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ARTICLE

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High-resolution diving data collected from foraging area reveal that leatherback turtles dive faster to forage longer

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Abstract

Despite multiple studies examining the diving behavior of leatherback sea turtles (*Dermochelys coriacea*) at coarse resolution over broad distances, there is still a paucity of high-resolution diving data collected in areas where foraging has been confirmed. Short-term (~1–3 h) deployments of suction cup tags with time–depth recorders (TDRs) on 10 free-swimming leatherback turtles in a foraging area off Nova Scotia, Canada during August and September (2007–2014), captured a total of 161 dives. High-resolution (1–5 s sampling rate) dive profile data indicated variability in diving behavior between and within individuals. On average, turtles spent 55.7% of their time diving and 44.3% at the surface. Turtles generally performed short (mean duration = 250.4 s [SD = 47.9 s]) and shallow dives (mean depth = 24.3 m [SD = 5.8 m]). We recorded a mean dive descent rate of 0.32 m/s, which is faster than values recorded for leatherbacks in tropical waters. This may reflect differences in environment, behavioral mode (e.g., foraging vs. inter-nesting), and body condition. Linear mixed-effects models suggest a significant positive correlation between descent rate and mean depth, maximum depth, and integrated vertical bottom movement (IVBM). Turtles with faster descent rates dove deeper and increased their predicted foraging behavior (IVBM, or the sum of absolute differences in depth changes while at the bottom portion of their dives). Models additionally showed that dive time, bottom time, and IVBM were all positively correlated to the post-dive surfacing. This suggests that turtles required more time at the surface to recover and/or handle prey following longer dives characterized by increased vertical movement at the bottom portion of the dive. Dives were complex; the application of standard dive type/shape analysis may be over-simplified and inappropriate for leatherbacks foraging in these habitats. These results portray a novel and detailed look at the foraging dynamics of a diving marine reptile.

KEYWORDS
biologging, *Dermochelys coriacea*, diving behavior, endangered species, energy expenditure, feeding ecology, jellyfish, leatherback turtle, marine reptile, telemetry

INTRODUCTION

The leatherback sea turtle (*Dermochelys coriacea*) is a marine predator that feeds on jellyfish and migrates long distances between northern foraging grounds and breeding areas in the tropics. Most behavioral research on this species has occurred at low latitudes where adult females are readily encountered on nesting beaches (Hochscheid, 2014). Leatherbacks are comparatively difficult to locate and study on their high-latitude foraging grounds, where the collection of characteristic behavioral data sets in discrete areas can be affected by short-term tagging and/or handling effects if turtles are captured to facilitate attachment of biologgers (Sherrill-Mix & James, 2008). Previous research on the diving behavior of leatherbacks in tropical waters revealed diel diving patterns, with longer dives at night and more time spent at the surface during the day (Asada et al., 2021, 2022; Eckert et al., 1996). In some tropical areas of the Atlantic, this pattern is believed to mirror the diel movements of the leatherback's gelatinous zooplankton prey, with turtles utilizing shallower depth strata surface at night, then diving deeper during daylight hours (Hays et al., 2004). Most fine-scale dive data have been collected in tropical regions, particularly off nesting beaches, where foraging behavior may be infrequent relative to northern waters (Myers & Hays, 2006) and among reproductive females, fasting may even be the norm (Asada et al., 2022; Fossette et al., 2010).

Many North Atlantic leatherbacks migrate annually to temperate foraging areas to exploit seasonally abundant jellyfish. While jellyfish have relatively low energy content (Doyle, 2007), they are consumed in large quantities. A single foraging season can fuel 59% of a nonbreeding leatherback's annual energy budget, and 29% of energetic requirements for a female on a typical 2-year reproductive cycle (Wallace et al., 2018). When foraging in the temperate northwest Atlantic, most behavior is concentrated on the continental shelf, where leatherbacks perform relatively short and shallow dives at or above the main thermocline (Hamelin et al., 2014). This may reflect the concentration of prey above the thermocline and/or visually mediated foraging activity as turtles are known to limit dives to depths where sufficient ambient light is available to locate prey (Hamelin et al., 2014).

While several studies have examined leatherback diving behavior at coarse resolution across broad distances (Eckert et al., 1989; Okuyama et al., 2021; Reina et al., 2005; Sale et al., 2006), few have considered high-resolution diving data in discrete high-use areas where foraging has been confirmed. Traditional approaches to analyzing the diving behavior of air-breathing marine vertebrates often consider dive parameters such as dive time, bottom time, post-dive surfacing interval, and depth. Here, we focus on three dive metrics that have received comparatively little previous consideration in dive studies of leatherbacks in northern waters: integrated vertical bottom movement (IVBM; Hays et al., 2012), descent rate, and post-dive surfacing time. Previous research has suggested that in foraging areas, prey may be predominately captured at plateau portions of dives when rapid fluctuations of depth occur (quantified here as IVBM), or during ascent. We hypothesize that complex behavior can be observed in the rapid fluctuations in depth occurring while at the bottom portion of a dive, which, based on previous research, can be inferred as foraging behavior (Wallace et al., 2015).

Descent rate is the speed at which descent occurs in a dive. This metric may provide insight into organismal morphology, physiology, and energy expenditure. We hypothesize that for leatherbacks foraging in Canadian Atlantic waters, an increased descent rate will predict an increase in other dive parameters such as depth, bottom time, IVBM, and post-dive surfacing time.

Here, the post-dive surface duration will be used as a proxy for potential at-surface prey handling time. Thus, we predict that IVBM will be positively correlated with post-dive duration, with turtles utilizing this time possibly to handle and consume large jellyfish captured at depth more readily. This behavior has been suggested previously (James & Herman, 2001), but to our knowledge it has not been found to be significant in other studies (Wallace et al., 2015). We describe the relationship between these metrics and suggest how they may be used to better understand leatherback foraging strategy, success, and associated energy acquisition in areas where short-term biologger deployments are feasible.

METHODS

Time–depth recorders (TDRs; LAT1000 series, Lotek Wireless Inc., St. John's, NL, Canada) were deployed by hand on free-swimming leatherbacks from a platform suspended below the bowsprit of a commercial fishing vessel using a noninvasive positively buoyant suction cup tag pressed on the carapace as turtles surfaced (Figure 1). This technique was used to eliminate potential capture and handling effects. TDRs logged vertical dimensions of leatherback movement through changes in pressure, external temperature, and the suction cup tag incorporated a mechanical timed release and VHF transmitter for instrument tracking and recovery. TDR deployments occurred opportunistically over the span of 8 years in August and September ($n = 3$ in 2007, $n = 2$ in 2008, $n = 1$ in 2010, $n = 2$ in 2011, and $n = 2$ in 2014) in continental shelf waters (<200-m depth) off Cape Breton Island, Nova Scotia, Canada (~47° N, 60° W). All

FIGURE 1 Leatherback turtle with time–depth recorder, for the Nova Scotia Leatherback Field Research Programme. Photograph: Michael James, Fisheries and Oceans Canada.

deployments occurred during daylight hours to facilitate the recovery of tags following release. TDRs deployed in 2007 ($n = 3$ turtles) were programmed to sample at an interval of 5 s; all subsequent TDRs ($n = 7$) sampled at a 1-s interval. The tags deployed in 2014 ($n = 2$ turtles; Lotek, LAT2810) provided higher resolution temperature readings (faster thermistor response time). Suction cup tags were programmed to release between 1 and 4 h after deployment; however, a few corresponding datasets were truncated when tags detached prematurely (e.g., slid off carapace, knocked off by wave turbulence, etc.).

When possible, the sex of the turtle was assessed in situ at the time of tagging (tail length is markedly sexually dimorphic among mature leatherbacks, with males having longer tails; Stewart et al., 2007). Tagged turtles were directly observed resuming foraging activity immediately following tag deployment, including biting and swallowing jellyfish prey at the surface. Other evidence for the lack of apparent disruption to regular behavior associated with tagging included the discovery of jellyfish tentacles caught on suction cup tags at the time of tag recapture.

Dive analysis

The initial analyses of leatherback diving behavior were performed in R (R Core Team, 2020) using the package "diveMove" (Luque, 2007), which calibrates depth readings and separates individual dives into phases such as descent, bottom time, and ascent. The function "diveStats" quantifies diving parameters for dive time, post-dive duration, depth (both maximum and mean), descent time, and IVBM. Descent rate was quantified as the descent distance (in meters) divided by the descent

time (in seconds). Bottom distance (renamed in this study as IVBM for clarification purposes) was defined as a "numeric vector with the sum of absolute depth differences while at the bottom of each dive, or the measure of the amount of wiggling while at the bottom" (Luque, 2007). IVBM has been used previously in diving studies and is complimentarily defined as "the sum of the absolute differences in depth between readings n and n þ 1. For example, if depth readings over 5 mins were 4.6, 5.2, 1.7, 2.6 and 3.6 m, this equates to absolute changes in depth of 0.6, 3.5, 0.9 and 1 m, which sum to an IVBM of 6 m" (Hays et al., 2012). Using the "offset" function in diveMove, the minimum depth value for each turtle was offset to 0, enabling a consistent approach to classify post-dive surface time (Luque & Fried, 2011). Additional data recording time before the first dive (before tag deployment) and following the last dive (after tag release) were removed. To account for and to eliminate the potential effect of the amount of tag movement at the surface due to wave turbulence, any dives <45 s were omitted from the analysis following the use of the "divestats" function. Ambient sea surface temperature values were recorded for each turtle at each TDR sampling interval. All values are reported as mean ± SD, unless stated otherwise.

Behavioral analysis

For each individual dataset, the "diveStats" function in diveMove was used to record the following: the number of dives, the total time from the beginning of the first dive to the end of the last dive, the percentage of time spent at depth and at the surface, mean dive duration and post-dive duration, mean bottom time, mean IVBM, mean depth, maximum depth, and the mean descent rate. The relationships between various parameters were examined through tests for significance and collinearity.

Statistical analysis

ANOVA tests were performed for dive time, post-dive time, bottom time, IVBM, maximum depth, and mean depth to test for variation between individual turtles. For each parameter, Tukey–Kramer honestly significant difference post hoc tests were applied to evaluate which individuals were significantly different from each other. Linear mixed-effects models were fitted between parameters to identify any significant correlations, as well as significance among individuals, where turtle ID was used as a random effect. Modeling focused on the relationship between descent rate and other parameters as well as

post-dive duration and IVBM. Mean descent rate (in meters per second) was used as the control variable to test the response of post-dive duration, bottom time, dive time, IVBM, mean depth, and max depth. Dive time, bottom time, IVBM, mean depth, and max depth were tested for the response of post-dive duration. This was done using the R packages "lme4" (Bates et al., 2015) and "MuMIn" (Bartoń, 2020). To select the model, Akaike information criterion differences were used (Burnham & Anderson, 2002). ANOVA χ^2 tests were performed on the models to gather significance values and R^2 values. Model checks were done for heteroscedasticity and residual plots were assessed to check for normality within the data.

RESULTS

Summary dive data

A total of 161 dives ($n = 10$ turtles) were used to support dive analyses. Tagged turtles were labeled alphabetically for clarity (A–J). The average TDR recording time while tags were attached to turtles was 7255 ± 2033.1 s or 120.92 min. On average, turtles spent 55.7% of their time diving and 44.3% at the surface. The average dive duration was 250.4 ± 47.9 s or 4.17 min, and the average post-dive surface duration was 218.2 ± 73.3 s or 3.47 min. The mean dive depth among all turtles was 24.3 ± 5.8 m and the average maximum depth reached during deployments was 40.7 ± 14.2 m. The maximum depth recorded across all turtles was 65.6 m (Turtle B). The average descent rate was 0.32 m/s with a mean descent time of 76.2 ± 19.9 s. On average, Turtle H exhibited the greatest IVBM = 44.3 ± 17.2 m, meaning that the absolute differences in depth at the bottom portion of the dive were the largest (Figure 2). Turtle H also spent on average the longest time at the bottom while diving (mean = 152.1 ± 58.0 s). Turtles E and F traveled average IVBMs of 38.2 ± 25.1 m and 26.6 ± 31.3 m, respectively, and visually showed more variable diving behavior at the individual level (Figure 2). Individual values to summarize diving data are shown in Tables 1 and 2.

Diving behavior

Direct observation of leatherbacks engaging in foraging behavior following tag deployments suggested an absence of tagging effects. High variability was observed between individual dive profiles (Figure 2). Many dives involved intricate "wiggling" during the bottom portion of dives, which resulted in a variability in IVBM values (Table 2).

The high-resolution data yielded detailed dive profiles (e.g., Figure 3, Turtle H) which were poorly suited for classification into a narrow subset of dive shape types (e.g., V, U, W, etc., as is commonly applied to coarser scale dive data) due to the multitude of depth changes within a single dive. While dive profiles displayed unique patterns within individuals, all turtles performed relatively short and shallow dives, as expected from previous research (Figure 2; James et al., 2006). When data were organized into depth ranges, it was clear that 5 out of 10 leatherbacks (Turtles D, E, H, I, and J) spent most of their time between 15 and 20 m when diving (Figure 4). The 20–25 m range was also highly utilized. It should be noted that the lack of a salt-water switch, the depth resolution of the TDR tags, and the implementation of zero-depth offset correction may result in a proportion of the subsurface time being classified as post-dive surface time.

Temperature

A mean ambient temperature of $15.3 \pm 0.9°C$ was recorded from all TDR deployments. Temperature at maximum depth across all deployments ranged from 2.5°C at a depth of 38.1 m (Turtle I, Figure 5) to 14.7°C at a depth of 25.2 m (Table 2). Turtle J reached a maximum depth of 32.3 m at a temperature of 3.5°C (bottom, Figure 5).

Individual variation

There was significant variation between individual turtles across all diving parameters analyzed (ANOVA; $p < 0.001$; Table 3). Tukey pairwise comparison tests showed large variability among individuals for the different parameters. For example, Turtle J had a significantly slower descent rate compared to Turtles D, E, F, G, and H ($p < 0.05$), and Turtle I's descents were significantly slower than Turtles D, E, and G ($p < 0.05$; Figure 6). Turtle B consistently displayed significantly longer dives than four other turtles (Turtles A, C, D, and G; $p < 0.05$). The remaining turtles were more variable or consistently dove for shorter durations (Figure 6). Post-dive surface interval durations were generally consistent within individual dive records. However, there were exceptions as Turtle E exhibited longer post-dive surface durations on average (Figure 6). This display of inconsistent post-dive surfacing time was significant from Turtles B, C, D, F, G, and J ($p < 0.001$). Turtle H traveled significantly greater IVBMs (mean 44.3 ± 17.2 m) compared with the majority of other turtles ($p < 0.01$), traveling over double the IVBM of Turtles A, B, C, G, I, and J on average (Figure 6).
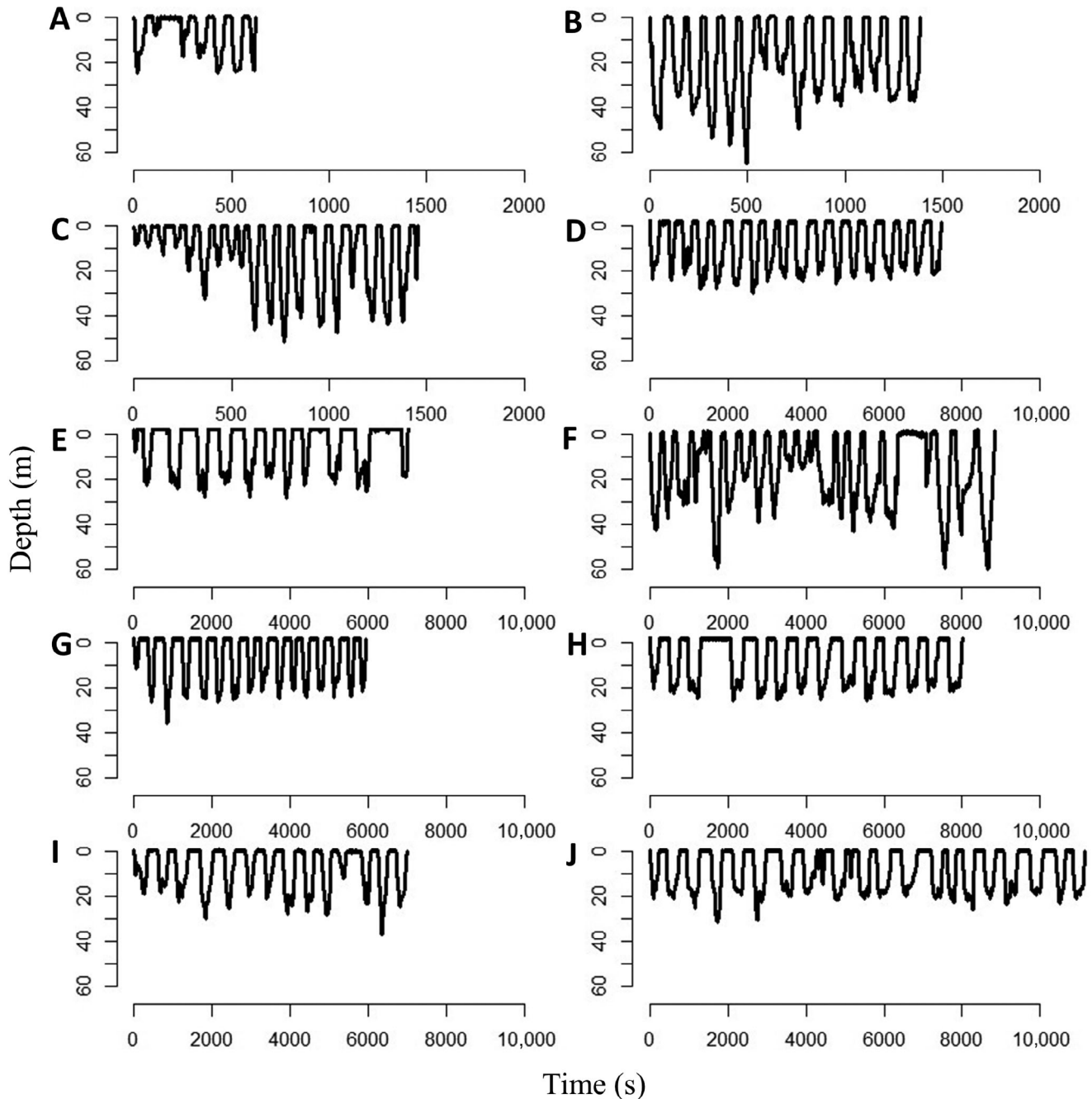
FIGURE 2 Dive profiles from 10 leatherback turtles (Turtles A–J) foraging off Nova Scotia, Canada, during August and September (2007–2014).

Model results

Linear mixed-effects models indicated that mean bottom depth during dives was predicted by and positively correlated with descent rate (i.e., mean depth increased with descent rate) (LMER: $\chi^2 = 18.9$, $p < 0.001$). R^2 values showed a marginal value of 0.12 and a conditional value of 0.35 suggesting that while the descent rate predicts depth, this is also changed by individual-level effects. Similar results were derived for maximum depth and descent rate (LMER: $\chi^2 = 217.2$, $p < 0.001$), where 28.7%

of the variation in descent rate was predicted by maximum depth through a positive correlation (marginal $R^2 = 0.16$, conditional $R^2 = 0.44$). Descent rate was predicted by IVBM (LMER: $\chi^2 = 9.05$, $p < 0.01$) with a marginal R^2 value of 0.06 and a conditional R^2 value of 0.31, suggesting that approximately 25% of the variation in descent rate is explained by IVBM. These models suggest that when turtles descended at a higher rate, they reached deeper mean and maximum depths, and achieved greater IVBMs (Figure 7). Several factors were shown to significantly predict post-dive duration,

TABLE 1 Dive behavior parameter data (mean and SD for dive length) from 10 leatherback sea turtles (*Dermochelys coriacea*) foraging off Nova Scotia, Canada.

ID	No. dives	Total time (s)	Time at depth (%)	Time at surface (%)	Dive length (s)
A	8	3100	50	50	193.8 ± 100.7
B	15	6905	70.9	29.1	326.3 ± 40.7
C	20	7255	57.3	42.7	207.8 ± 65.8
D	18	7456	58.6	41.4	242.6 ± 35.0
E	12	7008	42.2	57.8	246.3 ± 84.3
F	21	8827	70.8	29.2	291.5 ± 101.0
G	16	5933	47.6	52.4	176.6 ± 26.9
H	14	7982	53.2	46.8	303.6 ± 37.5
I	14	6971	51.3	48.7	255.4 ± 48.3
J	23	11,113	55.5	44.5	268.0 ± 95.1

TABLE 2 Continued dive behavior parameter data (mean ± SD) from 10 leatherback sea turtles (*Dermochelys coriacea*) foraging off Nova Scotia, Canada.

ID	Post-dive time (s)	Bottom time (s)	IVBM (m)	Depth (m)	Max depth (m)	Descent (m/s)
A	221.4 ± 155.7	66.9 ± 66.8	6.8 ± 8.8	15.8 ± 7.4	25.1	0.22 ± 0.06
B	143.6 ± 32.9	133.7 ± 42.7	20.4 ± 14.1	34.7 ± 8.2	65.6	0.33 ± 0.10
C	163.2 ± 46.6	48.0 ± 39.2	6.0 ± 6.6	27.3 ± 15.3	51.6	0.29 ± 0.13
D	181.7 ± 34.1	91.2 ± 41.1	27.6 ± 12.9	23.6 ± 2.8	32.5	0.35 ± 0.08
E	368.4 ± 178.9	124.2 ± 76.5	38.2 ± 25.1	21.8 ± 4.5	32.0	0.39 ± 0.10
F	122.0 ± 142.1	74.8 ± 89.4	26.6 ± 31.3	32.8 ± 14.7	62.0	0.30 ± 0.10
G	207.2 ± 35.1	37.1 ± 42.0	10.8 ± 12.8	24.8 ± 5.2	38.6	0.30 ± 0.10
H	287.1 ± 151.0	152.1 ± 58.0	44.3 ± 17.2	22.5 ± 2.2	28.5	0.37 ± 0.09
I	261.2 ± 60.1	78.1 ± 58.0	13.0 ± 9.1	21.2 ± 5.8	38.1	0.25 ± 0.07
J	225.0 ± 92.1	112.4 ± 71.6	13.2 ± 8.7	18.6 ± 4.2	32.3	0.21 ± 0.08

Abbreviation: IVBM, integrated vertical bottom movement.

including overall dive time (LMER: $\chi^2 = 4.12$, $p < 0.05$), bottom time (LMER: $\chi^2 = 6.61$, $p < 0.05$), and IVBM (LMER: $\chi^2 = 11.28$, $p < 0.001$). Dive time variation accounted for 31.1% of the variation in post-dive time (marginal $R^2 = 0$, conditional $R^2 = 0.31$) and bottom time accounted for approximately 27.2% of the variation in post-dive duration (marginal $R^2 = 0.04$, conditional $R^2 = 0.31$).

The most significant predictor of post-dive surface duration was IVBM (marginal $R^2 = 0.07$, conditional $R^2 = 0.33$). Approximately 26% of the variation in post-dive surface duration is explained by the absolute depth distance traveled while at the bottom phase of the dive. Models suggested that turtles generally spent more time at the surface following longer dives, longer bottom times, and after traveling greater IVBMs. Visual representations of all significant models are shown in Figure 7. No relationship was found between descent rate and bottom time, descent rate and dive time, nor descent rate

and post-dive surface duration ($p > 0.05$). Unlike mean depth, maximum depth was found not to be a predictor of post-dive surface duration ($p > 0.05$).

DISCUSSION

Deployment of suction cup tags with archival TDRs on free-swimming leatherback turtles provides novel insights into the fine-scale behavior of this species in a coastal, temperate foraging habitat. This is only the second study to collect high-resolution archival dive and temperature data to investigate the behavior of leatherbacks on foraging grounds using a comparatively large sample size for leatherback turtles in northern waters (Wallace et al., 2015). While instruments used in the present study did not incorporate video recording, their simplistic design and relatively small size facilitate noninvasive deployment on turtles without apparent disruption
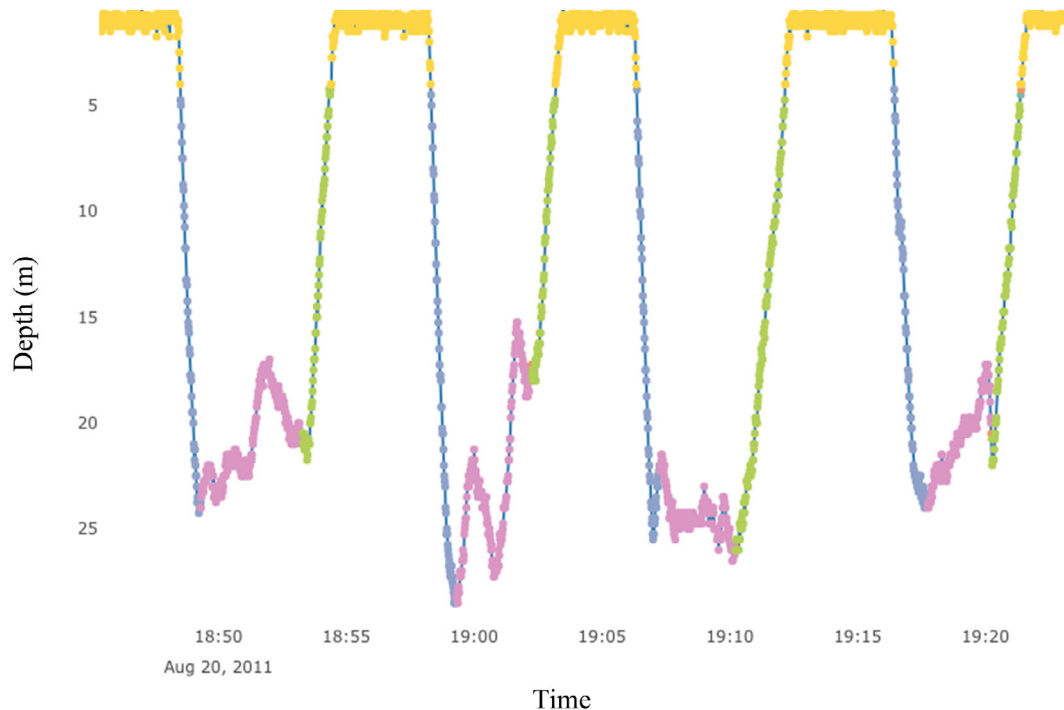
FIGURE 3 Four dives from Turtle H. Colors indicate phases of the dives; surfacing (yellow), descent (blue/purple), integrated vertical bottom movement (pink), and ascent (green). Figure produced using the R package "diveMove" (Luque, 2007).

of foraging activity. The present results indicate that foraging leatherbacks made repeated shallow (mean depth = 24.3 m) and short (mean duration = 4.17 min) dives. Wallace et al. (2015) reported similar dive durations among leatherbacks foraging off Canada (approximately, mean 4.50 min).

We found that turtles spent 56% of their time diving and 44% of their time at the surface. This is similar to Wallace et al. (2015) who observed 61% and 38%, respectively. An increase in time at the surface for leatherbacks in the present study versus those in tropical waters (e.g., Reina et al., 2005) likely reflects enhanced foraging effort (and success) in northern waters, with leatherbacks returning to the surface frequently, and for relatively long periods to process their jellyfish prey (James & Herman, 2001; Wallace et al., 2015). Initial calculations of leatherback aerobic dive limits suggest a range of 5–70 min (Lutcavage et al., 1992). More recent studies estimate around 12–48 min may be more accurate (Bradshaw et al., 2007; Wallace et al., 2005). With a mean dive duration of 4.17 min found in this study, it is very unlikely that leatherbacks foraging in Canadian waters are exceeding their dive limit.

Study of leatherbacks in Atlantic Canadian waters using animal-borne cameras has revealed that, although the majority of foraging occurs during bottom time, prey capture also regularly occurs during ascent (Wallace et al., 2015). This may help explain why turtles in the

present study spent so much of their time shallower than the maximum depths reached on individual dives. Half of the leatherbacks in the present study spent the highest proportion of dive time in the 15–20 m depth range, which likely reflects the shallowest depth at which their preferred prey are concentrated in those areas and at that time of year turtles were tagged. However, both the mean dive depth (24.3 m) and the maximum dive depth (mean = 40.7 m) were deeper than 15–20 m, suggesting that turtles often pass through this depth range. This may indicate that the turtles are silhouetting prey regularly found in the 15–20 m depth range by diving beneath them and capturing them upon their ascent, with extended time spent at this depth range associated with prey handling and ingestion. Other behavioral and environmental data from foraging leatherbacks suggest they are a visual predator at high latitudes, with foraging in temperate shelf waters focused at or above the thermocline and likely within the photic zone, where ambient light is available (Hamelin et al., 2014). Unfortunately, the dive profiles we collected were not sufficiently deep to establish the depth of a thermocline and the potential influence of this feature on behavior (Figure 5). Simultaneous independent deployments of depth profilers would help advance this understanding and are recommended.

There was high variability in depth range use among the turtles in our sample, a finding which has not been previously reported. The reasons for this are unclear, but
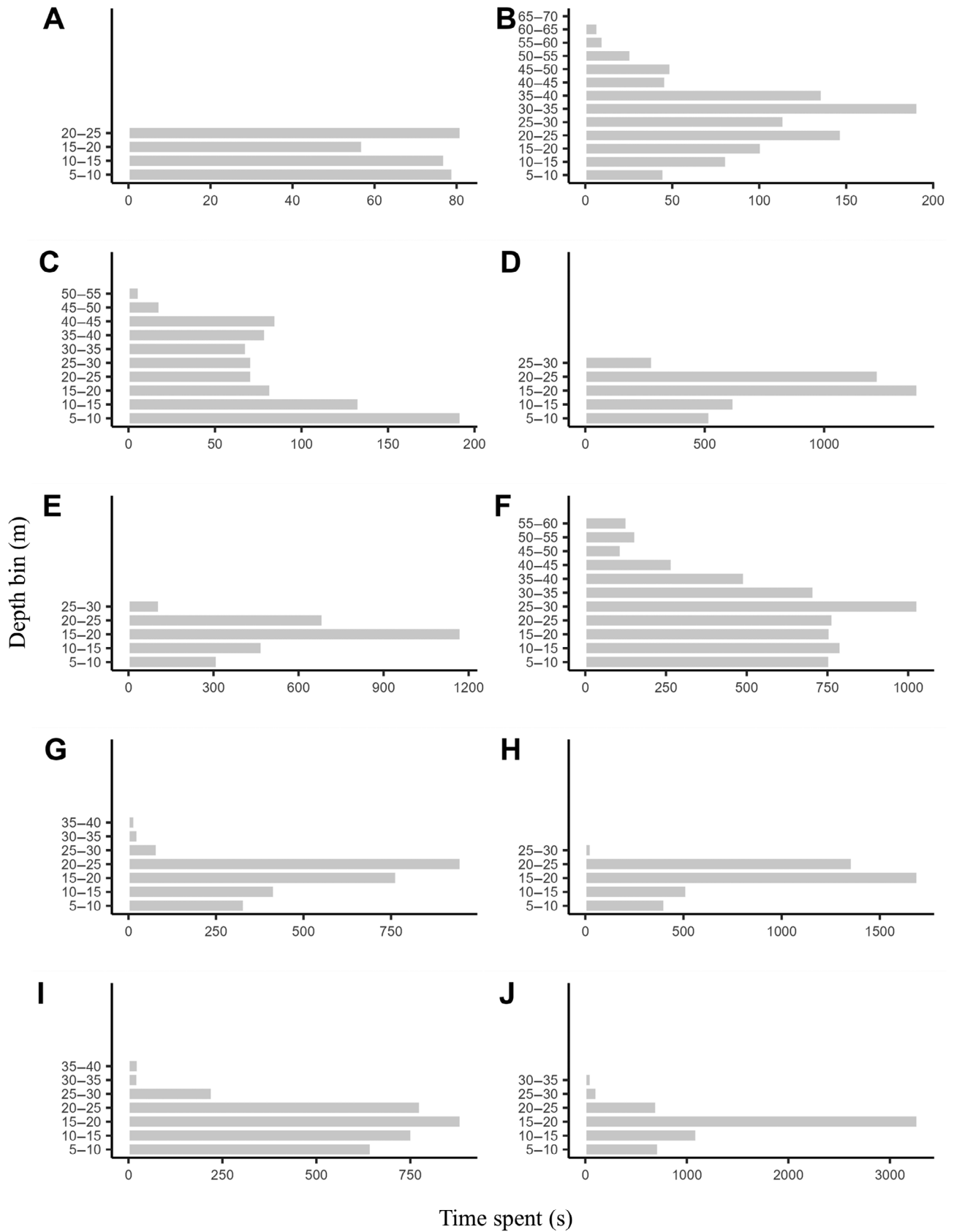
FIGURE 4 Proportion of time spent at depth for 10 leatherback turtles (identified alphabetically A–J) foraging off Nova Scotia, Canada.
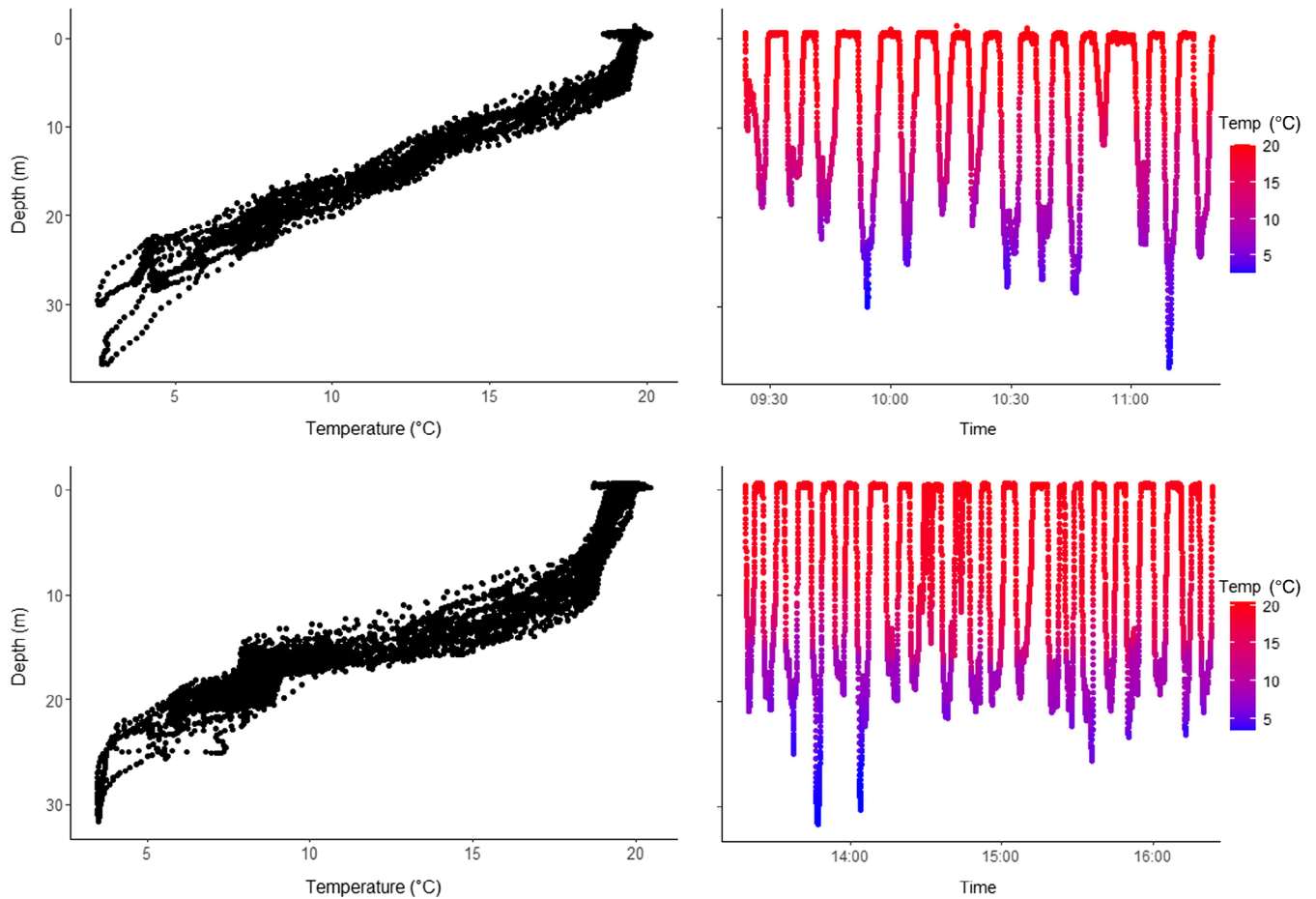
FIGURE 5 Ambient sea surface temperature recorded from time–depth recorders (TDRs) on two leatherback turtles foraging in 2014 off Nova Scotia, Canada. Top panels: Turtle I; bottom panels: Turtle J. Left panels: distribution of all temperature–depth records. Right panels: chronological temperature–depth record during TDR deployment.

TABLE 3 Results from ANOVA tests to identify variation in dive parameters, including integrated vertical bottom movement (IVBM), between leatherback turtles foraging off Nova Scotia, Canada.

Dive parameter	df	SS	MS	F	p
Dive time	9	317,711	35,301	7.225	1.08×10^{-8}
Bottom time	9	178,937	19,882	5.306	2.74×10^{-6}
IVBM	9	22,590	2510	8.913	1.02×10^{-10}
Post-dive	9	664,596	73,844	7.264	1.22×10^{-8}
Mean depth	9	4847	538.6	6.927	2.50×10^{-8}
Max depth	9	6639	737.6	8.593	2.43×10^{-10}
Mean descent rate	9	0.6206	0.06895	7.818	2.04×10^{-9}

it may indicate an individual preference for certain depth strata based on individual foraging success. Increased time spent at shallow depths of 5–10 m (as observed in Turtle C) could represent a behavioral thermoregulation strategy consistent with basking (Hochscheid et al., 2010) to facilitate warming and enhanced digestion in near-surface waters. Sunfish, also predators of gelatinous zooplankton, are known to rewarm at the surface in waters that have similar temperatures to those found in this study (18–3°C) (Nakamura et al., 2015). However, while time spent at surface waters may help facilitate digestion, Casey et al. (2014) found that metabolic processes were the primary source of heat for leatherback turtles. Alternatively, and more likely, it is possible that
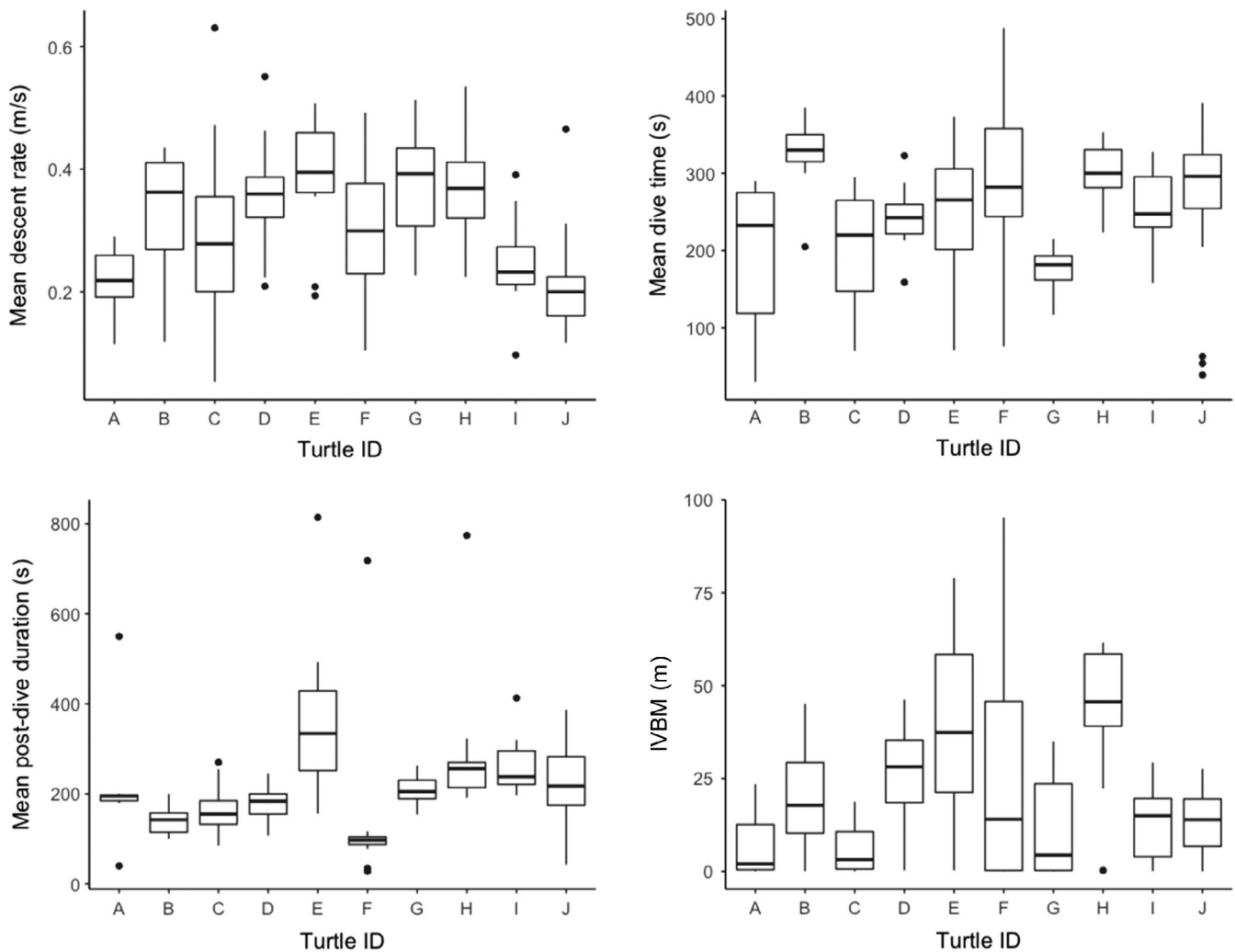
FIGURE 6 Boxplots depicting variation in mean descent rate (in meters per second) (top left panel), dive time (in seconds) (top right panel), post-dive duration (in seconds) (bottom left panel), and integrated vertical bottom movement (IVBM) (in meters) (bottom right panel) for 10 leatherback turtles off Nova Scotia, Canada. The lower and upper hinges correspond to the 25th and 75th percentiles. The upper whisker extends to the largest value within 1.5 times the interquartile range above the 75th percentile, lower whisker extends to the smallest value within 1.5 times the interquartile range below the 25th percentile. The midline corresponds to the median value. Outlying data points are plotted individually beyond the end of the whiskers.

variable depth use reflects dynamic ocean conditions and prey distributions as these data were collected over multiple years.

Model findings

The linear mixed-effects models we employed identified that mean bottom depth, maximum depth, and IVBM were predicted by descent rate (Figure 7). This suggests that foraging leatherbacks may select the depth they choose to descend to, as well as how much effort (time) they will put into foraging before they begin their descent, with targeted depth ranges reflecting relative prey density. Turtles descended at a faster rate for dives that were deeper and where a greater IVBM was covered (i.e., more wiggling/foraging) during bottom time. Fossette et al. (2010) described a similar relationship between descent rate and depth for inter-nesting leatherbacks in the tropics. However, this is the first time the descent rate has been investigated during the high-latitude foraging phase of the migratory cycle and is specifically related to foraging behavior. Other marine species, such as rockhopper penguins (*Eudyptes chrysocome*), also increase their descent rate to optimize time spent at the bottom (Tremblay & Cherel, 2000). Descent rates of 0.23 m/s (Eckert, 2002) and between 0.20 and 0.26 m/s (Fossette et al., 2008) have been
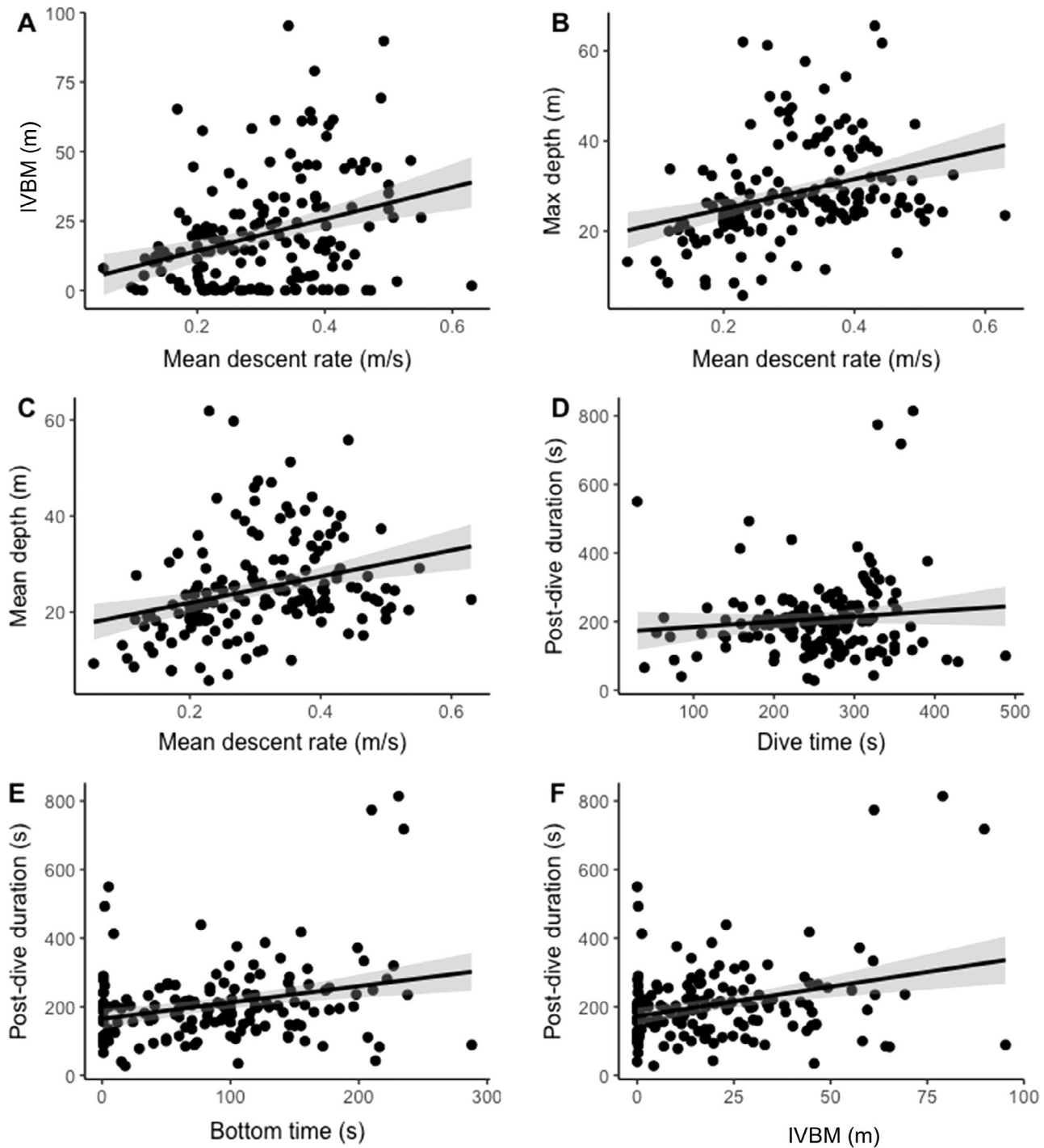
FIGURE 7 Correlations between diving parameters in 10 leatherback turtles off Nova Scotia, Canada. Black line indicates the line of best fit and the surrounding gray band indicates the CI. IVBM, integrated vertical bottom movement.

previously recorded for leatherbacks in the tropics. The mean descent rate recorded from our sample in Canada was 0.32 m/s, which is marginally faster on average than that recorded by Eckert (2002). Due to our larger sample size than previous studies (Eckert, 2002), the mean descent rate recorded here is likely more realistic, specifically for turtles in northern foraging grounds.

In the present study, dive time, bottom time, and IVBM (an index of foraging success; Wallace et al. (2015)) were all positively correlated with post-dive surface duration (Figure 7). This may reflect both the relatively large size of the jellyfish that leatherbacks encounter off Atlantic Canada (e.g., *Cyanea* sp.) and prey density. Leatherbacks may require more at-surface prey handling

time when encountering such large and relatively abundant prey in temperate coastal waters off Eastern Canada. Extended at-surface prey handling time in Canadian waters has been previously reported (James et al., 2006; James & Herman, 2001).

Future research

The high-resolution dive profiles we collected from leatherbacks in a discrete foraging area off Nova Scotia, Canada could not be easily classified into a series of dive types (e.g., V, U, W, etc.), using automated dive shape analysis that has been previously applied to leatherback diving data in tropical areas (Fossette et al., 2007, 2008; Reina et al., 2005). By contrast, the dive profiles of the leatherbacks we studied are typically comprised of a steep ascent and descent (similar in this sense to "V" type dives). Importantly, these dives include multiple steps in depth, both up and down, of varying number and magnitude, corresponding to the bottom portion of the dive. As such, the nature of these dive profiles does not readily fit widely used dive shape categories. The leatherbacks in our sample performed complex dives which incorporate extended bottom time where classic "wiggling" behavior is observed. Applying the classification of dive type to diving datasets has been identified as problematic by others due to inconsistencies in the methodology used across various studies (Hochscheid, 2014). The present data support movement away from simple dive-type categorization to avoid missing dynamic behavior in a dynamic oceanographic context. Instead, for leatherbacks foraging in coastal temperate northwest Atlantic waters, particular attention should be paid to bottom dive time, IVBM, and associated behaviors (i.e., wiggling), as it has been established that most prey capture occurs during these rapid fluctuations in depth in the bottom portion of dives and on ascent (Wallace et al., 2015). Although TDRs provide insight into the vertical dimensions of leatherback movement, further research should be done to study the three-dimensional dive paths of foraging leatherbacks in cold, temperate regions using instruments such as tri-axel acceleration data loggers.

Understanding the diving behavior of endangered, highly migratory marine vertebrates is important for promoting species recovery. In the case of leatherback turtles, expanding high-resolution behavioral research far beyond nesting beaches to the largely inaccessible, but critically important high-latitude parts of their foraging range, is essential. Not only does a sizeable component of the northwest Atlantic leatherback turtle population inhabit northern waters for several months each year (James et al., 2005; James & Herman, 2001),

but leatherbacks are also vulnerable to entanglement in vertical lines associated with fishing gear in a multitude of areas (Dodge et al., 2022; Doyle et al., 2008; Hamelin et al., 2017; Houghton et al., 2006). Further investigation of leatherback movements and diving behavior in northern waters may therefore be integral to understanding and mitigating leatherback-fishery interactions.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data were collected through collaboration with fishing industry participants, correspond to movements of a species listed as *Endangered* under Canada's Species At Risk Act, and are available to qualified researchers from the Canadian Sea Turtle Network by contacting the Canadian Sea Turtle Network, info@seaturtle.ca.

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