct modes of behavior, with most pilot whales showing a strong affinity for the continental shelf break and others following offshore meanders of the Gulf Stream for all or part of the observed track. We used first passage time (FPT) to assess area-restricted search behavior, and found that FPT was significantly higher close to the shelf break and in submarine canyons. Our results demonstrate the importance of steep bathymetric features to the foraging habitat and distribution of short-finned pilot whales in this region. In addition, our findings suggest that pilot whales in the Mid-Atlantic Bight may have developed specialized foraging behaviors for targeting steep bathymetric gradients, and that their latitudinal distribution may be limited to regions where this foraging strategy is effective.

KEY WORDS: Pilot whale · Foraging behavior · Shelf break · Submarine canyon · Gulf Stream · Distribution · First passage time

INTRODUCTION

The presence of steep bathymetric slopes along the continental shelf break has strong influences on physical oceanography and biological productivity, and as such, shelf break systems are important regions of trophic transfer (Acha et al. 2004, Genin 2004, Yen et al. 2004, Ryan et al. 2005, He et al. 2011, Hazen et al. 2013). Enhanced productivity in shelf break regions both aggregates and attracts lower- and mid-trophic level species (Herman et al. 1981, Munk et al. 1995, Mackas et al. 1997, Young et al. 2001, Colloca et al. 2004, Genin 2004). The resulting increase in prey densities at these fixed locations creates persistent and predictable foraging areas for marine predators, and notably for air-breathing predators whose prey can be aggregated or advected into shallower, more accessible waters (Waring et al.

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2001, Yen et al. 2004, Freeman et al. 2010, Okkonen et al. 2011). In particular, submarine canyons along the shelf break have steep and complex bathymetry and create foraging habitat for deep-diving odontocetes such as sperm whales and beaked whales (e.g. Hooker et al. 1999, Waring et al. 2001, Moors-Murphy 2014). Examining the habitat use of marine predators within shelf break systems is necessary to understand the impact of these systems on food web dynamics in pelagic ecosystems. While the influence of shelf break systems on the abundance and distribution of marine predators has been well documented (Springer et al. 1996, Catard et al. 2000, Waring et al. 2001, Yen et al. 2004, Suryan et al. 2006, Freeman et al. 2010), fewer studies have analyzed animal movement to elucidate how shelf break regions influence foraging behavior specifically (Suryan et al. 2006).

Pilot whales *Globicephala* spp. are deep-diving odontocetes that occur in shelf break regions and forage at depths of >800 m (Baird et al. 2002, Heide-Jørgensen et al. 2002, Garrison 2007, Aguilar Soto et al. 2008, Jensen et al. 2011, Baird 2016, Quick et al. 2017). Information on the spatial habitat use of pilot whales in the northwest Atlantic is limited and, until recently, most information on their habitat use in this region was derived from shipboard and aerial surveys (although see Mate et al. 2005). Like many marine mammals, pilot whales use habitats over large spatial and temporal scales (e.g. Lewison et al. 2004, Moore 2008), making it difficult to understand patterns of movement from survey data alone. Furthermore, 2 species of pilot whale exist in the northwest Atlantic: short-finned (*G. macrorhynchus*) and long-finned (*G. melas*) pilot whales. These 2 species are difficult to distinguish reliably at sea, except with close approaches under ideal conditions (Rone & Pace 2012). The 2 species are believed to differ in their ecology and habitat use (Gannon et al. 1997, Mintzer et al. 2008, Hayes et al. 2017), but our understanding of their individual distribution, habitat use, and demography is incomplete (Hayes et al. 2017).

In the northwest Atlantic, short-finned pilot whales typically occur in subtropical and tropical waters while long-finned pilot whales are distributed further north in boreal waters, but the limits of their ranges and the area of overlap remain unclear. Long-finned pilot whales occur from Norway to New Jersey (Abend & Smith 1999, Taylor et al. 2008, Hayes et al. 2017). Short-finned pilot whales are thought to range from the southern end of Georges Bank south into the tropics (Taylor et al. 2011, Hayes et al. 2017). The 2 species likely overlap along the shelf break between New Jersey and Georges Bank, but information on the spatial and seasonal distribution of both species is limited (Hayes et al. 2017). In the United States, the respective distributions of short-finned and long-finned pilot whales are estimated by confirming species identity with biopsy samples and modeling these observations in relation to sea surface temperature (SST). Abundance estimates from shipboard surveys are then partitioned by species using the probability of each species' occurrence based on SST (Hayes et al. 2017). Most pilot whale sightings can be attributed to a species using this approach, but the sightings represent only a snapshot in time and space of each species' habitat use and may not reflect the dynamic nature of the ranges of these species. Detailed information on species-specific habitat use is required to develop a more precise understanding of the distribution of both species and their overlap.

In addition, a better understanding of patterns of movement, habitat use, and behavior is necessary in order to generate a full assessment of the threats faced by these species. Off the US Atlantic coast, short-finned pilot whales interact with a pelagic longline fishery for swordfish and tuna (Garrison 2007). As a result of interactions with the pelagic longline fishery, entanglements resulting in mortality and serious injury (M/SI) are relatively common; the short-finned pilot whale is the most frequently taken marine mammal species in this fishery (Garrison 2007). Under the US Marine Mammal Protection Act, if M/SI exceeds sustainable levels, estimated as the potential biological removal (PBR) level, fishermen, scientists, and managers must work together to develop strategies to reduce takes to below PBR. The total annual estimated fishery-related M/SI of short-finned pilot whales in the pelagic longline fishery recently exceeded PBR for this stock (Hayes et al. 2017). With our current level of understanding of pilot whale habitat use, it is difficult to develop effective management strategies for the species. An improved understanding would provide managers with knowledge regarding where the risk of pilot whale–longline interactions is greatest. Observations of short-finned pilot whale bycatch in the pelagic longline fishery have suggested that they occur in proximity to the deep slope waters of the continental shelf within the Mid-Atlantic Bight (MAB) (Garrison 2007), but the influence of the shelf break and submarine canyons on pilot whale foraging behavior has not been investigated to date.

Foraging behaviors of marine mammals can be developed through social learning (Rendell & Whitehead 2001), and as a result, marine mammals can show a great deal of intraspecific variability in foraging behavior (e.g. Baird & Dill 1995, Nowacek 2002, Estes et al. 2003, Sargeant et al. 2005). In addition, animals respond to spatial heterogeneity in resources, and foraging behavior can be focused at different spatial scales (Fauchald 1999, Pinaud & Weimerskirch 2005). Thus, to understand patterns of pilot whale foraging behavior relative to environmental features, it is important to account for both individual effects and to control for the spatial scales at which animals interact with their environment (Levin 1992, Pinaud & Weimerskirch 2005).

The objectives of the present study were to (1) describe the movements and scales of foraging behavior for individual satellite-tagged short-finned pilot whales in the MAB, and (2) investigate how their patterns of habitat use and foraging behavior are influenced by bathymetric features.

MATERIALS AND METHODS

Study area

The continental shelf break in the MAB is characterized by steep bathymetric relief between depths of 200 and 1000 m (Fig. 1). A series of submarine canyons are located along the shelf break, extending from waters offshore of Norfolk, Virginia north to the Gulf of Maine. North of Cape Hatteras, North Carolina, the Gulf Stream separates from the continental shelf and flows northeast, and the location of the Gulf Stream and associated Gulf Stream warm core rings strongly impact the oceanography and ecology of organisms in the MAB (e.g. Planque & Taylor 1998, Conversi et al. 2001, Borkman & Smayda 2009, Nye et al. 2011).

Satellite telemetry

We deployed 29 Wildlife Computer SPOT5 tags in the Low Impact Minimally Percutaneous External-electronics Transmitter (LIMPET) configuration on short-finned pilot whales *Globicephala macrorhynchus* off Cape Hatteras in 2014 and 2015 (Fig. 1). The tags were programmed to transmit data daily for the first 60 d of the deployment, every 3rd day for the subsequent 21 d, and every 5th day for the remainder of the deployment. In addition, we deployed Mk10-A satellite-linked depth-recording tags (Wildlife Computers) on 8 short-finned pilot whales. Mk10 tags were programmed to transmit data daily for the first 20 d of the deployment, every third day for the subsequent 30 d, and every ninth day for the remainder of the deployment. Tags were remotely deployed into the dorsal fin or base of the dorsal fin using a pneumatic projector and attached with two 6.8 cm titanium darts with backward-facing petals. Tags were deployed in both the spring and fall of 2014 and 2015, and tag transmissions through the first week of January 2016 were included in the analysis. Tag data used in analyses covered the months of May through the end of December in 2014, and May 2015 through early January 2016 (see Table 1). Two tags transmit-

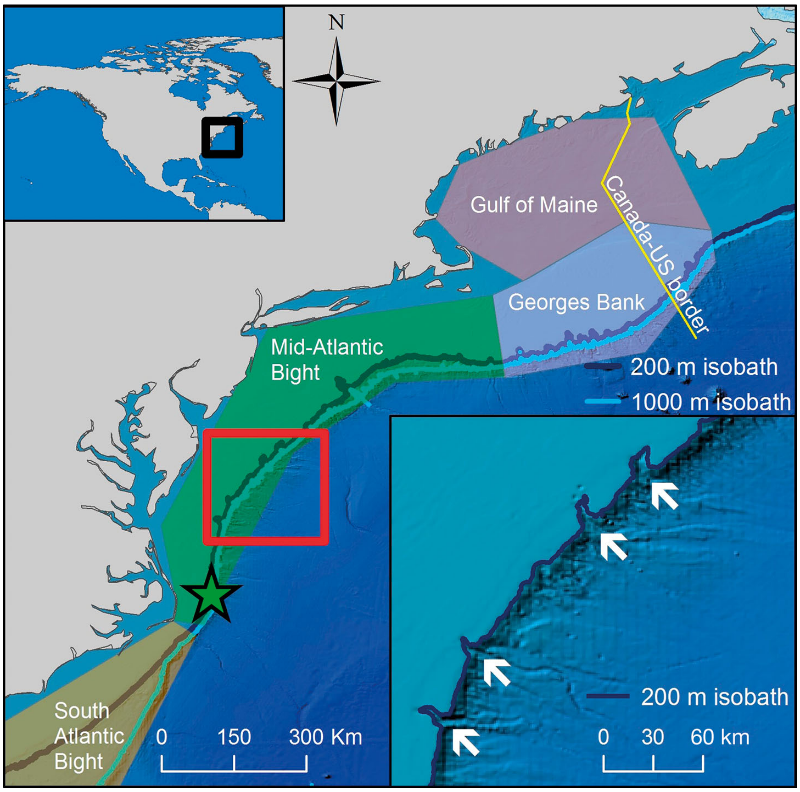

Fig. 1. Bathymetric relief and regional designations. Upper-left inset: Black square indicates the study area in North America. Lower-right inset is a zoom-in of the area marked by the red square and highlights submarine canyons (indicated with arrows, from lower left to top right: Norfolk Canyon, Washington Canyon, Baltimore Canyon, and Wilmington Canyon) relative to the 200 m isobath. Green star: *Globicephala macrorhynchus* tagging location off of Cape Hatteras, North Carolina. Regional designations follow those used by the US Northeast Fisheries Science Center (e.g. Fratantoni et al. 2015)

ted locations for < 1 d and were excluded from analyses. In 4 cases, tags were deployed on pairs of pilot whales from the same social group that showed similar patterns of movement over the course of their tracks. We therefore removed the shorter track of each pair from analyses to avoid pseudoreplication, resulting in a sample size of 33 tags. Tag data were processed with the Douglas Argos-Filter to remove erroneous location estimates (Douglas et al. 2012; user-defined settings: maximum rate of movements = 15 km h^{-1}, maximum redundant distance = 3 km, default rate coefficient for marine mammals = 25, location classes 2 and 3 retained). Filtered data were used to produce 75% and 95% kernel density estimates (KDEs) in the Geospatial Modelling Environment (www.spatialecology.com/gme/) to represent habitats frequently used by pilot whales (e.g. Cianfrani et al. 2011, Pendoley et al. 2014, Mei et al. 2017).

Environmental data

A close relationship between pilot whale movements and both shelf break and canyon features was apparent during our exploratory data analysis. To assess the influence of these features on pilot whale foraging behavior, we used the 200 m isobath, generated from GEBCO bathymetric grids (30 arc-second resolution; www.gebco.net/data_and_products/gridded_bathymetry_data/), as a proxy for the location of the shelf break. Short-finned pilot whales typically forage at depths of 200–1000 m in our study area (Quick et al. 2017), so consequently we identified canyons by examining valleys in the continental shelf slope that were evident in both the 200 m and 1000 m isobaths. We defined canyons as deep, steep-sided valleys that extended into the continental shelf for >5 km in the cross-shelf direction of the 200 m isobath (Fig. 1, lower-right inset).

Environmental effects on foraging behavior

We used first passage time (FPT) to evaluate pilot whale foraging behavior. FPT is a scale-dependent metric used to indicate how much time an animal spends in a given area along its path of movement (Fauchald & Tveraa 2003, Kappes et al. 2010). FPT can be calculated across a range of scales for each animal's path to identify the spatial extent of area-restricted search (ARS) for that individual (Suryan et al. 2006, Robinson et al. 2007). ARS behavior, demonstrated by decreased speed and increased turning rates, is often used to restrict movements to areas of increased resource density (Curio 1976, Kareiva & Odell 1987). Thus, FPT can be used to indicate foraging behavior along an animal's track, with regions of high FPT representing intensive foraging behavior (Kappes et al. 2010). The extent of the ARS can be identified from FPT by identifying the scale at which there is a peak in the variance of log-transformed FPT (Fauchald & Tveraa 2003).

We restricted our analysis of FPT to initial periods of each track with daily satellite transmissions, because duty-cycled data may influence the apparent spatial scale of the ARS. We calculated FPT at spatial scales of 2–150 km at increments of 2 km and identified the ARS scale for each individual. To compare FPT among individuals, we then scaled FPT by the spatial scale of the ARS (FPT divided by the area of a circle whose radius is the ARS scale; Kappes et al. 2010). We used the approach of Suryan et al. (2006) to reduce spatial autocorrelation in FPT data. Briefly, we identified the location with the maximum FPT value (representing the most intensively searched area) within the ARS radius, excluded all other locations within 2× the ARS radius of that location to exclude locations with overlapping radii, and then selected the location with the maximum FPT from the remaining locations. Following exploratory analyses, we assessed differences in FPT close (less than the median distance of 4500 m) vs. far (greater than the median value) from the shelf break and within vs. outside of canyons, using nested ranks tests with 10 000 bootstrap iterations. Ranks tests are mixed-model extensions of the Wilcoxon test in which treatment (distance to shelf break, inside or outside canyons) is a fixed effect and group membership (individual) is a random effect. We restricted the sample for the nested ranks test to individuals tracked in regions both close and far from the shelf break (n = 18) and inside and outside canyons (n = 14). Lastly, we examined locations of maximum FPT on a weekly basis to investigate broader relationships of foraging effort with bathymetry. FPT analyses were conducted in the R statistical package (version 3.1.2) using the adehabitatLT (version 0.3.20) and the nestedRanksTest (version 0.1) libraries.

RESULTS

Patterns of habitat use

Tagged pilot whales were highly mobile, traveling 192–7879 km (mean: 2758 km), and extending 50–1314 km (mean: 356 km) from the tagging location,

Table 1. Tag deployments for *Globicephala macrorhynchus* tagged off of Cape Hatteras in 2014 and 2015. Tags were programmed to switch from daily to less frequent transmissions after 20–60 d of deployment (detailed in 'Materials and methods'), and only daily transmissions were used for analyses of first passage time (FPT). Prop.: proportion

Tag ID	Date of deployment (mo/d/yr)	End date (mo/d/yr)	Duration (d)	Total min. horizontal distance traveled (km)	Farthest horizontal distance traveled (km)	Min. latitude (°N)	Max. latitude (°N)	Min. longitude (°W)	Max. longitude (°W)	Duration included in FPT analysis (d)	Prop. time in Gulf Stream
GmTag085	5/14/14	6/20/14	37.43	1252	195	35.57	37.41	74.36	75.05	14.48	0.00
GmTag086	5/14/14	7/31/14	78.46	3764	330	34.84	38.40	73.48	75.34	57.49	0.00
GmTag087	5/18/14	11/27/14	193.72	7879	881	34.08	40.36	66.43	75.98	57.79	0.02
GmTag088	6/7/14	9/23/14	108.84	6273	1191	35.26	40.00	62.18	74.84	57.88	1.00
GmTag090	6/8/14	8/1/14	54.29	2832	385	35.25	38.83	72.83	74.91	54.29	0.00
GmTag092	6/11/14	7/29/14	48.91	2241	304	35.13	38.47	73.44	75.00	48.91	0.00
GmTag094	6/11/14	9/2/14	83.48	3049	471	35.43	39.56	72.20	74.95	57.70	0.00
GmTag095	6/11/14	9/2/14	83.50	2646	428	35.62	39.20	72.43	74.90	57.23	0.00
GmTag097	9/11/14	10/12/14	31.34	1227	50	35.20	35.90	74.64	74.98	31.34	0.00
GmTag098	9/11/14	10/8/14	27.61	1372	226	33.82	35.71	74.50	75.97	18.90	0.00
GmTag099	9/11/14	11/13/14	63.31	2754	209	35.45	37.44	74.29	74.94	57.91	0.00
GmTag101	9/13/14	10/15/14	32.12	1483	187	35.42	37.34	74.37	74.95	32.12	0.00
GmTag102	9/13/14	9/22/14	9.29	533	156	35.47	37.08	74.57	74.89	9.29	0.00
GmTag103	9/13/14	12/31/14	109.18	4085	248	35.15	37.22	72.69	75.01	58.14	0.15
GmTag122	5/16/15	7/13/15	58.04	2834	338	35.55	38.51	73.22	74.94	58.04	0.00
GmTag123	5/16/15	5/24/15	8.76	518	166	35.59	37.08	74.53	74.94	8.76	0.00
GmTag124	5/16/15	7/15/15	60.78	3043	342	35.49	37.71	71.88	75.08	57.79	0.42
GmTag125	5/19/15	10/5/15	139.12	3211	214	35.48	37.53	74.44	75.04	58.03	0.00
GmTag126	5/19/15	7/2/15	44.53	2168	530	35.62	39.77	71.77	74.96	44.53	0.00
GmTag127	5/19/15	6/18/15	30.77	1364	166	35.53	37.13	74.54	74.97	19.09	0.00
GmTag128	6/16/15	7/24/15	38.43	1734	154	35.46	37.10	74.49	74.93	38.43	0.00
GmTag129	6/16/15	6/24/15	8.75	471	163	35.63	37.11	74.57	74.96	8.75	0.00
GmTag130	6/16/15	12/31/15	198.48	6001	484	33.51	39.53	72.15	76.47	57.86	0.00
GmTag131	6/16/15	9/18/15	94.07	6974	1315	35.65	41.99	60.76	74.83	58.03	1.00
GmTag134	10/15/15	12/11/15	57.18	2595	191	34.10	36.30	73.89	75.79	57.18	0.11
GmTag135	10/15/15	11/14/15	30.83	1660	193	34.10	36.33	73.88	75.75	19.10	0.20
GmTag136	10/16/15	1/3/16	79.19	2280	173	35.23	37.09	74.47	74.96	58.17	0.01
GmTag137	10/20/15	1/4/16	76.25	4288	330	35.38	38.32	73.25	74.92	58.29	0.00
GmTag138	10/20/15	11/13/15	24.55	1465	266	35.78	38.10	72.89	74.74	18.99	0.18
GmTag139	10/20/15	12/23/15	64.08	6890	1215	33.89	39.17	61.49	75.00	64.08	0.76
GmTag140	10/20/15	10/26/15	6.49	192	156	35.64	37.05	74.63	74.72	6.49	0.00
GmTag141	10/20/15	11/23/15	34.20	2152	198	35.49	37.47	73.16	74.89	34.20	0.48
GmTag142	10/21/15	1/5/16	76.43	2856	217	35.44	37.23	73.22	74.97	58.35	0.13

ters, with some individuals using both habitats (Fig. 3). Most animals were associated with the shelf break for much or all of their track. More than 75% of all locations occurred within 10 km of the shelf break and more than half (57%) occurred within 5 km of the shelf break. Pilot whales that were associated with the shelf break moved back and forth along the shelf break repeatedly. This behavior was observed in all months in which tags were transmitting (Figs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m584p245_supp.pdf). Twelve pilot whales were associated with offshore Gulf Stream waters for some portion of their track. Of these animals, 3 were observed in offshore Gulf Stream waters for more than half of their track (Table 1), closely following Gulf Stream meanders into distant offshore waters (Fig. 4); the others spent shorter periods in Gulf Stream waters before returning to the shelf break.

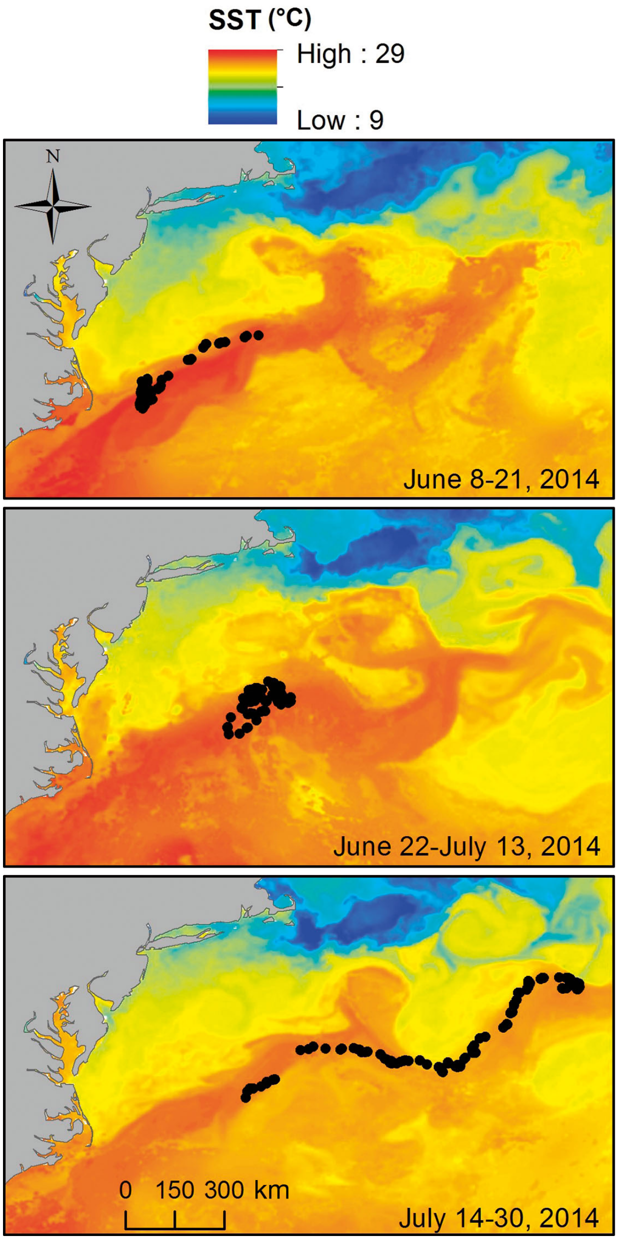

Fig. 4. Sequential locations of an individual satellite-tagged *Globicephala macrorhynchus* (GmTag088; see Table 1) in the Gulf Stream in June and July 2014. Only the outbound portion of the track is shown to highlight the close relationship between pilot whale movements and Gulf Stream features. Sea surface temperatures (SSTs) shown are daily Level 4 Group for High Resolution Sea Surface Temperature (GHRSST) SST data from June 15, June 30, and July 22, respectively

Area-restricted foraging behavior

All tagged pilot whales showed ARS behavior, but there was considerable variability in the scale of their ARS (Fig. 5). ARS scales varied from 2 to 148 km (mean: 24 km), with 27 of 31 tracks showing an ARS scale of 40 km or less. Due to the limited sample of animals that associated with the Gulf Stream during daily satellite transmissions, we focused our analysis of FPT on tagged whales showing the shelf break-associated foraging pattern. FPT was significantly higher close to the shelf break (nested ranks test, $p = 0.0004$) and within submarine canyons (nested ranks test, $p = 0.0001$), reflecting higher foraging effort in these regions (Fig. 6). Analyses of high FPT along individual tracks and maximum FPT for each individual on a weekly basis further highlighted the importance of submarine canyons to their foraging habitat (Fig. 7, Fig. S3 in the Supplement).

DISCUSSION

Our analyses demonstrate that the continental shelf break provides important foraging habitat for short-finned pilot whales in the northwest Atlantic. Most of the tagged pilot whales in this study focused their foraging efforts close to the shelf break, and long-duration tag deployments on pilot whales that foraged in the Gulf Stream indicated that these animals returned to forage on the shelf break following excursions into offshore Gulf Stream waters. The biological effects of ocean currents interacting with steep slopes along the continental shelf break likely carry up to these upper trophic level species by aggregating prey species and/or by making prey more accessible, thus highlighting the importance of biophysical coupling and trophic transfer in shelf break ecosystems.

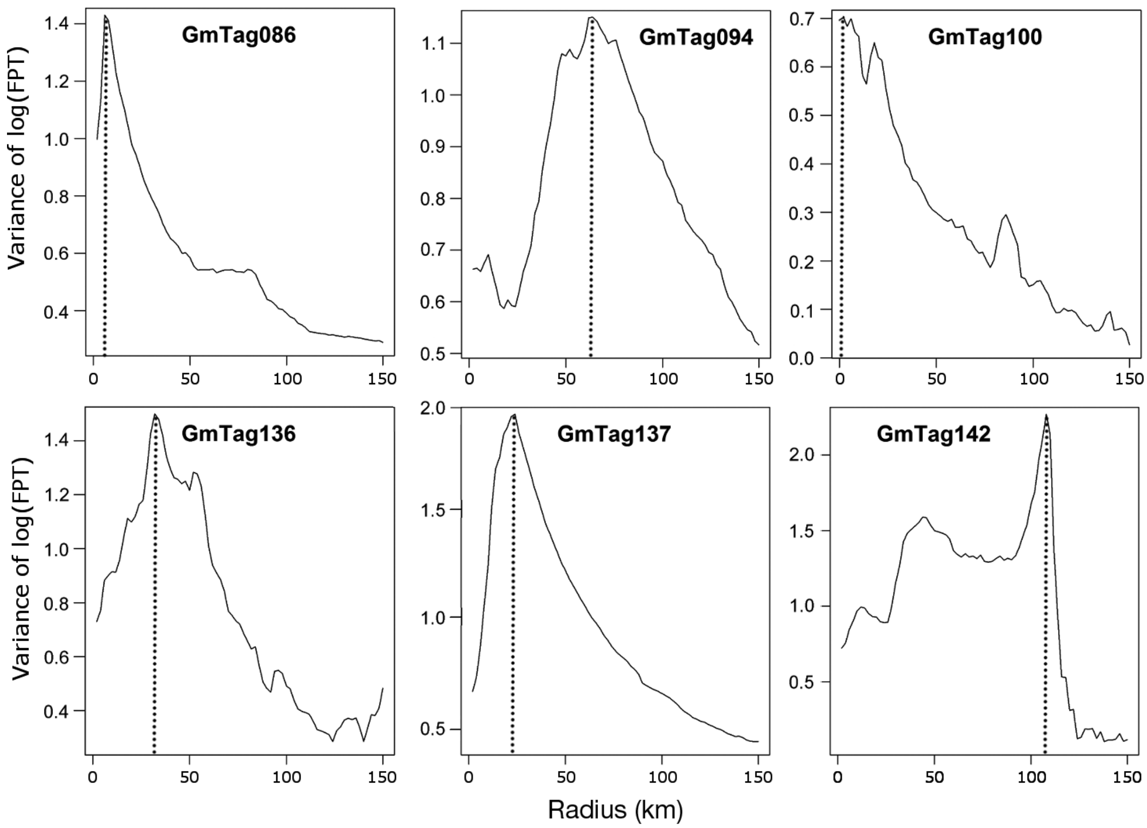

Fig. 5. Examples of variance in log(FPT) as a function of radius for *Globicephala macrorhynchus* telemetry tracks (see Table 1 for tag IDs). Peak in variance was used to indicate scale of the area-restricted search (dashed line). FPT: first passage time. GmTag 100 was not included in the final analysis

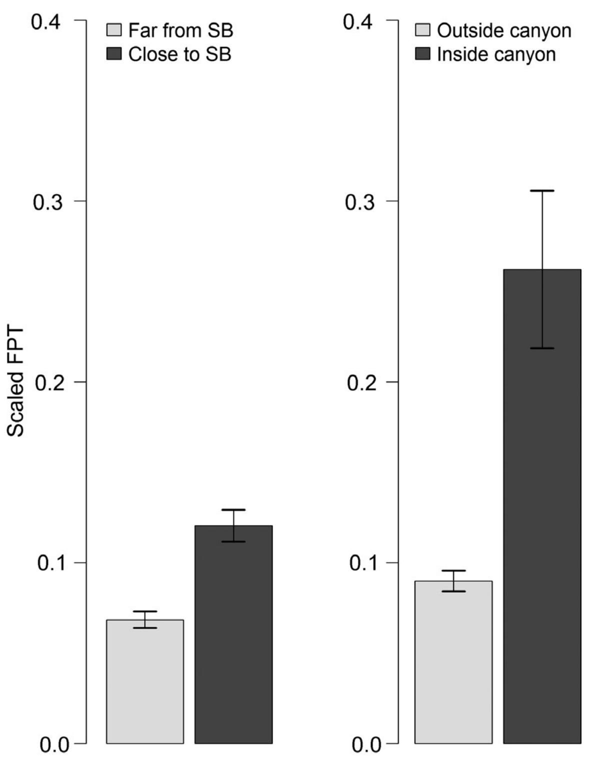

Fig. 6. Scaled first passage time (FPT) of *Globicephala macrorhynchus* relative to proximity to shelf break (SB; close: <4.5 km from 200 m isobath, far: >4.5 km from 200 m isobath) and occurrence within submarine canyons (mean ± SE). Units of scaled FPT are h km^{-2}; e.g. FPT of 30 h within a 6 km area-restricted search radius would result in a scaled FPT of 0.27 (30 h divided by the area of a 6 km-radius circle)

Our results have implications for stock structure and management of short-finned pilot whales. In the US Atlantic exclusive economic zone (EEZ), the species is managed as a single stock that ranges from Florida to New England (Hayes et al. 2017). Despite the extensive northward movements of whales tagged off Cape Hatteras, we were surprised that none of the tagged whales moved further south into the South Atlantic Bight (SAB). We hypothesize that shelf break waters off of Cape Lookout may act as a biogeographic boundary that could influence the stock structure of short-finned pilot whales. Further, we postulate that the use of shelf break habitats by short-finned pilot whales in the MAB may play a role in limiting the distribution of these animals to waters

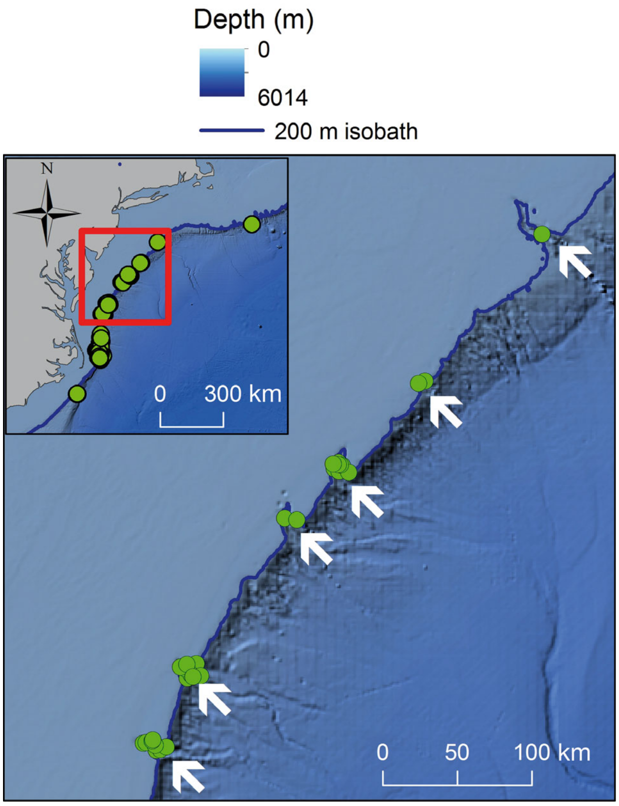

Fig. 7. Location of maximum first passage time (FPT) by week for all individual *Globicephala macrorhynchus* foraging in shelf break waters (inset: study area) relative to submarine canyons (indicated by arrows, from lower left to top right: Norfolk Canyon, Washington Canyon, Baltimore Canyon, Wilmington Canyon, Lindenkohl Canyon, and Hudson Canyon)

north of the SAB. The distribution of our tagged pilot whales was closely linked to steep bathymetric slopes occurring within their typical foraging depth range (approximately 200–1000 m depth). This may explain why the distribution of tagged pilot whales was focused north of Cape Lookout, since the continental shelf drops off much more gradually and steeper slopes are located in deeper waters south of this region (Fig. 1). Data from satellite tags deployed on 4 short-finned pilot whales in the SAB suggest that animals in the SAB show very different movement patterns than those to the north, with little or no association with the shelf break (A. J. Read unpubl. data). We suggest that the pilot whales occurring north of Cape Lookout might have developed specialized foraging behaviors for targeting steep bathymetric gradients in this region, and their latitudinal distribution may be limited by regions along the shelf break with steep gradients where this foraging strategy is effective.

Individual pilot whales varied considerably in the scale of their ARS behavior, though individuals consistently used shelf break and canyon habitats while foraging. Observed scales of ARS were generally small (mean: 24 km) compared to scales of movement (Table 1), indicating that pilot whales focus their foraging efforts at a fine scale in spite of their highly mobile nature. In addition to showing considerable individual variability, cetacean foraging behavior can vary geographically, and foraging behavior can influence population structure (e.g. Lusseau et al. 2006, Hoelzel et al. 2007, Ansmann et al. 2012, Daura-Jorge et al. 2012, Mann et al. 2012). If the shelf break foraging behavior of short-finned pilot whales limits their distribution to waters of the MAB, this foraging specialization could limit interactions with pilot whales further south. Comparisons of the movements, foraging behavior, and habitat associations of short-finned pilot whales in the SAB and MAB are needed in order to assess whether there might be separate stocks of short-finned pilot whales in the US Atlantic EEZ, and to determine whether foraging behavior might play a role in maintaining stock structure. In addition to broad-scale geographical differences in foraging behavior, pilot whales have long-term social bonds which could lead to foraging specializations within social groups (Amos et al. 1993, Ottensmeyer & Whitehead 2003, Mahaffy et al. 2015). Tracks from multiple individuals within different social groups are required to investigate how social structure might influence foraging behavior between groups of short-finned pilot whales in the MAB.

The limited information on pilot whale diet in the northwest Atlantic suggests that short-finned pilot whales forage on pelagic cephalopods (e.g. *Brachioteuthis riisei*, *Taonius pavo*, *Histioteuthis reversa*; Mintzer et al. 2008), but the distribution of these prey species has not been well documented. Pilot whales may use steep bathymetric gradients and fine-scale variation in bottom topography along the shelf break as a physical barrier against which to herd prey, much like other cetaceans which herd prey against the surface (Würsig 1986, Vaughn et al. 2008). Submarine canyons occurring along the shelf break were used intensively by foraging short-finned pilot whales. Canyons provide important foraging areas for marine mammals (e.g. Schoenherr 1991, Hooker et al. 1999, Waring et al. 2001, Benoit-Bird et al. 2004, Croll et al. 2005, Rennie et al. 2009), and our telemetry data demonstrate the extent to which the foraging habitat of individual pilot whales was dominated by canyons. Like other types of abrupt topographies, canyons can create concentrations of lower trophic level species, and upwelling flow within canyons can influence the vertical and horizontal distribution of marine organisms (Allen et al. 2001, Bosley et al. 2004). Euphasiids and mesopelagic prey can be advected upward and towards canyon walls (Bosley et al. 2004), and upwelling that aggregates and advects prey into shallower waters is likely an important mechanism providing enhanced foraging opportunities for marine mammals (Schoenherr 1991, MacLeod & Zuur 2005). Analyses of dive behavior will be useful for examining foraging behavior within and outside of canyons.

Shelf break canyons vary considerably in size, and previous studies have suggested that large canyons are likely to support larger numbers of cetaceans than smaller features (Wimmer & Whitehead 2004). The largest canyon within our study area is Hudson Canyon, which is also the northernmost canyon targeted by foraging pilot whales in our study. Hudson Canyon clearly stands out in plots of pilot whale habitat use as a region of increased density (see the 75% KDE in Fig. 2), suggesting that pilot whales may travel north to forage within this large submarine canyon.

Submarine canyons contain a diversity of undersea habitats, support high densities of marine organisms, and are considered to be important conservation hotspots in marine environments (Vetter & Dayton 1998, Hooker et al. 1999, Yen et al. 2004, Mortenson & Buhl-Mortenson 2005, De Leo et al. 2010, Vetter et al. 2010). The Gully, a large submarine canyon off eastern Canada, was designated as a Marine Protected Area in 2004, due in large part to a small population of northern bottlenose whales *Hyperoodon ampullatus* occurring in this region and increasing threats due to oil and gas exploration and development (Whitehead et al. 1997, Gowans et al. 2000, Wimmer & Whitehead 2004). Hudson Canyon was recently nominated as a national marine sanctuary due to its importance as habitat to a variety of marine organisms, and our results suggest that sanctuary designation in Hudson Canyon could protect important foraging habitat for short-finned pilot whales. However, pilot whales are highly mobile and regularly transit out of canyons and along shelf break regions throughout the MAB and thus conservation and management efforts for the species should include additional areas and measures in order to be effective.

Tagged short-finned pilot whales moved further north than expected, with 1 animal traveling into Canadian waters as far north as 42° N latitude, near the Northeast Channel, during August 2015. As far as we are aware, this is the first confirmed record of the species occurring in waters off eastern Canada, although short-finned pilot whales occur regularly in waters off western Canada (Stacey & Baird 1993). Waters on the continental shelf of the northeast USA have experienced high rates of warming in the last few decades (Friedland & Hare 2007, Belkin 2009, Pershing et al. 2015), and it is unclear whether our observations of short-finned pilot whales in more northerly waters represent a distributional shift in association with increases in water temperature, or whether limited observations with genetic samples confirming species identity in previous studies prevented a more complete understanding of short-finned pilot whale range. Regardless, our results suggest that short-finned pilot whales regularly use habitats throughout the northeastern seaboard of the USA, where the majority of interactions between pilot whales and the US pelagic longline fishery occur (Garrison 2007). Movements and foraging behavior of tagged short-finned pilot whales indicate that this species is closely associated with the shelf break, except when foraging in offshore Gulf Stream waters where interactions with the US pelagic longline fishery are not observed (Garrison 2007). This constrained distribution suggests that spatial approaches to mitigating pilot whale–longline interactions with the US fishery may be feasible and merits further investigation.

Some of our tagged pilot whales periodically ventured from the Cape Hatteras region into distant pelagic waters, following Gulf Stream meanders before returning to the shelf break. These offshore movements into international waters suggest that pilot whales are potentially also overlapping with fisheries outside of US waters, and that interactions between pilot whales and longlines in the high seas could represent an additional source of mortality for the northwest Atlantic stock of short-finned pilot whales. At the present time it is unclear what triggers pilot whales to undertake movements into distant offshore waters, or what impels them to return to the shelf break. Of course, it is possible that the Gulf Stream foraging strategy we observed is simply a bias associated with the location of our tag deployments on the shelf break off Cape Hatteras. Tagging efforts in Cape Hatteras are ongoing and future deployments in other regions will help to investigate pilot whale movements in association with the Gulf Stream in more detail.

We found that the Cape Hatteras region is an important hotspot of short-finned pilot whale density and foraging habitat (Figs. 2 & 7). We selected the

Cape Hatteras shelf break as the site for tag deployment due to the extremely high densities of pilot whales occurring there, and we found that tagged pilot whales returned to Cape Hatteras repeatedly during tag deployments. Off Cape Hatteras, cool, low-salinity waters of the MAB converge with warm, high-salinity waters of the SAB along the continental slope, creating a strong temperature and salinity front known as the Hatteras Front (Berger et al. 1995, Savidge 2002). The Hatteras region hosts an abundance of fish and upper trophic level predators (e.g. Magnuson et al. 1981, LaBrecque 2006, Mansfield et al. 2009), and likely creates enhanced foraging opportunities for pilot whales.

Our results demonstrate the foraging associations and highly mobile nature of short-finned pilot whales and emphasize the importance of shelf break systems and associated submarine canyons to the foraging habitat of deep-diving marine predators. Further, our results have implications for the management of short-finned pilot whales within the US Atlantic EEZ; our findings raise questions about the stock structure of short-finned pilot whales, and suggest that the shelf break and associated submarine canyons in this region should be the focus of conservation and management efforts for this species.

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