



Regional variation in leatherback dive behavior in the northwest Atlantic

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ABSTRACT: Understanding the movement patterns and behaviors of a migratory species across all stages of migration is critical to informing successful conservation management strategies. While the movement patterns of northwestern Atlantic leatherbacks *Dermochelys coriacea* have been widely studied, there is still a need to understand area-specific behaviors. We collected and analyzed dive data from 52 satellite-tagged leatherbacks that inhabited documented or proposed foraging areas: the northeastern Gulf of Mexico (NEGOM), the Mid-Atlantic Bight (MAB), and southern New England (SNE). We fit generalized linear mixed models (GLMMs) to these data to determine area-specific dive metrics and their relationship to several environmental variables. The most notable result from the GLMMs revealed area-specific relationships between dive behavior and sea surface temperature (SST). As SST increased, leatherbacks in the NEGOM and MAB were observed to increase their surface duration and decrease dive duration, while the opposite trend was observed off SNE. Additionally, leatherbacks in the NEGOM performed more deep dives to cooler waters with rising SSTs. Our results suggest that leatherbacks in the NEGOM are performing thermoregulatory dive behavior that may reduce time available for feeding, potentially inhibiting foraging success relative to the MAB and SNE. These findings offer a deeper comprehension of leatherback movement ecology in each area, provide critical information needed for population assessments and management, and highlight areas of conservation concern in a warming climate.

KEY WORDS: Dive behavior · Movement ecology · Satellite telemetry · *Dermochelys coriacea* · Sea turtle · Gulf of Mexico · Mid-Atlantic Bight

1. INTRODUCTION

Understanding the movement patterns and behaviors of a migratory species throughout all stages of migration is essential for developing effective conservation management strategies (Lascelles et al. 2014). Not only does such research elucidate important bio-

logical and ecological aspects of a population, but it can also provide useful information for population assessments and predicting potential overlap with anthropogenic activities. For example, by studying the dive behavior of Atlantic bluefin tuna *Thunnus thynnus* in the northwestern Mediterranean Sea, Bauer et al. (2017) were able to infer tuna foraging behavior as well

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as provide important information on the suitability of their study region for aerial surveys aimed at estimating abundances. Additionally, analyses of dive behavior in blue whales *Balaenoptera musculus* have aided in determining the ability of large whales to avoid collisions with ships (McKenna et al. 2015). For migratory species, population assessments and analyses of perceived threats are only possible with an acute understanding of regional variation in behavioral patterns.

For most migratory marine species, assessing region-specific behaviors can be difficult as these animals can traverse entire ocean basins and geopolitical boundaries, making *in situ* observations nearly impossible (Shillinger et al. 2008, Block et al. 2011). However, advances in tracking technology and associated analyses have allowed researchers to expand the remote study of animal behavior (Hays & Hawkes 2018). Currently, satellite transmitters can record detailed dive information that also includes bathy–thermal conditions in the form of depth–temperature profiles. Paired with increasingly advanced statistical analyses, such information has been useful in refining our understanding of animal behaviors in remote areas, especially for air-breathing animals like sea turtles. For instance, both horizontal and vertical movement metrics have been employed as data streams in hidden Markov models to highlight potential foraging areas for several sea turtle species such as loggerheads *Caretta caretta* (Chimienti et al. 2020) and leatherbacks *Dermochelys coriacea* (Rider et al. 2024).

Accurately characterizing region-specific behaviors is particularly challenging for leatherbacks as they can migrate thousands of kilometers from tropical nesting beaches to a myriad of foraging areas that can span a wide breadth of latitudes (James et al. 2005a,b, Hays et al. 2006, Fossette et al. 2010, Evans et al. 2021, Rider et al. 2024). Further, leatherbacks have been suggested to display behavioral plasticity, altering their dive behavior based on the stage of their migration cycle and distribution of their prey in the water column (James et al. 2005b, Hays et al. 2006), making it even more difficult to accurately define foraging behavior. Thus, foraging has only been verified in a few areas in the northwest Atlantic where telemetry data were successfully paired with direct field observations: Nova Scotia (Heaslip et al. 2012, Wallace et al. 2015) and southern New England (Dodge et al. 2018, Patel & Siemann 2020). Within these areas, leatherback horizontal and vertical behavior were recorded as they consumed large quantities of gelatinous zooplankton, in some cases up to 73% of their body mass per day (Doyle et al. 2007, Heaslip et al. 2012). These measurements have subsequently been

used as a reference to compare to leatherback movement in high use areas where foraging has only been suggested and not directly observed (Okuyama et al. 2021, Rider et al. 2024).

Understanding variation in behavior among different regions is especially important in areas of high human usage such as along the northwest Atlantic shelf, where leatherbacks encounter impacts of commercial fisheries, climate change, and offshore energy development. (NMFS & USFWS 2020). Thorough investigations into region-specific dive behavior in the northwest Atlantic only exist for leatherbacks along the Scotian Shelf (Wallace et al. 2015) and Cape Cod, Massachusetts (Dodge et al. 2018, Patel & Siemann 2020, Rogers et al. 2024). In comparison, there is relatively limited information on dive behavior in other high use areas described as potential foraging areas, such as the northeastern Gulf of Mexico (Aleksa et al. 2018b, Sasso et al. 2021) and along the South and Mid-Atlantic Bights (Eckert et al. 2006, Rider et al. 2024).

In the present study, we compared leatherback dive behavior across 3 areas in the northwest Atlantic Ocean that have been either documented or suggested as foraging areas: the northeastern Gulf of Mexico (NEGOM; suggested by Aleksa et al. 2018b and observed during the tagging research underlying Sasso et al. 2021), the Mid-Atlantic Bight (MAB; suggested by Rider et al. 2024), and southern New England (SNE; documented by Dodge et al. 2018 and Patel & Siemann 2020; and observed during the tagging research underlying Rider et al. 2024 and Rogers et al. 2024). In each of these areas, leatherbacks were affixed with satellite transmitters capable of recording depth and temperature metrics, and resulting telemetry data were evaluated to determine how dive behavior changed with respect to the area's bathy–thermal conditions. Analyzing such data allowed us to infer if and how leatherbacks are foraging in each area and how this information will aid in population assessments and mitigating harmful interactions with anthropogenic activities.

2. MATERIALS AND METHODS

2.1. Study sites

We compared diving behavior among 3 different areas along the gulf and east coasts of the United States: the NEGOM, the MAB, and SNE (see Fig. 1). In the NEGOM, a large area off the coast of the Florida Panhandle was recently documented as a foraging area for leatherbacks during the summer and fall

(Aleksa et al. 2018b). Initial data indicated that leatherbacks displayed area-restricted searching behavior (indicative of foraging) along the 200 m isobath between Louisiana and Panama City, Florida. However, subsequent tracking demonstrated that this behavior also extended farther south along the shelf slope and on the West Florida Shelf (Sasso et al. 2021). While there are no direct observations of foraging behavior along the MAB, both horizontal and vertical movement data from tagged leatherbacks suggest that foraging is taking place between Cape Hatteras and Delaware Bay (Rider et al. 2024). The waters off Cape Cod correspond to a known foraging ground for leatherbacks migrating along the east coast of the United States (Rider et al. 2024). Foraging behavior was observed to take place within Vineyard Sound and Nantucket Sound, and along Nantucket Shoals (Dodge et al. 2018, Patel & Siemann 2020).

For this study, we defined the bounds of each foraging area based on previous research. In the NEGOM, the foraging area spanned from 84.5 to 92° W and 25.5 to 30.2° N, with the northern boundary following the 200 m isobath. The MAB foraging area included the entire continental shelf region from Cape Hatteras, North Carolina (35° N) to the cross section between Sandy Hook, New Jersey (40.5° N), and the Hudson Canyon (30.5° N). The foraging area along SNE was much smaller and spanned from 68.6 to 71.3° W and 40.1 to 41.7° N. All leatherback locations within each of these regions can be seen in Fig. 1.

2.2. Leatherback tagging and tracking

Tagging took place between 2015 and 2022 at 3 locations along the Gulf and East coasts of the United States: Destin, Florida (September to October), Cape Cod, Massachusetts (August to October), and Cape Lookout, North Carolina (May). Detailed capture and tagging methods can be found in Sasso et al. (2021) and Rider et al. (2024). Each leatherback was affixed with a satellite transmitter (MK-10AF, Wildlife Computers) to the caudal peduncle via a monofilament tether. Transmitters were capable of recording Argos-derived locations, Fastloc GPS-derived locations, depth, and temperature and transmitting those data via the Argos satellite system. There was no limit to the number of Argos locations transmitted per day, but we programmed all transmitters to relay only 4 Fastloc GPS locations per day to conserve battery life. All depth and temperature data were measured via pressure and temperature sensors with resolutions of ± 0.5 m and $\pm 0.05^\circ\text{C}$, respectively.

Most dive data were aggregated within 6 h time intervals starting at 00:00 h GMT and within preprogrammed depth, duration, and temperature bins before transmission. We chose to aggregate dive data within 6 h time intervals to reduce the amount of data processed during each transmission and thus conserve battery life, as these data were also used in studies aimed at understanding leatherback migration patterns (i.e. Sasso et al. 2021, Rider et al. 2024). Transmitters logged the proportion of time-at-depth (TAD) and the number of dives within depth bins corresponding to 0, 2, 5, 10, 25, 50, 100, 200, 300, 400, 500, 750, 1000, and >1000 m. Similarly, the number of dives corresponding to duration bins 0.5, 1, 2, 3, 4, 5, 10, 15, 20, 25, 30, 35, 40, and >40 min were also recorded. A dive was logged if the turtle surpassed a depth of 2 m for more than 30 s. Proportions of time-at-temperature (TAT) were logged within temperature bins corresponding to 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 26, 28, 30, and $>30^\circ\text{C}$.

Transmitters were also capable of logging temperature and depth summary data, henceforth referred to as profiles of depth and temperature (PDTs). The PDT summary data contained the minimum and maximum temperatures recorded at different depth intervals (8 m resolution) during each 6 h interval. The proportion of time that the wet/dry sensor was dry was also recorded per hour.

Before analyzing leatherback dive behavior, raw location data were filtered and processed following methods outlined in Rider et al. (2024). Argos and GPS-derived locations were filtered to remove erroneous locations such as those on land or those with a lack of estimation error (i.e. location class Z). We also used a speed filter from the R package *argosfilter* (Freitas 2012) to remove locations that resulted in travel rates above 5 km h^{-1} (James et al. 2005c). The first 24 h of each deployment period were also removed from further analysis to control for any potential alteration in movement behavior as a result of the tagging process. Finally, we removed any instance of a premature tag detachment, which was characterized as total TAD below 2 m approaching and remaining at zero for the remainder of the deployment. After necessary filtering, the remaining data were used to reconstruct the most probable path for each leatherback on a time-regularized interval by employing a continuous time move persistence state space model (CTMP SSM) using the R package *aniMotum* (Jonsen et al. 2023). The CTMP SSM allowed us to account for the uncertainty of location and irregular time series of the Argos and GPS positions while simultaneously estimating move persistence, which is an index of

movement behavior (Jonsen et al. 2023). We chose a time-regularized interval of 6 h as this matched the temporal resolution of the dive and temperature data collected by the transmitters. We ran a separate CTMP SSM for groups of leatherbacks based on their tagging locations (i.e. Florida, North Carolina, and Massachusetts). Model fit was evaluated by calculating one-step-ahead prediction residuals using the *osar* function in *aniMotum* (Jonsen et al. 2023) and assessing for homogeneity, normality, and autocorrelation of the residuals.

The move persistence index estimated by the CTMP SSM measures the autocorrelation between consecutive displacements and accounts for variability in both speed and turning angle (Jonsen et al. 2019). Move persistence models have been successfully used to infer the movement behavior of various highly migratory marine species such as orcas *Orcinus orca* (Vogel et al. 2021) and Atlantic tarpon *Megalops atlanticus* (Drymon et al. 2021). Move persistence values for leatherbacks were estimated for each predicted location, with values ranging continuously from 0 to 1, where 0 characterized slower and indirect movements, and 1 indicated faster and more directed movements. For this study, a move persistence value between 0 and 0.25 was interpreted as area-restricted searching behavior, between 0.25 and 0.75 as searching or intermediate behavior, and between 0.75 and 1 as transient or directed behavior. It is important to note the benefit of using a continuous value for move persistence as opposed to discrete values, since leatherbacks can demonstrate varying degrees of move persistence while foraging. For example, leatherbacks migrating in the north Atlantic Ocean and in the Gulf of Mexico engaged in searching behavior during which they were inferred to be seeking out small patches of prey spread across large geographic areas (Hays et al. 2006, Sasso et al. 2021). Thus, this behavior may be identified by an intermediate move persistence value closer to 0.5.

After processing the location data through the CTMP SSM, locations were filtered to only include those within the 3 foraging areas specified above (i.e. NEGOM, MAB, and SNE). Finally, depth and temperature data were joined to their respective processed locations for further analyses.

2.3. Leatherback dive behavior

To determine the relationship between leatherback dive behavior and environmental conditions across foraging areas, we followed methods outlined by Iver-

son et al. (2019) and used a model selection approach using 5 measurements of dive behavior: (1) time at the surface, (2) number of shallow dives, (3) number of intermediate dives, (4) number of deep dives, and (5) average dive duration. Each of these metrics was derived from the binned data and either summed or averaged over 6 h time intervals. The amount of time at the surface was quantified using the percentage of time the wet/dry sensor was dry per hour. We used the wet/dry sensor as a proxy for surface time rather than TAD within the first 2 m of the water column to control for any uncertainty as a result of drift in the pressure sensor (Rider et al. 2022, Rogers et al. 2024). Those values were summed across each 6 h time interval to keep consistent with the temporal resolution of the other binned data. To quantify the number of shallow, intermediate, and deep dives per 6 h interval, we used the binned data to sum the number dives between 2 and 10 m, between 10 and 50 m, and greater than 50 m, respectively. We chose these depth bins since leatherbacks were observed to spend most of their time in waters <50 m in neritic areas across the northern Atlantic, but spent a lot of time past 50 m in the Gulf of Mexico (Fossette et al. 2010). The durations of individual dives were averaged across the 6 h time interval using the binned data as well.

We fit a suite of generalized linear mixed models (GLMMs) with binomial (fraction of dives in a 6 h time block that were shallow, and the same for intermediate, and deep dives) and Gaussian (time at surface and dive duration) error distributions using the R package *glmmTMB* (Brooks et al. 2017). To meet assumptions of normality and homogeneity for the GLMMs with Gaussian error distributions, both time at the surface and dive duration were transformed, using a square-root and natural log transformation respectively. We chose 5 fixed effects: sea surface temperature (SST), chlorophyll *a* (*chl a*), diel period, foraging area, and move persistence. SST was selected as leatherbacks were observed to alter their movement behavior in relation to it in the northwest Atlantic (Dodge et al. 2014), while *chl a* was used as a proxy for food availability following Iverson et al. (2019). Leatherbacks were observed to alter their dive behavior with respect to diel periods in the north Atlantic Ocean (Hays et al. 2006). The move persistence value was included since leatherbacks were observed to alter their dive behavior in relation to different movement behaviors (i.e. area-restricted and transitory behaviors, James et al. 2005b). Additionally, including move persistence allowed us to account for the days that leatherbacks were within

the foraging area but not performing foraging-like behavior (i.e. migrating in and out of the area).

Both SST and chl *a* were extracted for each interpolated location from the SSM using the `rerddapXtracto` package in R (Mendelssohn 2021). For each parameter, the mean value was calculated within a 0.05° longitude by 0.05° latitude bounding box centered at the position of each interpolated location. We chose a value of 0.05° as this roughly corresponded with the average error radius of the interpolated locations. SST data were retrieved from the Multi-scale Ultra-high Resolution Sea Surface Temperature analysis (daily 0.01° resolution) data product from NASA's Jet Propulsion Laboratory (JPL MUR MEASURES Project 2015). Chl *a* was downloaded from the NOAA S-NPP VIIRS (weekly 4 km resolution) data product from NOAA's National Environmental Satellite, Data, and Information Service (<https://coastwatch.pfeg.noaa.gov/erddap/info/nesdisVHNSQchlaWeekly/index.html>). Before running each model, we assessed for correlation between SST and chl *a* within each area by computing the Spearman rank correlation coefficient.

Diel periods were based on the 6 h intervals for which dive data were collected. While the 6 h intervals do not accurately correspond to sunrise and sunset in each region, we were able to roughly compare depth metrics by combining the time bins that ranged from 07:00 to 13:00 and 13:00 to 19:00 h (Central Time Zone) to represent diurnal measurements and the 2 bins that ranged from 19:00 to 01:00 and 01:00 to 07:00 h to represent nocturnal measurements. We included individual leatherback as a random effect as there were repeated observations for each turtle (Bolker et al. 2009).

Since we wanted to see how the relationship between dive behavior and environmental conditions varied among foraging areas, we included an interaction term between foraging area and each of the remaining fixed effects. We applied data dredge statistics to run the GLMMs with all valid combinations of fixed effects using the dredge function from the R package `MuMIn` (Bartón 2023). This allowed us to test every possible combination of fixed effects and generate Bayesian information criterion (BIC) and BIC weights for every model. The preferred model was selected based on the BIC, which penalizes models with more parameters with consideration for the sample size (Neath & Cavanaugh 2012). Models with a $\Delta\text{BIC} < 2$ were considered to be equivalent to the best fitting model. We assessed the explanatory power of the model using both the conditional and marginal R^2 values, which consider the variance of both random and fixed effects and just fixed effects, respectively. The R^2 values were calcu-

lated using the R package `performance` (Lüdtke et al. 2021). Diagnostic plots using empirical quantile residuals were generated using the `DHARMA` package (Hartig 2022) to assess model fit.

To gain insight into leatherback association with vertical features (i.e. thermocline and mixed-layer depth), we examined PDT data within each foraging area. Following Rider et al. (2024), PDT data were joined with predicted locations within the bounds of each foraging area. We used those data to synthesize continuous temperature profiles using the R package `RchivalTag` (Bauer 2021), which allowed us to linearly interpolate the average between the minimum and maximum recorded temperatures across 8 m intervals for each 6 h time bin. The estimated depths of the thermocline were derived from the interpolated temperatures using methods outlined in Bauer et al. (2015). For every 6 h bin, we used TAD data to calculate the mean ($\pm\text{SD}$) depth of all leatherbacks within each area by year. Both the average leatherback depth and derived estimates of the thermocline were plotted onto PDTs averaged by area and year.

3. RESULTS

3.1. Leatherback tagging and tracking

Between 2015 and 2022, we tracked a total of 52 leatherbacks across the 3 foraging areas: NEGOM ($n = 14$), MAB ($n = 24$), and SNE ($n = 17$; Table 1, Table S1 in the Supplement at www.int-res.com/articles/suppl/n055p169_supp.pdf). Four individuals (IDs MA18.01, NC18.03, NC18.05, and NC18.07) spent time in both the MAB and SNE. On average, tagged leatherbacks spent similar amounts of time ($\pm\text{SD}$) in the NEGOM (26.78 ± 22.75 d) and SNE (21.12 ± 13.12 d) and spent the most time in the MAB (43.75 ± 27.57 d). Based on curved carapace length (CCL), all turtles analyzed in this study were considered adults (CCL > 130 cm; Avens et al. 2020), and the average ($\pm\text{SD}$) CCL was comparable among foraging areas: NEGOM (153.81 ± 10.06 cm), MAB (150.76 ± 10.18 cm), and SNE (150.53 ± 8.51 cm).

Based on the interpolated tracks and move persistence, we observed that leatherbacks in the NEGOM did not focus on a particular area, while those in the MAB and SNE concentrated their movements in specific areas (Fig. 1). In the NEGOM, leatherbacks displayed area-restricted movement along the Florida Escarpment, with most of their interpolated locations on the continental shelf between the 200 and 1500 m isobaths. Leatherbacks utilized most of the MAB area,

Table 1. Summary (mean ± SD) of tagging, tracking, and physiological calculations for leatherbacks foraging in the northeastern Gulf of Mexico (NEGOM), Mid-Atlantic Bight (MAB), and southern New England (SNE). Leatherbacks were either tagged in the NEGOM, Massachusetts, or North Carolina

Foraging area	N	Days in foraging area	Curved carapace length (cm)	Curved carapace width (cm)
NEGOM	14	26.8 ± 22.8	153.8 ± 10.1	123.7 ± 13.1
MAB	24	43.8 ± 27.6	150.7 ± 10.9	110.5 ± 10.7
SNE	17	21.1 ± 13.1	150.5 ± 8.5	110.2 ± 6.3

but displayed lower move persistence both along the coast between Cape Hatteras and Delaware Bay as well as in the southern portion of the MAB, along the coast of North Carolina and the mouth of the Chesapeake Bay. In SNE, leatherbacks performed more concentrated movements on the continental shelf across

Nantucket Shoals, south of Martha's Vineyard, and throughout Vineyard Sound (Fig. 1).

3.2. Leatherback dive behavior

Based on the BIC values, there was 1 model within 2 ΔBIC of the best model to predict time at surface (Table S2). Both models contained the fixed effects of diel period, foraging area, move persistence, SST, and interactions between foraging area and diel period, and move persistence and SST (Table 2). The preferred model also contained the fixed effect of chl *a* (weight = 0.591), whereas the other did not (weight = 0.408). Across all areas, SST had a significant relationship with time

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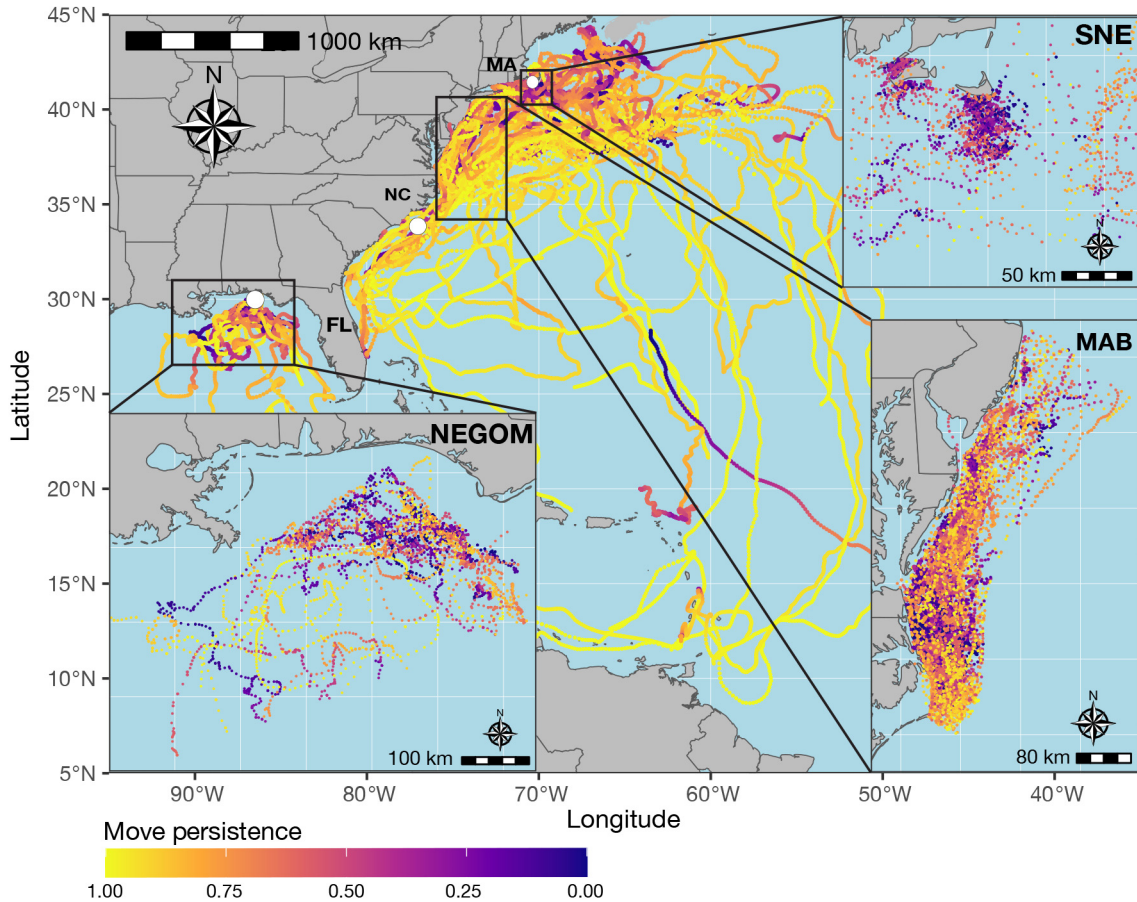


Fig. 1. Interpolated leatherback locations with associated move persistence values for all transmitters deployed off Florida Panhandle (FL), North Carolina (NC), and Massachusetts (MA). For all analyses involving dive behavior, locations were filtered to only include those within the 3 documented and suggested foraging areas in the northeastern Gulf of Mexico (NEGOM), Mid-Atlantic Bight (MAB), and southern New England (SNE). The color of each point corresponds to the move persistence value, which ranges from 0 to 1. We classified values between 0 and 0.25 as area-restricted movement, between 0.25 and 0.75 as searching or intermediate persistence, and 0.75 and 1 as transient or directed movement. White points represent tagging locations

Table 2. Estimated parameters from the best model selected for each diving metric. The reference levels for foraging area and diel period were northeastern Gulf of Mexico (NEGOM) and day, respectively. DP: diel period, FA: foraging area, MP: move persistence, SST: sea surface temperature, MAB: Mid-Atlantic Bight, SNE: southern New England

	Estimate	SE	z-value	p
Time-at-surface				
Intercept	-5.53	1.46	-3.79	<0.001
DP (Night)	-0.23	0.12	-1.86	0.063
FA (MAB)	8.13	1.56	5.22	<0.001
FA (SNE)	19.65	1.76	11.19	<0.001
MP	-0.82	0.25	-3.25	<0.001
log ₁₀ (chl <i>a</i>)	-0.14	0.05	-2.99	0.002
SST	0.46	0.05	9.73	<0.001
DP (Night) × FL (MAB)	0.74	0.14	5.29	<0.001
DP (Night) × FL (SNE)	1.17	0.18	6.36	<0.001
FA (MAB) × MP	-2.48	0.30	-8.20	<0.001
FA (SNE) × MP	-1.75	0.42	-4.18	<0.001
FA (MAB) × SST	-0.27	0.05	-5.31	<0.001
FA (SNE) × SST	-0.92	0.07	-13.74	<0.001
	Conditional R ²	0.560	Marginal R ²	0.285
Shallow dives (2–10 m)				
Intercept	3.76	0.47	8.03	<0.001
DP (Night)	-0.28	0.07	-4.18	<0.001
FA (MAB)	-2.56	0.30	-8.41	<0.001
FA (SNE)	-1.92	0.33	-5.89	<0.001
MP	0.89	0.30	3.03	<0.001
SST	-0.13	0.01	-9.76	<0.001
DP (Night) × FA (MAB)	0.54	0.08	6.51	<0.001
DP (Night) × FA (SNE)	0.44	0.09	5.13	<0.001
FA (MAB) × MP	-1.68	0.35	-4.79	<0.001
FA (SNE) × MP	-1.71	0.39	-4.43	<0.001
	Conditional R ²	0.312	Marginal R ²	0.167
Intermediate dives (10–50 m)				
Intercept	-4.55	0.48	-9.56	<0.001
DP (Night)	-0.27	0.03	-8.29	<0.001
FA (MAB)	3.29	0.31	10.71	<0.001
FA (SNE)	2.74	0.33	8.23	<0.001
MP	-0.97	0.39	-2.49	0.013
log ₁₀ (chl <i>a</i>)	0.13	0.04	3.63	<0.001
SST	0.13	0.01	9.24	<0.001
FA (MAB) × MP	1.87	0.43	4.36	<0.001
FA (SNE) × MP	2.00	0.46	4.33	<0.001
	Conditional R ²	0.398	Marginal R ²	0.273
Deep dives (>50 m)				
Intercept	-9.44	1.46	-6.47	<0.001
DP (Night)	0.59	0.08	7.48	<0.001
FA (MAB)	14.10	2.85	4.94	<0.001
FA (SNE)	13.78	2.51	5.49	<0.001
log ₁₀ (chl <i>a</i>)	0.07	0.09	0.79	0.431
SST	0.27	0.05	5.86	<0.001
FA (MAB) × log ₁₀ (chl <i>a</i>)	-6.72	0.68	-9.84	<0.001
FA (SNE) × log ₁₀ (chl <i>a</i>)	-3.49	0.80	-4.34	<0.001
FA (MAB) × SST	-0.95	0.12	-7.95	<0.001
FA (SNE) × SST	-0.86	0.11	-7.88	<0.001
	Conditional R ²	0.900	Marginal R ²	0.812
Dive duration				
Intercept	3.99	0.66	6.08	<0.001
FA (MAB)	-0.54	0.68	-0.78	0.433
FA (SNE)	-3.77	0.75	-5.05	<0.001
MP	0.03	0.1	0.24	0.810
SST	-0.07	0.02	-2.96	0.003
FA (MAB) × MP	0.80	0.12	6.55	<0.001
FA (SNE) × MP	0.820	0.16	5.02	<0.001
FA (MAB) × SST	0.010	0.02	0.40	0.686
FA (SNE) × SST	0.16	0.03	5.68	<0.001
	Conditional R ²	0.537	Marginal R ²	0.303

at surface (Table 2), but the nature of this relationship varied between foraging areas. There was a positive relationship in the NEGOM and MAB and a negative relationship in SNE (Fig. 2A). For all 3 locations, there was a significantly negative relationship between move persistence and the time at surface (Table 2, Fig. S1). The model indicated that leatherbacks spent relatively similar amounts of time at the surface in the NEGOM and MAB but less time in the SNE (Fig. S1). There was no discernible difference in the time spent at the surface between diel periods among any of the areas (Fig. S1). There was a significant but weak negative relationship between chl *a* and time at surface across all 3 regions (Table 2, Fig. S1).

The preferred model for explaining the number of shallow dives included diel period, foraging area, move persistence, SST, and the interaction between foraging area and diel period and move persistence as fixed effects (Table 2, Table S2). Leatherbacks foraging in the NEGOM exhibited more shallow dives compared to those foraging in the MAB and SNE (Fig. 2B). In both the MAB and SNE, there was a slightly higher proportion of shallow dives at night while the opposite was true for turtles in the NEGOM (Fig. 2B). Among all areas, the proportion of shallow dives decreased with increasing temperature (Fig. S2). In terms of move persistence, as leatherbacks became more transitory (i.e. showed higher move persistence), the proportion of shallow dives increased in the NEGOM, and slightly decreased in the MAB and SNE (Fig. S2). However, these relationships were weak.

Similar to surface time, there were 2 models within 2 ΔBIC of the best model for explaining the proportion of intermediate dives (Table S2). The model with the third lowest BIC included diel period, foraging area, move persistence, SST, and the interaction between move persistence and foraging area. The model with the second lowest BIC in-

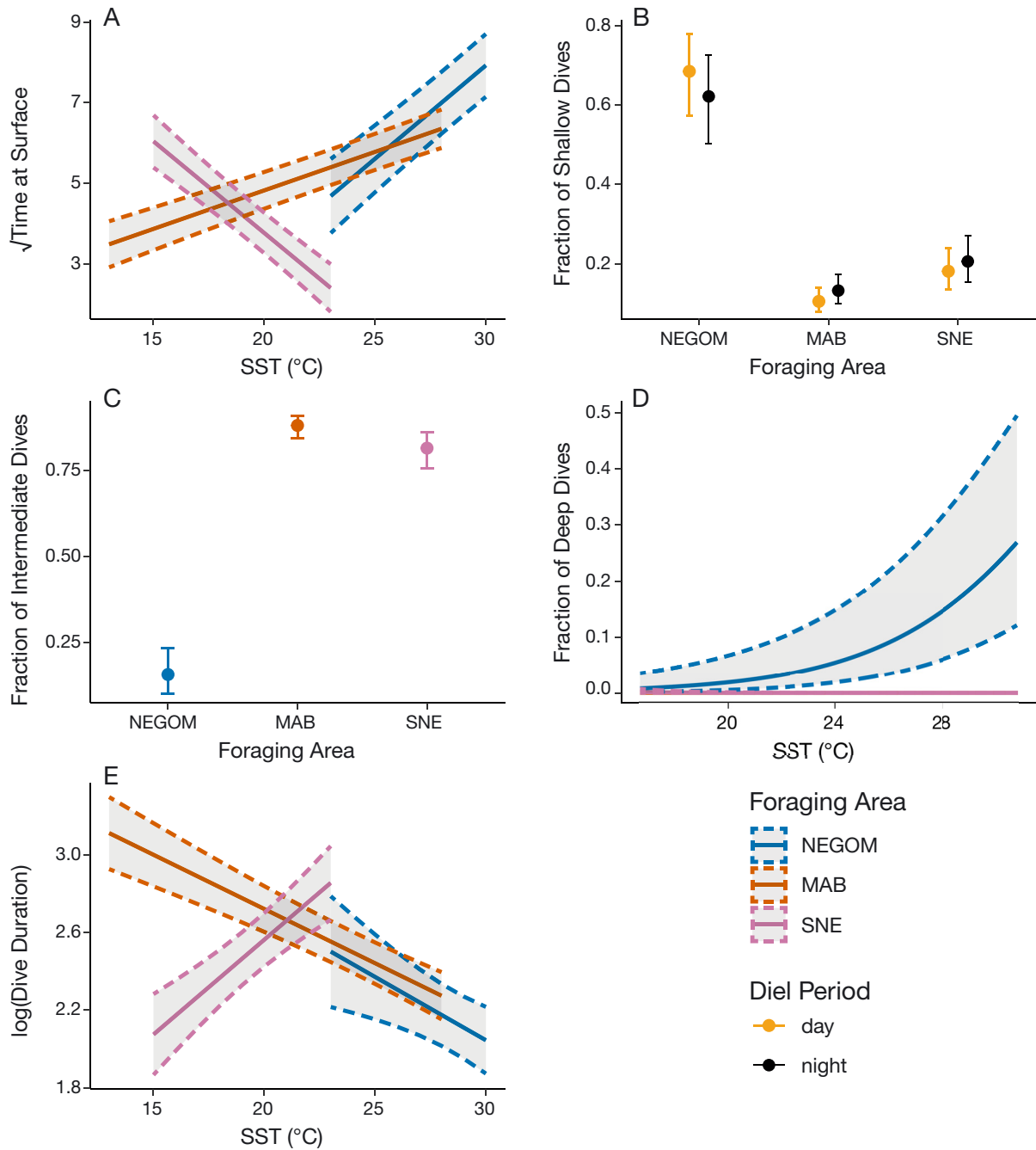


Fig. 2. Prediction plots generated using results of the generalized linear mixed models (GLMMs) used to determine the relationship between leatherback dive behavior and environmental conditions at each foraging area. Plots represent relationships between (A) percent time spent at the surface and the interaction between foraging area and sea surface temperature (SST), (B) fraction of shallow dives (2–10 m) and the interaction between foraging area and diel period, (C) fraction of intermediate dives (10–50 m) and foraging area, (D) fraction of deep dives (>50 m) and the interaction between foraging area and SST, and (E) dive duration and the interaction between foraging area and SST. Given the low percentage of deep dives in the MAB and SNE, the lines corresponding to these 2 regions are overlapping in panel D. Percent time spent at the surface and dive duration were square root and log-transformed, respectively. Shaded regions in A, D, and E, and error bars in B and C represent the 95% confidence interval

cluded the effects of diel period, foraging area, move persistence, chl *a*, and SST (weight = 0.236). The preferred model included those effects as well as the inter-

action between foraging area and move persistence (weight = 0.570; Table 2). Contrary to the patterns observed for shallow dives, the proportion of intermediate

dives was higher in the MAB and SNE compared to the NEGOM (Fig. 2C). There was no discernible difference in proportion of intermediate dives between diel periods (Fig. S3). Both chl *a* and SST had significantly positive relationships with the proportion of intermediate dives, but the effect of chl *a* appeared to be weak (Table 2). As leatherbacks exhibited more restricted movement behavior, they performed slightly fewer intermediate dives in the SNE and MAB and more in the NEGOM. However, these relationships appeared to be weak as well (Fig. S3).

Since the bathymetry of the foraging areas in the MAB and SNE is relatively shallow (<50 m) compared to the NEGOM, the majority of deep dives among all areas were conducted in the NEGOM (86.8%). Thus, the relationships presented here should mainly be considered for the NEGOM. The best predictors of deep dives (past 50 m) included diel period, foraging area, chl *a*, SST, and the interaction between foraging area and chl *a* and SST (Table 2). Leatherbacks performed slightly more deep dives at night (Fig. S4). The effect of chl *a* was negligible among all areas (Fig. S4). The effect of SST was significant and most prominent in the NEGOM as the proportion of deep dives increased with increasing SST (Table 2, Fig. 2D). Even at the highest SSTs, the predicted proportion of deep dives was still relatively low (~0.3; Fig. 2D), indicating that the majority of dives in the NEGOM were shallow.

Foraging area, move persistence, SST, and the interaction of foraging area with SST and move persistence were the best explanatory variables for the average dive duration (Table 2, Table S2). Dive durations were longest in SNE and shortest in the NEGOM and MAB (Fig. S5). There was a significant relationship between SST and dive duration across all areas (Table 2). Leatherbacks dove for shorter periods of time as SST increased in the NEGOM and MAB, while we observed the opposite pattern in SNE (Fig. 2E). As leatherbacks increased their move persistence, their dive durations increased as well (Fig. S5). This was ev-

ident in the MAB and SNE, but there appeared to be little to no effect of move persistence in the NEGOM.

We were able to synthesize average PDT plots for each foraging area (Fig. 3). In the NEGOM, leatherbacks' average depths occurred between 20 and 50 m,

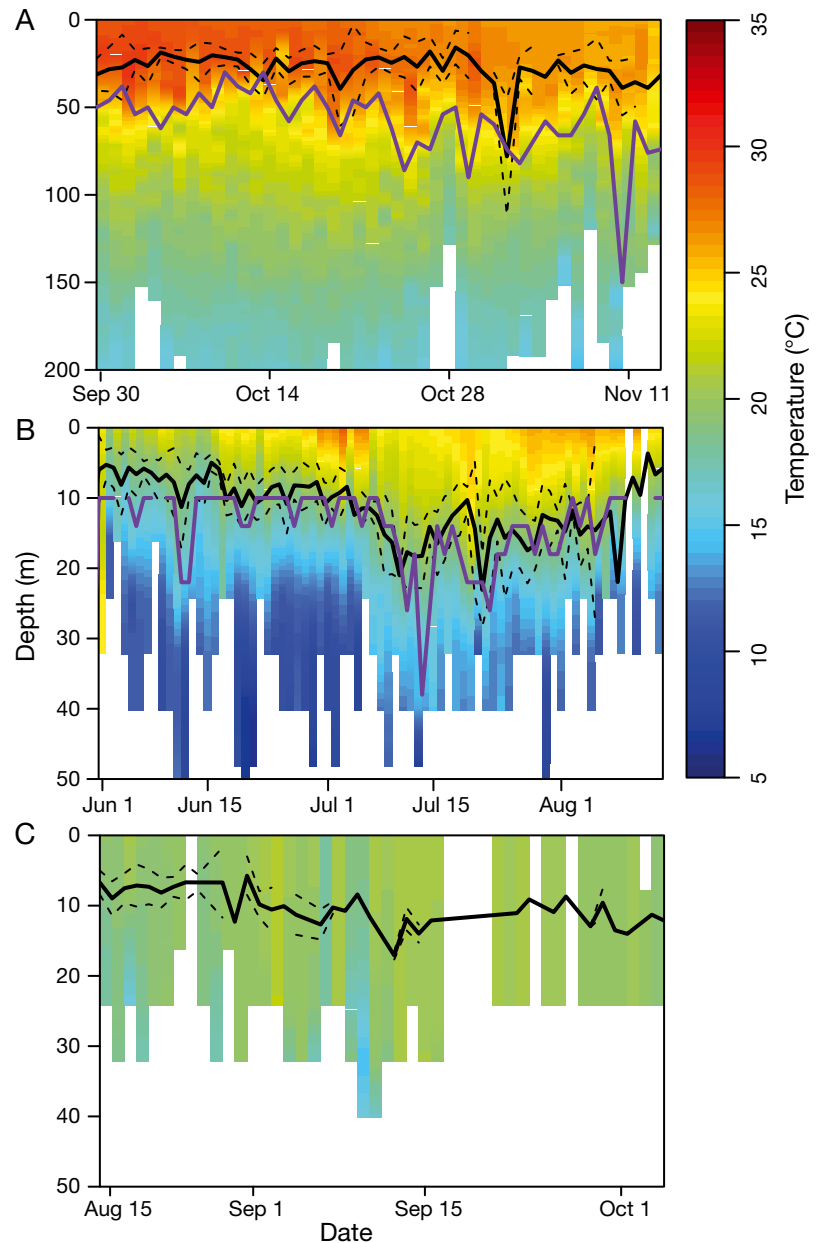


Fig. 3. Average depth–temperature profiles (PDTs) derived from all leatherback locations within the (A) northeastern Gulf of Mexico (NEGOM), (B) Mid-Atlantic Bight (MAB), and (C) southern New England (SNE) foraging areas. Solid black lines represent the mean depth of turtles, while dashed lines represent SD. The purple line is the estimated depth of the thermocline. There is no estimated depth of the thermocline in SNE due to the high amount of vertical mixing of the water column. Each plot represents 1 foraging season: 2019 for the NEGOM and MAB and 2018 for SNE. Plots were created using the R package RchivalTag (Bauer 2021)

while the depth of the thermocline was deeper, between 50 and 100 m (Fig. 3AB). Turtles in this area spent a large proportion of their time (mean \pm SD) between 0 and 5 m ($51.1 \pm 23.4\%$) as well as between 50 and 100 m ($16.3 \pm 10.3\%$, Fig. 4). However, there were occasional dives past 300 and as deep as 600 m ($<0.001\%$). With respect to temperature, their time was mostly spent above 29°C ($68.2 \pm 51.0\%$, Fig. 4).

Within the MAB, the average depth of all leatherbacks closely aligned with the thermocline, which typically occurred above 20 m (Fig. 3C). A large pro-

portion of their time (mean \pm SD) was spent between 11 and 25 m ($39.8 \pm 23.4\%$, Fig. 4), with little time spent beyond 50 ($0.9 \pm 5.5\%$) and 100 m ($0.1 \pm 1.4\%$). They displayed a large thermal range between 6 and 34°C , with most of their time spent between 15 and 30°C ($97.0 \pm 53.8\%$, Fig. 4).

Since the temperatures in SNE were uniform throughout the water column, it was not possible to estimate a thermocline using our methods (Fig. 3D). The average depth of all leatherbacks in this area was approximately 10 m. Most of their time (mean \pm SD)

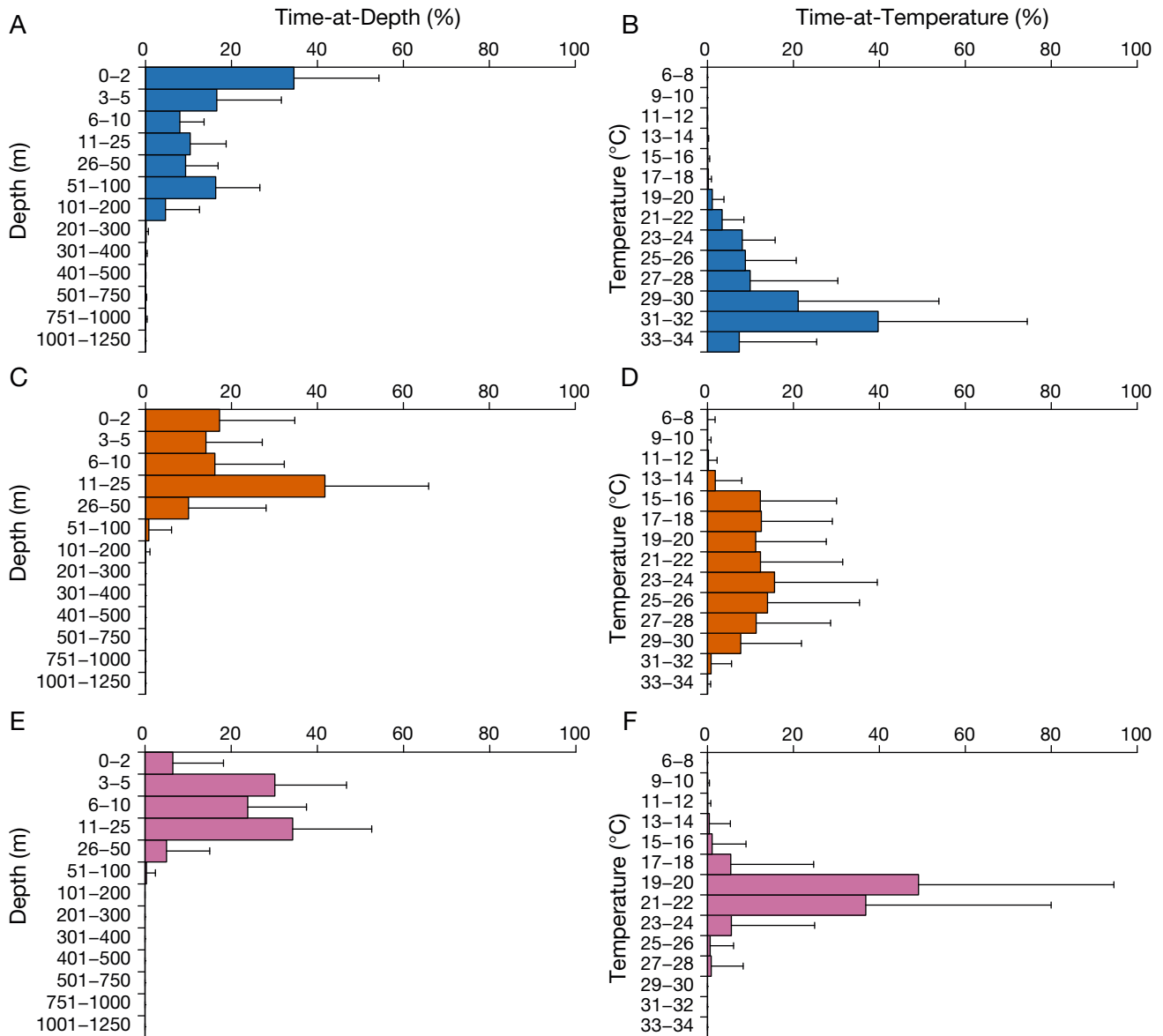


Fig. 4. Time-at-depth (TAD) and time-at-temperature (TAT) for leatherbacks in (A,B) the northeastern Gulf of Mexico (NEGOM; n = 14 tags), (C,D) the Mid-Atlantic Bight (MAB; n = 23 tags), and (E,F) southern New England (SNE; n = 13 tags) foraging areas. TAD and TAT were averaged (\pm SD) using all binned depth data collected in each foraging area. Plots were created using the R package RchivalTag (Bauer 2021)

was spent between 2 and 25 m ($82.9 \pm 29.5\%$), with relatively little time spent either at the surface ($9.9 \pm 14.7\%$) or beyond 25 m ($7.2 \pm 11.8\%$, Fig. 4). Their thermal range did span between 9 and 28°C , but they spent most of their time between 19 and 22°C ($77.4 \pm 60.6\%$, Fig. 4).

4. DISCUSSION

In the present study, we used depth and temperature data derived from satellite transmitters to determine dive behavior of leatherback sea turtles within documented and suggested foraging areas in the NEGOM, MAB, and SNE. While current literature highlights leatherback dive behavior off SNE (Dodge et al. 2018, Patel & Siemann 2020), research into the movement ecology of leatherbacks in the NEGOM and MAB is relatively new, and no in-depth study of dive behavior in these areas exists. Our findings indicated clear distinctions in leatherback use of the water column and how it relates to each area's bathy-thermal conditions. We used these findings to infer foraging strategies and provide an explanation as to why this information is critical to informing region-based population assessments and conservation management strategies.

4.1. Dive behavior

Leatherbacks exhibited distinct diving patterns within each area. In the NEGOM, turtles spent more time near the surface and engaged in brief, shallow dives limited to 10 m, as well as deeper dives exceeding 50 m (Fig. 2). In the MAB, leatherbacks also spent a large proportion of their time at the surface, but their diving behavior primarily consisted of brief intermediate dives ranging from 10 to 50 m (Fig. 2). In SNE, dive behavior also consisted of intermediate dives, but these dives lasted longer, resulting in less time at the surface compared to turtles in the other 2 areas (Fig. 2). Combining these findings with observations from TAT, TAD, and PDT plots (Figs. 3 & 4), we can infer the foraging strategies exhibited in each area. While we cannot definitively classify this behavior as foraging without direct observation, inference of foraging in our results is based on movements and dive behavior similar to those seen during direct foraging observations in nearby areas (Wallace et al. 2015, Dodge et al. 2018, Patel & Siemann 2020).

Potential foraging strategies appeared to be similar between the NEGOM and MAB, as leatherbacks ap-

peared to target prey at and above the thermocline. Based on the PDT plots, the average depths of leatherbacks in each area corresponded to estimated thermocline depths. While average depth may not be an ideal indicator as to where in the water column leatherbacks spend most of their time, TAD plots give a more detailed assessment. Based on the TAD plots, leatherbacks in the NEGOM and MAB were observed to spend relatively more time at depths containing the thermocline (i.e. 25–50 m in the NEGOM and 10–20 m in the MAB). This foraging strategy has been observed off the coast of Nova Scotia, where leatherbacks specifically targeted jellyfish that accumulate at this physical boundary (Wallace et al. 2015). However, it is possible leatherbacks are also feeding on prey throughout the entire layer, given the high proportion of time spent between the surface and the thermocline. While there is little knowledge of the vertical distribution of jellyfish in these regions, loggerheads have been recorded consuming and encountering jellyfish between 1 and 16 m in the MAB (Patel et al. 2016) which would support our inferences.

Studies of foraging leatherbacks using animal-borne camera systems observed foraging to take place both at the thermocline boundary as well as during their ascent to the surface (Wallace et al. 2015). Capturing prey during ascent may lead to increased time at the surface handling and consuming prey (Heaslip et al. 2012). Further, handling time at the surface may increase with larger and more abundant prey species. Off the coast of Nova Scotia, leatherbacks were observed to spend more time at the surface while consuming larger prey items such as lion's mane jellyfish *Cyanea capillata* (James et al. 2006, Migneault et al. 2023). While it is unclear what prey species leatherbacks are consuming in the MAB, there is evidence of leatherbacks in the NEGOM consuming pink meanies *Drymonema larsoni* (Aleksa et al. 2016) which are large Scyphomedusae with a bell diameter of up to 45 cm and wet mass of 5 kg. Leatherbacks foraging off SNE were observed to consume sea nettles *Chrysaora quinquecirrha*, which were smaller, reducing the need for turtles to surface for further handling (Patel & Siemann 2020).

Due to longer dive durations and uniform distribution across most depths, we suggest leatherbacks off SNE foraged throughout the entire water column. The waters off SNE are highly productive, promoting high abundance of jellyfish (Lilley et al. 2011, Patel & Siemann 2020). During leatherback capture and tagging, we observed dense aggregations of gelatinous zooplankton, including sea nettles, lion's mane, and moon jellies *Aurellia aurita*. These waters are also

well-mixed, resulting in no defined thermocline or pycnocline that would typically promote aggregations of jellyfish at particular depths. These key attributes paired with a relatively shallow habitat (<35 m) should have allowed leatherbacks to perform routine dives to the bottom in search of prey. Indeed, previous research using autonomous underwater vehicles and animal-borne cameras observed leatherbacks in this area diving to the bottom and capturing prey from the bottom to just underneath the surface (Dodge et al. 2018, Patel & Siemann 2020). Here, we did not observe a high proportion of shallow dives; rather, most dives were between 10 and 50 m. It is possible that leatherbacks are diving to the bottom and silhouetting their prey against the illuminated surface to facilitate prey detection and capture. These strategies have been observed before off Nova Scotia (Wallace et al. 2015), a foraging site also seasonally inhabited by leatherbacks tracked in SNE (Dodge et al. 2014).

4.2. Diving behavior with respect to bathy–thermal conditions and movement behavior

Our results indicated that leatherback dive behavior was significantly related to SST, though the directionality of the relationship was inconsistent among foraging areas. As SST increased, turtles in both the NEGOM and MAB increased their surface durations and decreased their dive durations, while the opposite trend occurred in SNE. A plausible explanation for these relationships may be related to behavioral thermoregulation.

As mesotherms, leatherbacks can maintain a constant core body temperature despite ambient water temperatures through a suite of anatomical, physiological, and behavioral mechanisms (Paladino et al. 1990, Southwood et al. 2005, Bostrom et al. 2010). In warmer climates, they have been suggested to avoid overheating by reducing their activity, and diving to cooler waters (Paladino et al. 1990, Southwood et al. 2005, Wallace et al. 2005). By spending more time at the surface and less time diving, leatherbacks in the NEGOM may be reducing their activity levels as a means of reducing their metabolic rates, a behavior observed in inter-nesting females as well as captive juveniles (Wallace et al. 2005, Bostrom et al. 2010). Indeed, our use of the wet/dry sensor to quantify surface duration leads us to further believe leatherbacks may be resting as this sensor is the most accurate for determining surfacing events (Rogers et al. 2024).

Spending more time at the surface when SSTs are high may also cause leatherbacks to seek colder

water to aid in thermoregulation. Wallace et al. (2005) suggested that an increase in metabolic rate during periods of high activity (i.e. foraging) could increase the likelihood that, in warmer waters, core temperature would increase to the point where the physiological capacity to heat dump is exceeded and behavioral means of heat dumping are required. This could explain why we observed leatherbacks in the NEGOM increasing the proportion of dives past 50 m as SST increased. Diving past the thermocline would enable turtles to access cooler waters to regulate their body temperature. Indeed, leatherback body temperatures were observed to decrease during prolonged deep dives to cooler waters in the tropics during the inter-nesting period (Southwood et al. 2005).

In the MAB, leatherbacks displayed similar behaviors, as they performed more intermediate dives while SSTs were higher. An increase in the number of intermediate dives corresponded to an increase in the average SST during the months of June, July, and August (Fig. S6), which further supports the idea that these leatherbacks may be accessing colder water for thermoregulation. During these months, an annual cold pool forms in the MAB between 30 and 70 m; the difference between the surface and the cold pool can be up to 10°C (Lentz 2017). It is possible that leatherbacks are taking advantage of this colder body of water until it begins to dissipate in October, which corresponds to when they depart the MAB for the Gulf Stream (Rider et al. 2024).

The water column in SNE is relatively cooler and well-mixed compared to the other 2 areas. To elevate their body temperatures relative to that of the surrounding water, leatherbacks in this area may be relying on both solar and endogenous heat production. At higher latitude foraging grounds, leatherbacks have been observed basking at the surface (James et al. 2006, Migneault et al. 2023). This behavior has been suggested to be a possible means for exogenously elevating body temperature, as variability in this measure has been linked to increased time at the surface (Casey et al. 2014). Casey et al. (2014) also noted that swimming activity and specific dynamic action (i.e. heat produced by ingesting and digesting prey) may play a role in maintaining body temperatures above the ambient water temperatures in foraging areas off Nova Scotia. The high abundance of prey throughout the water column in SNE (Patel & Siemann 2020) would promote these means of heat production.

Based on the variation in dive behavior responses to bathy–thermal conditions in each area, it is possible that thermoregulatory behavior is a subcomponent of

the overall energy budget. Our results suggest leatherbacks in the NEGOM may need to thermoregulate separately from foraging, while those in SNE, where water is well-mixed, and the MAB, where the cold water is much shallower and more accessible (mean thermocline depth: MAB = 20 m, NEGOM = 58 m) may be able to use foraging behavior to maintain a consistent body temperature. Currently, these trade-offs may be managed by the relative proximity to nesting sites from the NEGOM compared to SNE, as may also be the case in the Pacific (Okuyama et al. 2021). Similar energetic trade-offs have been observed in other animals (i.e. birds; Van de Ven et al. 2019, mammals; Mason et al. 2017). To further explore these trade-offs in more detail, future research should aim to use fine scale movement data to estimate energy budgets (e.g. Wallace et al. 2015, Asada et al. 2022) to help understand the long-term effects of balancing active thermoregulation at the cost of foraging within each region, especially in the NEGOM. As temperatures continue to increase, turtles in the NEGOM may not be able to effectively thermoregulate and forage, which could impact other components of their life history (e.g. remigration for nesting; Neeman et al. 2015).

Interestingly, we observed a weak relationship between dive behavior and chl a concentrations. Chl a has been observed to have varying relationships with the movement behavior of leatherbacks. In the western Pacific, the likelihood of leatherbacks engaging in area-restricted behaviors was strongly related to chl a concentrations, while there was little to no relationship in eastern Pacific population (Bailey et al. 2012). Along the northwest Atlantic shelf, the primary factors explaining restricted behavior did not include chl a but rather region, bathymetry, and SST (Dodge et al. 2014). Since information on the distributions and abundances of gelatinous zooplankton are limited, chl a is typically used as a proxy for prey abundance (e.g. Hays et al. 2006, Fossette et al. 2010, Bailey et al. 2012). However, the use of just chl a for this purpose may not be sufficient. On a global scale, there was no significant relationship between gelatinous zooplankton biomass and chl a (Lucas et al. 2014). Rather, SST, dissolved oxygen, and primary productivity together were better predictors (Lucas et al. 2014). Aleksa et al. (2018a) suggested that chl a can be used in conjunction with other environmental parameters such as salinity and temperature as a more robust alternative proxy for prey abundance. As we continue to expand our knowledge of leatherback movement behavior across this region, there should be careful consideration of the environmental parameters used as proxies for prey

abundance and how those change by region. As most foraging behavior in the northwest Atlantic occurs within neritic regions along the coast, environmental drivers associated with those areas, such as salinity and primary productivity, should be incorporated into behavior and distribution models, as they may have more of an impact on leatherback preferred prey abundance compared to chl a .

Within each site, we observed minimal changes in dive behavior across diel periods. Although there was a slight increase in surface duration at night for both the MAB and SNE and deep dives at night in the NEGOM, this difference was negligible. Our findings suggest that foraging activities persist consistently regardless of the time of day, aligning with previous conjectures about leatherbacks foraging off Nova Scotia (James et al. 2006). This behavior contrasts with that proposed for leatherbacks foraging in oceanic regions of the Atlantic and Pacific, where individuals were observed to adjust their dive frequency and depth between day and night (Hays et al. 2006, Okuyama et al. 2021). These behaviors have been proposed to synchronize with the nocturnal, vertical migrations of plankton (Hays 2003). In the case of the neritic locations in this study, where prey is uniformly distributed throughout the water column (i.e. SNE) or often near the surface (i.e. NEGOM and MAB), substantial alterations in diel behavior appear unnecessary as leatherbacks can feed continuously. The ability to constantly forage is especially important in foraging grounds at higher latitudes, such as those off SNE and Nova Scotia, where leatherbacks have limited time to forage before migrating to lower latitudes. It is important to note that the programmed time bins used to record dive metrics did not perfectly align with sunrise and sunset. Thus, these results should be verified with data recorded at a higher temporal resolution.

Results from the move persistence model closely aligned with other studies that analyzed movement behavior of the same leatherback tracks using different methods. Both Aleksa et al. (2018b) and Sasso et al. (2021) used a Bayesian state space model to characterize the movements of leatherbacks in the NEGOM and each highlighted area-restricted behavior along the edge of the shelf as well as searching behavior on the west Florida shelf. In the MAB and SNE, Rider et al. (2024) used hidden Markov models that used both horizontal (i.e. speed and turning angles) and vertical (i.e. dive frequency and duration) metrics to estimate locations of area-restricted behavior. Based on these comparisons, we are confident in the use of the move persistence model to estimate the locations of area-restricted and transient behaviors

and believe that the results can guide future research to elucidate potential foraging behavior through direct observation.

The relationship between move persistence and dive metrics varied between the NEGOM and the 2 Atlantic areas. Turtles from the MAB and SNE increased their surface duration while decreasing their move persistence, similar to behaviors of leatherbacks migrating to and from foraging grounds off Nova Scotia (James et al. 2005b). Movement persistence had little relationship with surface and dive durations in the NEGOM. This may be attributed to the dispersed nature of prey in this area. Unlike the SNE foraging areas, where prey can be concentrated (Patel & Siemann 2020), distributions of prey species appear to be more dispersed along the continental shelf, with few areas of high density (Aleksa et al. 2018a). Thus, NEGOM turtles appear to employ broad area searching behavior with sustained directional persistence (Sasso et al. 2021). By navigating between widely distributed prey patches, their move persistence is more consistent across transient and foraging behaviors. This behavior mirrors observations of leatherbacks movement in the Gulf Stream, where prey patches are proposed to be ephemeral and geographically widespread (Hays et al. 2006).

4.3. Conclusions and potential impacts of dynamic ocean conditions

The results of this study provide new understanding of leatherback ecology along the northwest Atlantic shelf. We observed key differences in leatherback dive behavior in relation to the bathy–thermal conditions within each area. These findings not only elucidate regional variation in diving behavior that is critical to informing successful region-based population assessments, but also introduce concern for potential impacts of climate change and offshore energy development on foraging success.

The regional differences in use of the water column can have significant implications for both population assessments and conservation management. The estimated surface time and dive duration calculated for each region should be considered when assessing the availability bias that affects aerial surveys. Currently, no values exist for the NEGOM and the estimates from Rider et al. (2022) are averaged across the entire U.S. coastline. The estimates presented here, along with their relation to SST, are specific to each high-use area and should be considered when estimating population abundances. Further, the TAD distributions presented

here should be considered when assessing fishing gear mitigation efforts to reduce bycatch. Leatherbacks have been incidentally caught by longline fisheries in the northern Gulf of Mexico and MAB (Garrison & Stokes 2023) and fixed-gear fisheries (i.e. pot and trap gear) in SNE (Dodge et al. 2022). The information presented in this study may allow for dynamic management strategies (Maxwell et al. 2015) that account for variations in vertical habitat use by region.

Warming oceans have the potential to disrupt foraging success, especially in the NEGOM where temperatures are relatively higher than the other 2 areas. Rising temperatures may exacerbate the need to thermoregulate by requiring leatherbacks to spend more time resting to lower metabolic rates and/or to perform deeper dives to access cooler waters. As noted above, the relationship between body and water temperatures in the tropics has been studied (Southwood et al. 2005, Asada et al. 2022) with observations of prolonged dives to cooler waters lowering body temperatures (Southwood et al. 2005). However, these studies took place during the inter-nesting period and noted water temperatures lower than what we reported in the NEGOM. Thus, it is essential that future research not only record behavior using animal-borne videography but also measure body temperatures to further understand how leatherbacks might be able to balance thermoregulation and foraging behaviors to maximize and sustain energy uptake.

Offshore development in the form of wind turbines has introduced a new concern for foraging leatherbacks along the northwest Atlantic shelf and NEGOM. On Nantucket Shoals, it is hypothesized that the development of offshore wind turbines may disrupt zooplankton prey fields (National Academies of Sciences, Engineering, and Medicine 2024). Combined with documented high densities of leatherback prey species (Patel & Siemann 2020), the concentrated movement (i.e. low move persistence values) along Nantucket Shoals highlighted in this study suggests that this area promotes high foraging efficiency and therefore may serve as a primary foraging ground. While it is unclear what will happen to the distributions and abundances of these prey fields, it is important that leatherback foraging behavior continue to be monitored in this area.

To validate our findings and provide a more robust characterization of these inferred behaviors, complementary direct field-based observations are also imperative. Although such studies can pose logistical and financial challenges, researchers have successfully used technology, including accelerometers (Fossette et al. 2012), animal-borne video cameras

(Wallace et al. 2015, Rogers et al. 2024), autonomous underwater vehicles (Dodge et al. 2018), and remotely operated underwater vehicles (Smolowitz et al. 2015, Patel et al. 2016), to closely observe fine-scale sea turtle behaviors. For example, Asada et al. (2022) effectively used animal-borne video cameras equipped with 3-axis accelerometers and magnetometers to elucidate dive behaviors and provide metrics that aided in calculations of energy expenditure during the inter-nesting season. Conducting similar investigations in the NEGOM and MAB could validate the dive behaviors we have documented here and provide more detailed insights into leatherbacks' energetic intake and how it may be influenced by environmental conditions. Such research will aid in assessing the productivity of foraging in each region and how foraging success impacts leatherback remigration interval and reproductive output, as well as provide critical monitoring of the effects of climate change and offshore development on leatherbacks.

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