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ARTICLE

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The impact of temperature at depth on estimates of thermal habitat for short-finned pilot whales

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Abstract

Short-finned pilot whales (*Globicephala macrorhynchus*) experience dramatic changes in temperature during deep dives, but studies of pilot whale habitat use typically rely solely on surface temperature measurements. We quantified vertically integrated thermal habitat for short-finned pilot whales using a novel metric, degree-hours, developed using data from digital acoustic recording tags (DTAGs) deployed off Cape Hatteras along with interpolated temperature profiles at depth from the Met Office Hadley Centre EN4 oceanographic data set. We then compared estimates of thermal habitat calculated from surface waters with estimates of vertically integrated thermal habitat calculated using EN4 data collected along the eastern seaboard of the U.S. to understand how available thermal habitat is influenced by seasonal and spatial variability in water temperature. Estimates of vertically integrated thermal habitat were typically lower than estimates produced using surface temperatures, and the difference was greatest at intermediate latitudes and in warmer seasons, where and when there is a high degree of variability between surface and bottom temperatures. Our work highlights the importance of considering temperature at depth to accurately assess the thermal habitat of deep-diving marine vertebrates, and presents a means of quantifying thermal habitat that will be useful for understanding the thermal ranges of these species.

KEYWORDS
dive behavior, DTAG, *Globicephala macrorhynchus*, short-finned pilot whale, spatiotemporal distribution, temperature at depth, thermal habitat

1 | INTRODUCTION

Temperature is an important driver of the spatial distribution of marine mammals (Becker et al., 2010; Brown and Winn, 1989; Griffin, 1999). The distribution of these animals is often associated with oceanographic features, such as thermal fronts, which can create enhanced foraging opportunities (Brown and Winn, 1989; Doniol-Valcroze et al., 2007; Griffin, 1999; Murase et al., 2002; Whitehead and Carscadden, 1985). Due to the association between temperature and marine mammal habitats, predictive spatial models often incorporate sea surface temperature (SST) as an important model parameter (e.g., Becker et al., 2010; Forney et al., 2012; Hazen et al. 2017; Kaschner et al., 2006; Thorne et al. 2019). To date, most studies have relied on measurements of surface temperature, and the role of temperature at depth in driving the habitat use, seasonal movements, and spatial distribution of most marine mammal species is very poorly understood.

Temperature at depth may be particularly important for deep-diving marine mammals. Many marine mammals dive to depths greater than several hundred meters, and Cuvier's beaked whales (*Ziphius cavirostris*) have been recorded diving to depths of nearly 3,000 m (Schorr, Falcone, Moretti, & Andrews, 2014; Shearer et al., 2019). Such deep dives result in extreme changes in the temperature regimes experienced by these animals (Aguilar Soto et al., 2008; Baird et al., 2002; Boyd, 1997; Schorr et al., 2014). The diving behavior of many deep-diving marine mammals is often studied with high resolution tags such as digital acoustic recording tags (DTAGs; Johnson and Tyack, 2003), which also provide temperature measurements at depth. However, we are not aware of studies that have assessed the potential for using temperature data recorded by DTAGs to define the thermal habitat of marine mammals at depth.

Short-finned pilot whales (*Globicephala macrorhynchus*) are deep-diving odontocetes that forage at depths of approximately 500 m to as deep as 1,500 m (Aguilar Soto et al., 2008; Quick et al., 2017). Recent telemetry studies have provided extensive observations of the movement and behavior of short-finned pilot whales in both horizontal and vertical dimensions (Quick et al., 2016; Thorne et al., 2017; Wells et al., 2013). Short-finned pilot whales are known to occur year-round at the shelf break at Cape Hatteras, off the Atlantic coast of the United States, but use waters further north during warmer months (Thorne et al. 2017, 2019). To date, however, studies examining how temperature influences patterns of habitat use in short-finned pilot whales have only relied on measurements of temperature at the surface (Garrison, 2007; Stepanuk, Read, Baird, Webster, & Thorne, 2018; Thorne et al., 2019). Due to the deep-diving nature of these whales, studies incorporating observations of temperature at depth are needed to provide a more thorough understanding of their thermal habitat use.

In the present paper, we developed a metric to compare thermal habitat in space and time, and compared estimates of thermal habitat calculated from SST with estimates of vertically integrated thermal habitat in order to understand how available thermal habitat is influenced by seasonal and spatial variability in water temperature. Specifically, we used data from DTAG deployments on short-finned pilot whales to (1) provide high resolution dive profiles in order to quantify vertically integrated thermal habitat available to short-finned pilot whales and (2) compare how estimates of thermal habitat calculated from SST and from temperature experienced at depth vary seasonally and latitudinally.

2 | MATERIALS AND METHODS

2.1 | DTAG data

We deployed Version 2 DTAGs (Johnson and Tyack, 2003) on 22 short-finned pilot whales off Cape Hatteras, North Carolina, (station 1 in Figure 1) from 2008 to 2014. DTAGs were deployed in May, June, July, September, and October (Quick et al., 2017; Table 1). Offshore waters of the Cape Hatteras region are defined by steep slopes along the continental shelf break and are heavily impacted by the Hatteras Front, a strong thermal front where cold, low-salinity waters and warm, high salinity waters converge (Berger et al., 1995; Churchill & Gawarkiewicz, 2009; Mellor & Paul, 1994; Savidge, 2002). The Hatteras region is a biologically important foraging site for short-finned pilot whales and other cetaceans (Hamazaki, 2002; Thorne et al., 2017).

DTAGs sampled pressure (depth) and temperature every 0.2 s, with the exception of one tag (Gm10_209), which was sampled at a frequency of 0.02 s and was subsequently down-sampled to 0.2 s to be consistent with the other data. Precision of the pressure and temperature data was to seven significant figures, but we rounded to two decimal places. Our classification of dive behavior followed Aguilar Soto et al. (2017) and Quick et al. (2017): *surface periods* were defined as time spent at ≤20 m, *dives* were submergences to depths >20 m but <500 m, and *deep dives* were excursions to depths ≥500 m. Two tags that did not include dives below 20 m were excluded from the analysis. All data recorded prior to the first dive were removed to account for potential behavioral changes following tag deployment.

DTAGs record temperature, but we identified temporal lags in DTAG temperature measurements relative to dive depth (described in more detail in results). As a result, we did not use these temperature measurements from the DTAGs to assess pilot whale thermal habitat.

2.2 | Vertically integrated estimates of thermal habitat

To develop estimates of vertically integrated thermal habitat, we first constructed a daily dive budget for pilot whales using the depth data collected from the DTAG deployments. We combined data from all tags and calculated the proportion of time spent in each 10 m depth bin for the combined tag data. We then extrapolated this value to a 24-hr period by multiplying the proportion of time in each 10 m depth bin by the number of hours in a day. For example, if we had 48 hr of dive data, 1 hr of which was spent at 10 m depth, the resultant proportion of time spent at 10 m would be 0.0208, and the time spent at 10 m in a 24-hr period is 0.49 hr or roughly 30 min.

To ensure that our dive data were representative of dive behavior both during the day and night, we tested for potential diel variation in time spent diving and time spent deep diving using chi-square tests. We found no significant differences in time spent diving or deep diving (for dives: $\chi^2 = 2.261$, $df = 3$, $p = .194$; for deep dives: $\chi^2 = 0.343$, $df = 3$, $p = .197$), so we did not account for diel variation in the dive budgets.

To assess available thermal habitat at depth, we used temperature profiles at the tagging location at 10 m intervals using interpolated and annually averaged temperature data from the Met Office Hadley Centre version 4 (EN 4.2.1; Good, Martin & Rayner, 2013; https://www.metoffice.gov.uk/hadobs/en4/) database with Gouretski and Resghetti (2010) corrections (Figure 2). The EN4 data set is a collection of previously recorded temperature and salinity profiles collated from various profiling instruments and oceanographic survey projects. When each profile is processed, numerous corrections are applied by the Met Office to account for differences in the sampling devices used and quality control checks are performed to provide a greater degree of accuracy and precision. The output of this data set is monthly averaged temperature profiles at 1° spatial resolution. To obtain precise temperature profiles at a fine spatial scale, linear interpolations were applied to these profiles. Since EN4 data were not available at the precise location where pilot whales were tagged, we interpolated data using a weighted sum of the nearest temperature measurements to determine temperature at the tagging location. Further, although several of the pilot whales

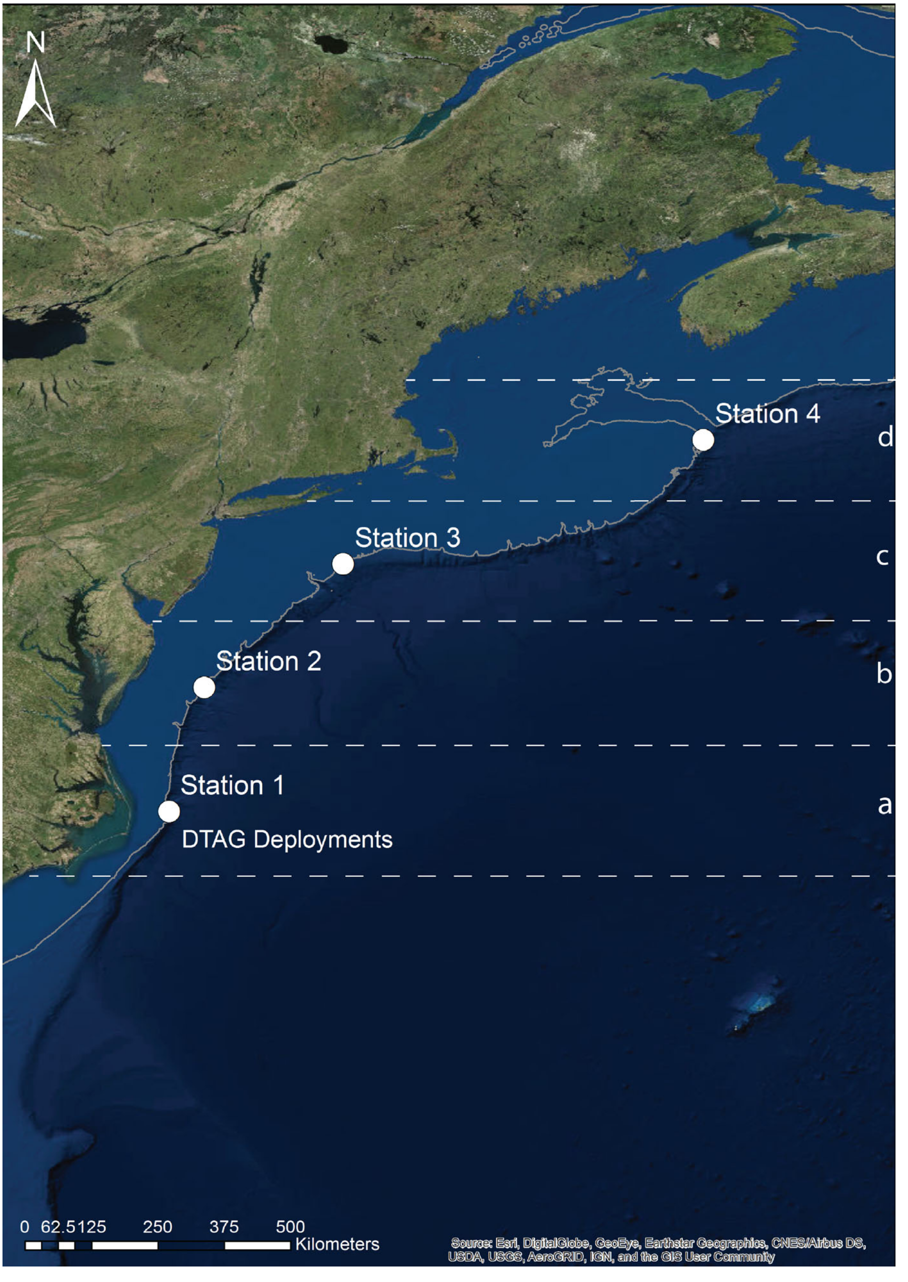

FIGURE 1 Map of four evenly spaced stations throughout the latitudinal range of short-finned pilot whales satellite tagged off Cape Hatteras used to develop estimates of available thermal habitat. Short-finned pilot whales occur in close proximity to the 200 m depth contour indicated by the dark gray line (Thorne et al., 2017), and thus all stations were located on this depth contour. Observations of satellite tagged pilot whales within regions a, b, c, and d were compared to degree-hour estimates from stations 1, 2, 3 and 4, respectively.

were tagged in waters <200 m, they later dived to depths of >200 m. Therefore, interpolated data generated from the nearest available offshore locations were used to generate temperature profiles at depth beyond 200 m. We constructed daily estimates of available thermal habitat at depth by integrating daily dive budgets with temperature

TABLE 1 Overview of DTAG deployments on short-finned pilot whales off Cape Hatteras used in analyses.

Tag name	Deployment date	Deployment latitude (°N)	Deployment longitude (°W)	Time on	Time off	Total deployment time
Gm08_143aprh	May 22, 2008	35.65	74.79	14:28	17:42	03:14
Gm08_143bprh	May 22, 2008	35.65	74.79	18:18	22:49	04:31
Gm08_147aprh	May 26, 2008	35.69	74.81	15:02	17:20	02:18
Gm08_151aprh	May 30, 2008	35.63	74.79	08:46	10:17	01:31
Gm08_151bprh	May 30, 2008	35.64	74.80	13:14	06:32	17:18
Gm10_185bprh	July 4, 2010	35.63	74.81	14:30	20:20	05:50
Gm10_186aprh	July 5, 2010	35.64	74.80	11:10	11:40	00:30
Gm10_186bprh	July 5, 2010	35.64	74.81	14:32	20:03	05:31
Gm10_187aprh	July 6, 2010	35.64	74.80	8:43	10:55	02:12
Gm10_187bprh	July 6, 2010	35.63	74.80	12:53	06:15	17:22
Gm10_208aprh	July 27, 2010	35.68	74.78	14:50	23:47	08:57
Gm10_209aprh	July 28, 2010	35.64	74.80	08:54	10:12	01:12
Gm10_209cprh	July 28, 2010	35.62	74.78	13:19	20:09	06:50
Gm10_266aprh	September 23, 2010	35.63	74.76	18:35	12:49	18:14
Gm10_267aprh	September 24, 2010	35.61	74.70	15:19	09:19	18:00
Gm11_149bprh	May 29, 2011	35.72	74.82	10:33	14:24	03:50
Gm11_150bprh	May 30, 2011	35.77	74.82	11:11	14:46	03:34
Gm11_156aprh	June 5, 2011	35.67	74.80	12:11	16:29	06:18
Gm11_165aprh	June 14, 2011	35.73	74.83	09:25	13:43	04:17
Gm14_279aprh	October 6, 2014	35.66	74.75	12:41	16:09	03:27

profiles. Vertically integrated thermal habitat was calculated in degree-hours, or the time (in hours) spent in each 1°C temperature bin multiplied by the temperature of that bin (i.e., 10 hr at 25°C would equate to 250-degree-hours).

2.3 | Comparisons of available thermal habitat in space and time

In addition to generating estimates of thermal habitat at the tagging location (represented by station 1 in Figure 1), we also generated estimates of thermal habitat at three other locations, referred to as stations, throughout the northern portion of the range of short-finned pilot whales in the Northwest Atlantic Ocean (Figure 1) to examine how available thermal habitat varied seasonally and latitudinally. These four stations were evenly spaced, with station 1 representing the tagging location at Cape Hatteras and station 4 representing the most northern latitude at which short-finned pilot whales have been observed in recent satellite tagging studies (Thorne et al., 2017). Short-finned pilot whales are strongly associated with the shelf break, as represented by the 200 m depth contour (Thorne et al., 2017), and thus all stations we sampled were located along this contour (Figure 1). We used monthly averaged data from 2007 to 2017 and averaged these values by season within 10 m depth bins (i.e., the temperature in the top 10 m bin was calculated as the average of temperatures observed at 0 m and 10 m) to generate temperature profiles representing each season. Seasons were defined as follows: Winter = February to April; Spring = May to July; Summer = August to October; Fall = November to January following Thorne et al. (2019) to allow for comparisons with this study.

We generated vertically integrated estimates of thermal habitat at each station in each season using the methodology described in Section 2.2. Since DTAG data providing high resolution dive data are not available north of

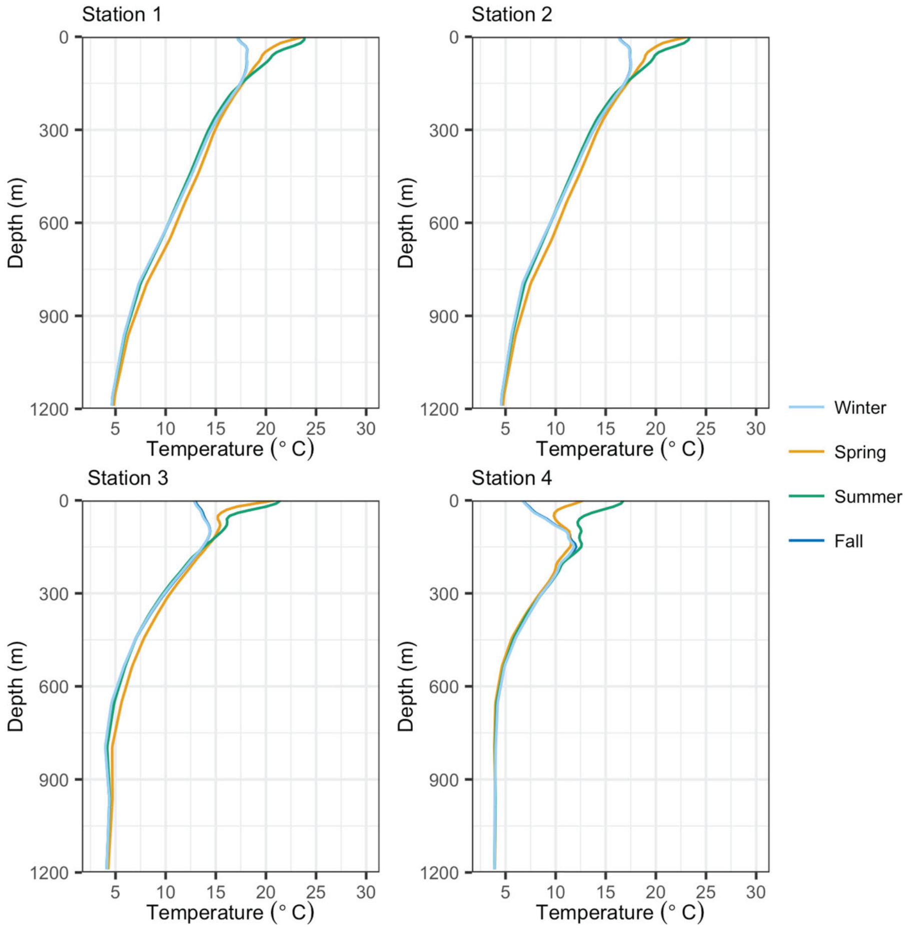

FIGURE 2 Temperature profiles in winter, spring, summer, and fall at four evenly spaced stations throughout short-finned pilot whale habitat in the northeast United States. For each respective station, fall and winter profiles were very similar, and therefore are not discernable. Temperature profiles were taken from interpolated temperature data made available by the Met Office Hadley Centre version 4 (EN 4.2.1) gridded temperature database (https://www.metoffice.gov.uk/hadobs/en4/) using the Gouretski and Resghetti (2010) correction.

Cape Hatteras, we used the daily dive budgets of pilot whales tagged at Cape Hatteras to construct estimates of available thermal habitat at all four stations. While we recognize that pilot whale dive behavior may vary considerably in space and time (Quick et al., 2017), our intention was to quantify the thermal habitat potentially available to short-finned pilot whales rather than to predict their realized thermal environment. This approach allowed us to examine seasonal and spatial variability in the estimated available thermal habitat based on variability in water temperature alone.

We compared estimates of vertically integrated thermal habitat with estimates of surface thermal habitat constructed using SST measurements derived from the EN4 interpolations (temperature at 0 m). Additionally, we used the projected vertically integrated thermal habitat to examine the proportion of time spent below 22°C. The threshold of 22°C was selected because it is commonly used to confirm sightings of short-finned pilot whales, particularly in NOAA Stock Assessment Reports (SARs),[1] as logistic regressions suggest that there is a near 0 probability of sighting a short-finned pilot whale in SSTs less than 22°C (Hayes, Josephson, Maze-Foley, & Rosel, 2017). Therefore, we used this threshold to determine if the 22°C threshold was representative of available short-finned pilot whale thermal environment below the surface. We used projected daily vertically integrated thermal habitat estimates to

TABLE 2 Mean temperature, temperature range in °C, and the proportion of time spent below 22°C (Prop. time) from estimates of depth-integrated thermal habitat for short-finned pilot whales by season at the four evenly spaced study stations in the northeast United States.

	Station 1			Station 2			Station 3			Station 4		
Season	Mean	Range	Prop. time	Mean	Range	Prop. time	Mean	Range	Prop. time	Mean	Range	Prop. time
Winter	16.32	5.16–18.14	1.00	15.54	5.00–17.53	1.00	11.99	3.98–14.40	1.00	7.45	3.93–11.84	1.00
Spring	20.29	5.46–23.74	0.45	19.66	5.30–23.18	0.45	16.68	4.47–20.80	1.00	10.88	3.89–12.76	1.00
Summer	20.51	5.21–23.87	0.39	19.92	5.06–23.37	0.40	17.24	4.18–21.45	1.00	13.73	3.95–16.77	1.00
Fall	16.35	5.18–18.13	1.00	15.59	5.02–17.49	1.00	12.09	4.02–14.43	1.00	7.50	3.93–12.04	1.00

examine the possible amount of time that would be spent below 22°C, the mean temperature, and the temperature range for short-finned pilot whales at the four stations in each season.

All analyses were conducted in the R version 3.2.1 base package (R Core Team, 2016).

3 | RESULTS

The length of DTAG deployments ranged from 1.23 hr to 18.23 hr (Table 1). The maximum dive depth was 1,077 m and lasted for a total of 20.60 min. We observed temporal lags in DTAG temperature measurements relative to dive depth. This phenomenon, termed hysteresis, has been documented in other marine mammal tagging technology resulting in biased data collection (Hooker & Boyd, 2003; Irvine, Windsor, Follett, Mate, &Palacios, 2020; Mensah et al., 2018; Nakanowatari et al., 2017). This bias can, at times, be corrected using post hoc calibration of the tags (Hooker & Boyd, 2003), however, this option was not available to us as the data had been collected years prior to these analyses. We found that time lag varied considerably among tag deployments (χ^2 = 49.18, p = 1.73 × 10^{-4}, df = 19; Figures S1 and S2) and were not dependent on dive depth or duration. Recorded DTAG temperature ranged from 4.66°C to 29.54°C, which had a higher maximum temperature than the temperature profile measurement at station 1 in both the spring and summer (Table 2), possibly due to solar radiation at the surface increasing the internal tag temperature. Since we could not quantify or correct for the temporal lags, we did not use DTAG temperature data in further analyses.

Tagged pilot whales spent most (57%) of their time at or above depths of 20 m (Figure 3). More time was spent in dives between 20 and 500 m (36%) than in deep dives below 500 m (7%; Figure 3). At all stations and in all seasons, a wide range of temperatures was observed in available thermal habitat (Table 2). At stations 1 and 2, where pilot whales are thought to occur year-round (Thorne et al. 2017, 2019), temperature at depth differed from surface temperatures by as much as 18°C.

For each representative station, temperature profiles in winter and fall were similar (Figure 2). Surface and subsurface temperatures in spring and summer were also similar for stations 1–3. Spring and summer surface profiles were considerably warmer than surface profiles for fall and winter for each station. The similar temperature profiles in winter and fall between stations resulted in very similar vertically integrated thermal habitat estimates for each station, while the warmer surface profiles during spring and summer resulted in warmer overall vertically integrated thermal habitat projections in these seasons and a greater amount of time spent in warmer waters (Table 2; Figure 2; Figure 4).

Estimates of thermal habitat generated using both the surface and vertically integrated methods were comparatively high at stations 1 and 2 year-round and at station 3 during spring and summer (Figure 4). For all stations, estimates of thermal habitat were highest in summer and lowest in winter and fall, though spring and summer estimates were similar for stations 1–3. Surface and vertically integrated estimates of thermal habitat showed similar trends,

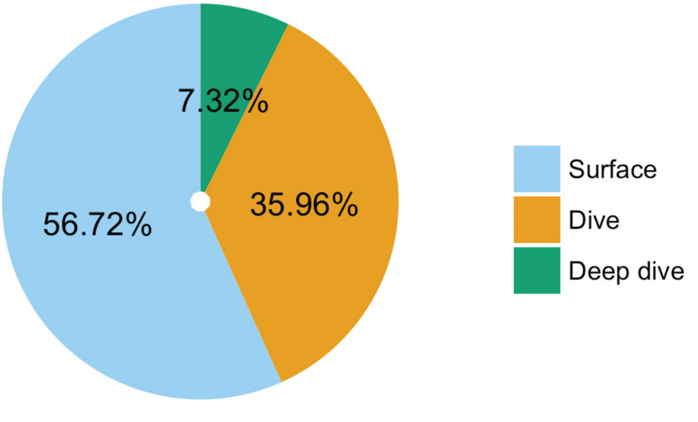

FIGURE 3 Daily dive budgets of short-finned pilot whales tagged with DTAGs off Cape Hatteras. Depth was separated into surface (≤20 m), dive (>20 m and < 500 m), and deep dive (≥500 m) behavior. Daily dive budgets were created by calculating the proportion of time spent in each dive behavior for all DTAGs combined, and then scaling these values by time in one day (86,400 s).

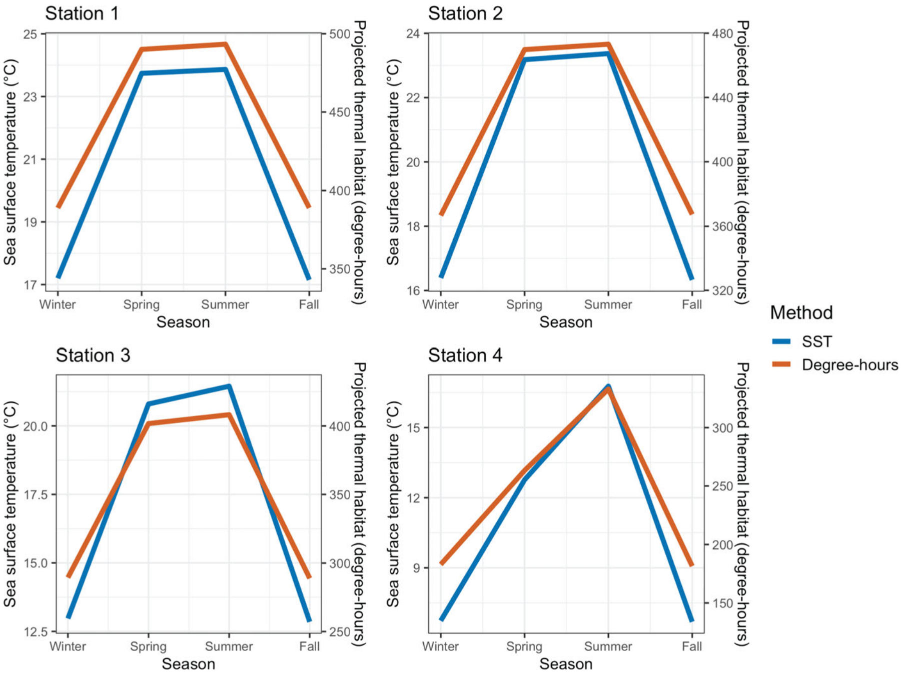

FIGURE 4 Estimates of available thermal habitat for short-finned pilot whales in degree-hours constructed with surface integrated and vertically integrated temperature throughout each season at stations 1–4.

but vertically integrated estimates were typically lower than those generated from surface data, alone. The difference between surface and vertically integrated estimates was greatest in warmer seasons (i.e., spring and summer) and at intermediate latitudes (stations 2 and 3).

Estimates of vertically integrated thermal habitat at stations 1 and 2 were similar, but were considerably higher than those at stations 3 and 4 in winter and fall (Figure 4). Mean temperatures from vertically integrated thermal habitat at stations 1 and 2 were as low as 15°C in the winter and as high as 21°C in the summer, while mean temperatures at station 3 varied from 12°C in the winter to only as high as 17°C in the summer (Table 2). At stations 1 and 2, estimates of vertically integrated thermal habitat suggested that pilot whales would spend 100% of their time at water temperatures below 22°C in winter and fall (Table 2). In spring and summer, 39%–44% of their time was spent below this threshold.

4 | DISCUSSION

Quantifying thermal habitat using the number of degree-hours allowed us to assess and compare how temperature at depth influenced potential short-finned pilot whale habitat between seasons and latitudes. The number of degree-hours is a metric that is employed in various fields such as engineering, meteorology, and horticulture to estimate the thermal energy experienced over a given time frame (Badescu & Zamfir, 1999; Balducci & Wong, 2008; Durmayaz, Kadioğlu & Şen, 2000). However, to our knowledge this is the first time it has been used to define the thermal habitat of animals. Applying this metric in future studies would provide a useful means of investigating the thermal habitats of deep diving marine mammals or predicting spatial patterns of marine mammals.

Our assessments of temperature at depth within the diving range of short-finned pilot whales at station 1 highlighted the wide range of temperatures experienced by these animals; pilot whales near Cape Hatteras regularly experience temperature differences of approximately 18°C during foraging dives or higher when occurring in

TABLE 3 Dive characteristics of deep-diving cetacean species. Maximum recorded dive depth and dive duration was determined from the literature.

Species	Scientific name	Maximum dive depth (m)	Maximum dive duration (minutes)	Literature
Blainville's beaked whale	*Mesoplodon densirostris*	1,408	61.47	Baird et al., 2006
Short-finned pilot whale	*Globicephala macrorhynchus*	1,018–1,500	27	Aguilar Soto et al., 2008
Gervais' beaked whale	*Mesoplodon europaeus*	1,251	57	Tyack et al., 2006
Long-finned pilot whale	*Globicephala melas*	648	12.7	Baird et al., 2002
Cuvier's beaked whale	*Ziphius cavirostris*	2,992	137.5	Schorr et al., 2014
Northern bottlenose whale	*Hyperoodon ampullatus*	1,453	70	Hooker & Baird, 1999
Sperm whale	*Physeter macrocephalus*	1,185	138	Watkins, Moore, & Tyack, 1985; Watkins, Daher, Fistrup, & Howald, 1993
Baird's beaked whale	*Berardius bairdii*	1,777	64.4	Minamikawa, Toshihide, & Kishiro, 2007

warm waters of the Gulf Stream. We used degree-hour estimates to evaluate how estimates of thermal habitat differed when using only surface temperatures versus when temperature at depth was incorporated and found differences between these methods that were particularly marked during spring and summer and at intermediate latitudes, when and where there is greater variability between surface temperature and temperature at depth. These findings suggest that incorporating temperature at depth is important to understanding the thermal habitat of deep-diving vertebrates, and that estimates of thermal habitat generated from surface temperatures during warmer months in temperate latitudes may present a considerably different picture of thermal habitat.

We examined estimates of thermal habitat relative to a reference value of 22°C since this temperature is important in distinguishing short- and long-finned pilot whales in SARs within the United States (sightings at SSTs <22°C are assigned a probability near 0 of being a short-finned pilot whale). In the southernmost region of the study site, where short-finned pilot whales are known to occur year-round, our results suggest that the thermal habitat available to pilot whales was always below 22°C during fall and winter (Table 2), though Gulf Stream meanders bring warmer waters into this region periodically. Pilot whales have been observed in the northernmost region of the study area represented by station 4, where the maximum (surface) water temperature observed was 16.77°C in summer. Thus, short-finned pilot whales are regularly occurring in cooler waters than expected in SARs, as observed in previous studies (Stepanuk et al., 2018, Thorne et al., 2019). Further, our results indicate that pilot whales experience temperatures as low as 5°C during dives, highlighting that much colder temperatures are experienced at depth than indicated by surface measurements, alone. Since abundance estimates in SARs rely on models that distinguish short- and long-finned pilot whales based on SST (Hayes et al., 2017), improving our understanding of the thermal ecology of these species could have important implications for the management of the species and should be the focus of further research.

Pilot whales take deep, but relatively short, foraging dives (the mean dive duration was 16 min, with a maximum duration of 38 min), but other deep-diving cetaceans engage in considerably longer deep dives (Table 3). Incorporating temperature at depth into estimates of thermal habitat is likely to be even more important for other deep-diving cetaceans, such as beaked whales, which can submerge for more than an hour and reach depths of nearly 3,000 m (Schorr et al., 2014; Shearer et al., 2019). Degree-hours would be a useful and practical approach for assessing and comparing the thermal habitat experienced by these and other deep-diving cetaceans.

This paper focused on comparing methods for assessing available thermal habitat within the dive depths and latitudinal range used by short-finned pilot whales, and we assumed a constant dive behavior at the four locations evaluated in doing so. However, we observed considerable individual variability in dive behavior, and habitat-dependent dive behavior could have a significant impact on temperatures experienced by short-finned pilot whales. Short-finned pilot whale dives are driven by availability of prey in the water column, and variations in the vertical distribution of prey will likely influence their overall dive behavior, and subsequently the water temperatures they experience (Baird et al., 2002; Heide-Jørgensen et al., 2002). For example, Georges Bank, around station 4, is defined by a submarine rise that results in a shallower region of productivity than that in other regions used by short-finned pilot whales in the northeast United States (Buckley & Lough, 1987; Thorne et al., 2017). This may result in shallower dives and warmer temperatures experienced at depth than would be expected from dive profiles observed at Cape Hatteras. Additional studies from a larger number of individuals tagged in different locations would provide a more comprehensive understanding of pilot whale dive behavior and available thermal habitat.

Some short-finned pilot whales follow the Gulf Stream and associated rings into offshore waters (Thorne et al., 2017). In deep diving marine ectotherms, such as tuna, low temperatures at deep depths result in physiological stress that force the animals to return to warmer waters (Schaefer, Fuller & Block, 2009; Schaefer & Fuller, 2010; Luo, Prince, Goodywar, Luckhurst, & Serafy, 2006). Endotherms and ectotherms possess different mechanisms for thermoregulation, but it is possible that deep diving marine mammals face similar physiological constraints on deep dives based on temperature. Dive behavior of marine mammals is predominantly limited by aerobic dive limits and larger animals with greater available oxygen stores tend to dive deeper and longer (Costa, Kuhn, Weise, Shaffer, & Arnould, 2004; Noren, Williams, Berry, & Butler, 2000). Pilot whale dive duration may be limited due to high energetic costs of foraging dives in which animals sprint to capture fast-moving prey species (Aguilar Soto et al., 2008). However, size is also indicative of differences in thermal ecology, with larger animals exhibiting improved capacity for heat retention (Worthy & Edwards, 1990). As a result, dive depth and duration may also be influenced by thermal ecology, particularly for mid-sized deep divers like pilot whales.

Analyses presented in this study would have greatly benefitted from reliable in situ measurements of temperature from tag devices. The temperature lags that were documented in this study precluded the use of DTAG temperature measurements to examine the thermal habitat of short-finned pilot whales. Tags providing accurate temperature measurements would allow more precise estimates of the temperatures these animals endure at depth, and an improved understanding of the impacts of temperature at depth on the spatial movements of deep-divers.

Our results highlight the importance of considering temperature at depth in order to accurately assess the thermal habitat of deep-diving marine vertebrates. This is likely to be particularly true for other deep-diving cetaceans which spend more time at depth, such as Cuvier's beaked whale or sperm whales (*Physeter macrocephalus*), and quantifying thermal habitat using degree-hours will be useful for understanding the thermal habitat of these species.

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AUTHOR CONTRIBUTIONS

Stephanie K. Adamczak: Conceptualization, formal analysis, methodology, writing-original draft; **William A. McLellan**: Conceptualization, writing-review & editing; **Andrew J. Read**: Conceptualization, data curation, writing-review & editing; **Christopher L. P. Wolfe**: Data curation, writing-review & editing; **Lesley H. Thorne**: Conceptualization, formal analysis, funding acquisition, methodology.

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ENDNOTE

[1] In the United States under the Marine Mammal Protection Act, Stock Assessment Reports are required for marine mammal management through the National Oceanic and Atmospheric Administration (NOAA).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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