






Deep diving by offshore bottlenose dolphins (*Tursiops* spp.)

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Abstract

We used satellite-linked tags to evaluate dive behavior in offshore bottlenose dolphins (*Tursiops* spp.) near the island of Bermuda. The data provide evidence that bottlenose dolphins commonly perform both long (>272 s) and deep (>199 m) dives, with the deepest and longest dives being to 1,000 m and 826 s (13.8 min), respectively. The data show a relationship between dive duration and dive depth for dives longer than about 272 s. There was a diurnal pattern to dive behavior, with most dives deeper than 50 m being performed at night; deep diving began at sunset and varied throughout the night. We used the cumulative frequency of dive duration to estimate a behavioral aerobic dive limit (bADL) of around 560–666 s (9.3–11.1 min) in adult dolphins in this population. Dives exceeding the bADL spent significantly longer time in the upper-most 50 m following a dive as compared with dives less than the bADL. We conclude that the offshore ecotype off Bermuda, unlike the shallow-diving near-shore bottlenose dolphin, is a deep-diving ecotype, and may provide a useful animal model to study extreme diving behavior and adaptations.

KEYWORDS

bADL, behavioral aerobic dive limit, cetacean, dive behavior, dive physiology, extreme diving, marine mammal

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1 | INTRODUCTION

Climate change and anthropogenic disturbance are becoming issues of greater concern for cetaceans as human impacts on the environment and oceans continue to increase. While studies on wild cetaceans are important to understand their in-situ behavior, a better understanding of their physiological capacity is vital to understand the constraints that may eventually limit survival. For example, climate change may result in changes in prey availability, and some species or ecotypes may be limited by their physiological capability as they try to capture enough food to survive. As the bottlenose dolphin (*Tursiops* spp.) is the most-studied and accessible dolphin species for understanding limitations to diving, it is important to better define the physiological capacity of its different ecotypes. It may also be that these differences in physiological capacity are further evidence that these ecotypes are distinct species, as has been suggested recently (Costa et al., 2021). If certain ecotypes of bottlenose dolphins can indeed be considered deep divers, it would provide evidence that the bottlenose dolphin is a useful animal model to study deep-diving adaptations and better understand the anthropogenic threats to less accessible deep-diving species.

The behavioral ecology of nearshore common bottlenose dolphins is well documented, and they live in a range of habitats from temperate to tropical waters, with different ecotypes inhabiting different habitats (Wells & Scott, 2018). Long-term studies of specific populations have provided detailed descriptions of their social behavior, ecology and, to some extent, physiology (Wells & Scott, 2018). The most-studied populations are nearshore dolphins, where most dives tend to be short and shallow following the nearshore bathymetry (Irvine et al., 2019; Wells et al., 2013; Würsig, 1978), and they therefore have rarely been considered a deep-diving species (e.g., Rowlands et al., 2021) despite reports that offshore populations of this species are capable of deep dives greater than 450 m (Fahlman et al., 2018b; Klatsky et al., 2007).

Bottlenose dolphin dives have been measured by direct radio-tracking, archival tags, and satellite-linked tags. Although direct comparisons are difficult between these different bio-logging devices and approaches due to their varying sampling techniques and schedules, comparisons of maximum dive efforts can still be made. For example, in Sarasota Bay, Florida, the maximum dive depths and dive durations in four female dolphins observed from an archival time-depth recorder (DTAG; Johnson & Tyack, 2003) were 5–10 m, and 110–129 s, respectively (Fahlman et al., 2018b). Dive depths of dolphins in Sarasota Bay, however, are limited by the shallow nature of the Bay (which has a maximum depth of 4 m) and nearshore waters. Studies with satellite-linked tags in Sarasota Bay in 2012, which reported dive duration data, found that most of the dives of three tagged bottlenose dolphins were <30 s in duration, with occasional dives exceeding 185 s, and shorter dives tended to occur at night (Wells et al., 2013). Radio-tagging studies suggest that the dive durations in nearshore populations from Argentina, and different locations in Florida, range from 20 to 40 s, with a maximum duration of about 265 s (Irvine et al., 1981; Würsig, 1978). A single female dolphin, studied with a satellite-linked tag in Tampa Bay, Florida, showed similar dive behavior, with short and shallow dives with a mean dive duration of 25–32 s depending on the time of day (Mate et al., 1995). This single female performed deeper and longer dives, and higher percentage time submerged in the afternoon than in the evening or at night (Mate et al., 1995). Tampa Bay is adjacent to Sarasota Bay, and in places is up to 13 m deep. Klatsky et al. (2007) tagged three bottlenose dolphins in the deep waters surrounding the Bermuda Pedestal and reported that the maximum dive depths of two of the dolphins exceeded the 500 m programming limit of the satellite-linked tags they used in the study. They also found that while a majority of dive durations for these three dolphins did not exceed 60 s, 46.4% of dive durations (defined as dives >6 m) surpassed 300 s. Finally, Ridgway (1985) reported that a coastal Atlantic bottlenose dolphin dove to 390 m for 450 s and a trained Pacific bottlenose dolphin dove to 535 m for 480 s. Despite the limited reports of dive behavior of offshore ecotypes, the bottlenose dolphin is often quoted to be a shallow-diving species, despite evidence of their capacity for deep and long dives. Such classification may be misleading when considering the response to climate change and warrants further investigation.

The aerobic dive limit (ADL) provides a useful index of the physiological diving capacity of a species, and allows predictions of their vulnerability to ecosystem changes due to climate change. The ADL, or lactate threshold, is defined as the dive duration powered by aerobic metabolism (Kooyman et al., 1980, 1983). It has also been

suggested that diving within the ADL improves foraging efficiency as it prevents the production and accumulation of anaerobic by-products, which eventually requires extended surface intervals or short and shallow dives to clear the lactate (Houston & Carbone, 1992; Houston et al., 2003; Kooyman et al., 1980). As it is logistically difficult to assess the ADL, the calculated ADL (cADL), or behavioral ADL (bADL) are two alternative estimates of aerobic diving capacity. The cADL is calculated by dividing the total O₂ stores by the resting metabolic rate, or an estimated diving metabolic rate (Butler & Jones, 1982). Thus, the cADL only provides a static estimate of the maximal diving capacity of a species, and variation in the metabolic rate or the O₂ stores during or following diving has only recently been estimated (Fahlman et al., 2023). The bADL was proposed as an alternative index of diving capacity based on data from the Weddell seal (*Leptonychotes weddellii*), where it was shown that 92%–96% of all dives were less than the measured ADL. The bADL has therefore been estimated as the dive duration where 95% of all dives were performed and has been used to examine physiological limits in both the Weddell seal and Cuvier's beaked whale (*Ziphius cavirostris*; Burns & Castellini, 1996; Quick et al., 2020).

In the current study, we used ARGOS-based satellite-linked time-depth transmitting tags to examine dive behavior in bottlenose dolphins around Bermuda. Previous research, and the habitat features in this region, provide evidence and opportunities to study dives that are deeper and longer than have been reported for nearshore bottlenose dolphins previously (Fahlman et al., 2018b, 2023; Klatsky et al., 2007). We examined dive depths, dive durations, and postdive shallow intervals of four tagged dolphins, estimated their bADL, and assessed diurnal changes in their dive behavior while they were inhabiting deep waters near Bermuda. Our data provide evidence that members of this ecotype regularly dive deeper than 500 m, to our knowledge the maximum depth previously reported for free-ranging bottlenose dolphins, and that on occasion, these animals dive up to 1,000 m and longer than 780 s. Based on the distribution of dive durations, we estimate the bADL of these dolphins to be approximately 620 s (560–666 s). These data provide clear evidence that the offshore bottlenose dolphin can perform deep and long dives and should be considered a deep-diving ecotype.

2 | MATERIAL AND METHODS

2.1 | Animals

Four bottlenose dolphins were studied off Bermuda in August 2016. Individual dolphins were caught by a break-away hoop netting technique (Asper, 1975). Once in the net, swimmers maneuvered the animal onto a buoyant foam mat. The animal was moved into a sling and then brought onto the sampling boat. Once on the boat, the dolphin was weighed (± 0.2 kg; Ohaus 3000 Series industrial floor scale) and underwent a brief basic health examination (e.g., Wells et al., 2004), including evaluation of lung function and resting metabolic rate (Fahlman et al., 2018c). The animal was then tagged with a satellite-linked tag attached to the trailing edge of the dorsal fin using a single 5/16" Delrin pin as detailed below (Figure 1).

Bermuda Tagged Bottlenose Dolphins - 2016



FIGURE 1 Photograph showing satellite-linked tag placement for each dolphin. See Table 1 for description of each animal.

All work was approved by the IACUC at Texas A&M University Corpus Christi (TAMUCC-IACUC AUP#04-11), the Bureau of Medicine (BUMED, NRD-1015), and by a research permit issued by the Bermuda Government, Department of Environment and Natural Resources (Research permit number SP160401r).

2.2 | Satellite-linked tag

Wildlife Computers SPLASH10-268D Single-point Finmount tags were used to record behavioral data. The tags were programmed for 400 transmissions per day, and the minimum time between transmissions was set to 46 s. The duty cycle was set to match optimal satellite passes, based on the ARGOS on-line satellite pass prediction values, looking for satellites with $>20^\circ$ elevation for at least 3 min. Data were transmitted during the following local time windows: 21:00–23:00, 03:00–09:00, 10:00–12:00, 14:00–16:00, and 18:00–20:00. All tags had the same duty cycle to allow assessment of whether the animals remained together postrelease.

The tag was placed against the fin, so that the connection of the tag wings fit snugly against the trailing edge of the fin (while not applying pressure to the fin edge) to stabilize the tag in a horizontal orientation and reduce the possibility of the tag moving vertically. For pain reduction, lidocaine with epinephrine, a commonly used analgesic, was injected in the center of the tag placement site on the fin for the core with 1–2 injections. A pre-cored Delrin pin was placed in the hole and secured the tag to the fin by means of 3/8" Tri-P 10–14 zinc-plated steel thread-forming screws for plastic, inserted through stainless steel washers on each side of the tag attachment wings to encourage corrosion that would eventually release the tag, usually in the range of 8–12 weeks. Photographs were taken of the attachment and tag serial number (Figure 1).

2.3 | Tag data programming and processing

To allow assessment of the deep diving patterns, tags were programmed with Mk10 Host 1.26.2008. Dives were defined as any submergence greater than 2 m; however, the tag was programmed to ignore dives <50 m or <30 s. This range was selected so that the dolphin's deep diving patterns could be characterized while optimizing battery life by not using up transmissions on more frequent shallow dives. This approach to collect relatively detailed dive data gave us an estimated battery life of 60 or more days.

Transmitted tag data were inspected to assess potential transducer failures or drifts that may have influenced dive depth recordings and for the presence of data gaps in the tag records (i.e., data validation). Specifically, the depth and zero depth offset information reported on the status files of each dolphin's tag was examined for extreme values as these have been reported to be indicative of possible transducer failure in other species (e.g., Cuvier's beaked whales; short-finned pilot whales, *Globicephala macrorhynchus*; Baird et al., 2019; Cioffi et al., 2022). In these files the depth is the last depth reading recorded before the tag transmitted data, while the zero-depth offset value is the amount of offset that the tag is applying to the depth sensor readings if this feature is enabled on the tag (Wildlife Computers, Redmond, WA). We followed definitions outlined by Baird et al. (2019), which considered cases where more than one depth value in the status record exceeded ± 10 m as indicative of potential transducer failure issue, and Cioffi et al. (2022), which defined unacceptably high pressure transducer drift as two or more consecutive absolute value zero depth readings >10 m, when assessing data records for possible failures or drifts. Data gaps were defined as any two consecutive records with more than 0 s missing between the end of dive i and the start of dive $i + 1$.

Behavioral dive data, including dive duration, dive depth, and time spent shallower than 50 m (hereafter referred to as postdive shallow interval), were summarized and inspected for outliers. Although only dives >50 m were recorded, the duration of those dives began at a depth of 2 m. Thus, the durations of these dives are slightly longer than reported here, i.e., the period from the surface to 2 m. Dive depths, durations and postdive shallow intervals are

reported as minimum and maximum values. We used the median of the reported minimum and maximum values of these metrics in our analyses. Only complete dive records (dive records that had a paired depth, duration, and postdive shallow interval) were considered in the analyses.

Statistical analyses were completed in SigmaPlot (V. 11; Systat Software, Palo Alto, CA), and in the R programming language (R Core Team, 2020). We used linear mixed effects models (*nlme*; Pinheiro et al., 2021), using animal as a random factor, to compare the means. A segmented linear regression was used to examine the relationship between dive duration and depth (*segmented*; Muggeo, 2003), with a single break point. Diurnal dive patterns were examined using the midpoint sunrise and sunset times obtained from the U.S. Naval Observatory (<http://aa.usno.navy.mil>) from the animal release dates and the last date of tag transmissions. All times are reported in local time (UTC minus 4 hr during daylight standard time). Figures were created using the following packages in R (R Core Team, 2020): “lubridate” (Grolemund & Wickham, 2011), “ggplot2” (Wickham, 2016), “tidyverse” (Wickham et al., 2019), “scales” (Wickham & Seidel, 2020), “cowplot” (Wilke, 2020), “viridis” (Garnier et al., 2023).

3 | RESULTS

Four dolphins (1 female and 3 males) were caught and tagged for this study. The three males remained in the vicinity of the Bermuda Pedestal, while the female ranged widely through the Sargasso Sea, up to several hundred kms from Bermuda. The tags transmitted data for 65–69 days (Table 1); however, to be conservative, data records from the behavioral files (e.g., dive depth, duration, and postdive shallow intervals) were removed if they were received after the last status message was received on each tag's status file. All four tagged animals had acceptable zero depth readings on their status files; however, the tag from Paget reported multiple consecutive depth records ≥ 10 m indicating the possibility of transducer failure or drift on this tag. To minimize possible influence on the reported behavioral records for Paget, data records transmitted after these consecutive extreme values were also omitted from this animal's tag record for data analysis. Further, incomplete dive records (i.e., dive records that did not have a paired depth, duration, and postdive shallow interval) were removed from the analysis for all four dolphins. A significant number of data gaps were identified between consecutive records in the tag's behavioral data for all four dolphins (Table 1). These data gaps could be found throughout the tag deployment periods and were present at comparable rates regardless of the time of day (see Figures S1 and S2). After accounting for these data gaps and removal of records based on our data validation steps listed above, 5.95 to 25.17 days of behavioral data were analyzed for each dolphin (Table 1). This included 249 to 1,562 paired dives and postdive shallow intervals (Table 2).

The basic dive descriptions are summarized for each dolphin in Table 2. The maximum dive depths and dive durations were similar among animals (Figure 2). The maximum dive depths ranged from 808 to 1,000 m, with an overall mean (median) \pm SD maximum dive depth of 880 (856) \pm 84 m (Table 2). The maximum dive durations ranged from 792 to 826 s, with an overall mean (median) \pm SD maximum dive duration of 809 (808) \pm 19 s. The deepest and

TABLE 1 Dolphin name, Tag ID (PTT ID), sex (male-m, female-f), straight length (SL), body mass (M_b), girth (G), satellite tag deployment date (DD), date of last data transmission (LDT), transmission duration (TD), last date that data were considered for analysis after data validation (LDA), number of gaps (>0 s) between consecutive behavioral records between DD and LD, and duration of time that the tags recorded behavioral data between DD and LD (DT) for dolphins studied off Bermuda in 2016.

| Name | PTT ID | Sex | SL (cm) | M_b (kg) | G (cm) | DD | LDT | LDA | Num gaps | DT (days) |
|------------|--------|-----|---------|------------|--------|--------|-------|--------|----------|-----------|
| Devonshire | 110606 | M | 256 | 294 | 142 | Aug 30 | Nov 4 | Oct 31 | 205 | 25.17 |
| Hamilton | 110607 | M | 261 | 282 | 142 | Aug 30 | Nov 3 | Oct 21 | 137 | 18.43 |
| Pembroke | 110608 | M | 251 | 282 | 144 | Aug 31 | Nov 8 | Oct 20 | 146 | 15.56 |
| Paget | 110610 | F | 238 | 173 | 144 | Aug 31 | Nov 8 | Sep 9 | 31 | 5.95 |

TABLE 2 Dolphin name; total number of dives analyzed; maximum, mean (median) \pm SD dive depth, dive duration, and postdive shallow duration; estimated behavioral aerobic dive limit (bADL); number and percent of dives longer than each dolphin's bADL; and the mean (median) \pm SD postdive shallow durations following dives longer and shorter than each dolphin's bADL for dolphins tagged off Bermuda in 2016.

| Name | # dives | Dive depth (m) | Dive duration (s) | Postdive shallow duration (s) | Estimated bADL (s) | # (%) Dives \geq bADL | Shallow duration for dives bADL (s) | Shallow duration for dives < bADL (s) |
|------------|---------|----------------------------|--------------------------|--------------------------------|--------------------|-------------------------|-------------------------------------|---------------------------------------|
| Devonshire | 1,562 | 872, 242 (222) \pm 168 | 824, 363 (378) \pm 154 | 40,560, 989 (231) \pm 3320 | 596 | 81 (5.2) | 1,133 (386) \pm 2,900 | 981 (226) \pm 334 |
| Hamilton | 1,059 | 1,000, 300 (296) \pm 199 | 826, 405 (430) \pm 169 | 34,320, 1,001 (262) \pm 2867 | 666 | 54 (5.1) | 1,855 (742) \pm 3,215 | 955 (254) \pm 2,842 |
| Pembroke | 1,025 | 840, 210 (156) \pm 157 | 792, 333 (330) \pm 150 | 31,500, 947 (218) \pm 2647 | 602 | 54 (5.3) | 1,638 (761) \pm 2,284 | 908 (204) \pm 2,661 |
| Paget | 249 | 808, 267 (288) \pm 147 | 792, 371 (410) \pm 144 | 47,040, 1,552 (268) \pm 5896 | 560 | 14 (5.6) | 1,301 (438) \pm 2,822 | 1,567 (260) \pm 6,033 |

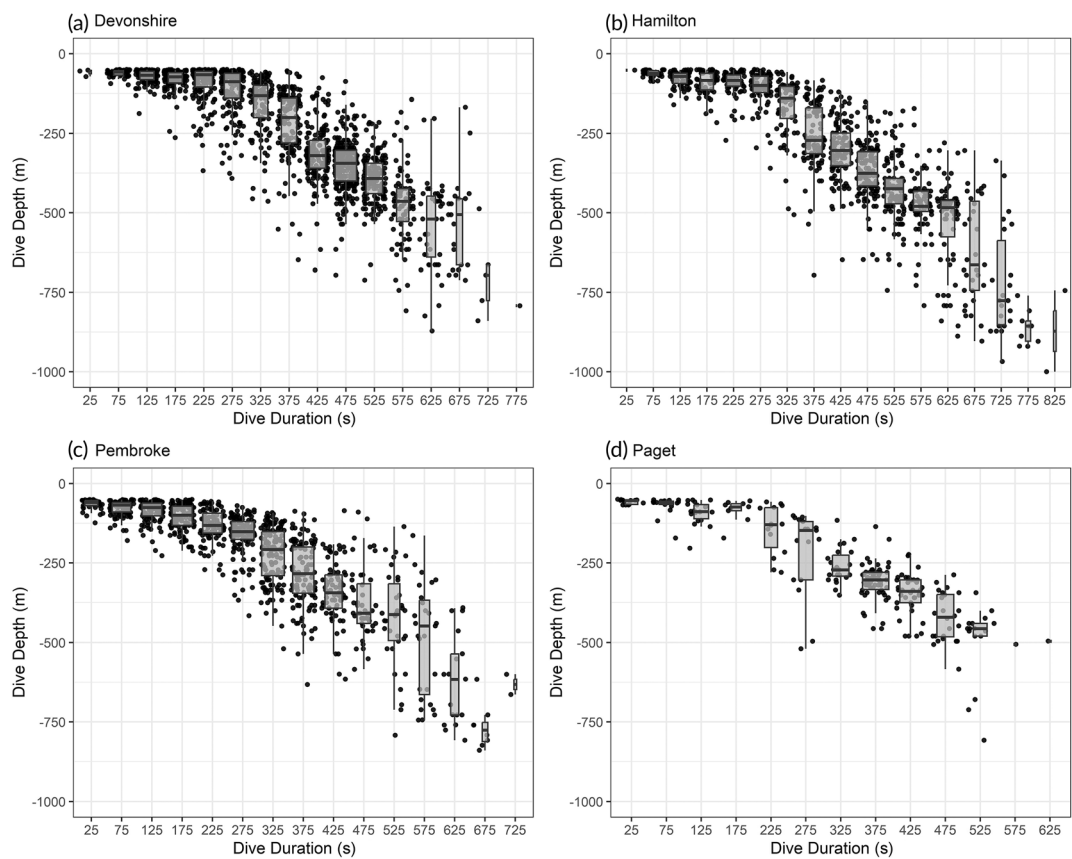


FIGURE 2 Scatter and boxplot of dive depth (m) versus dive duration (s) for each bottlenose dolphin instrumented with a satellite-linked tag. See Table 1 for description of each individual. Boxes span the interquartile range, and box widths are proportional to the square root of n . Thick horizontal lines show medians, and box whiskers extend no greater or less than $1.5 \times$ the interquartile range.

TABLE 3 Individual results from segmented linear regression analysis of dive depth and duration. Animal name, intercept (b_0), slope 1 (Depth 1, Duration 1), slope 2 (Depth 2, Duration 2), break-point depth and duration (Break point), and r^2 are included.

| Depth as independent variable | | | | | |
|---------------------------------------|-----------------|-----------------|------------------|-----------------|-------|
| Name | b_0 | Depth 1 | Depth 2 | Break point (m) | r^2 |
| Devonshire | 102.5 ± 6.7 | 1.44 ± 0.07 | -0.93 ± 0.07 | 200 ± 10 | 0.77 |
| Hamilton | 61.9 ± 10.4 | 1.75 ± 0.10 | -1.23 ± 0.10 | 184 ± 9 | 0.82 |
| Pembroke | 70.3 ± 8.7 | 1.61 ± 0.08 | -1.07 ± 0.08 | 188 ± 8 | 0.75 |
| Paget | 65.9 ± 14.5 | 1.47 ± 0.13 | -1.00 ± 0.14 | 223 ± 19 | 0.82 |
| Dive duration as independent variable | | | | | |
| Devonshire | 39.2 ± 11.0 | 0.25 ± 0.06 | 0.96 ± 0.06 | 279 ± 9 | 0.77 |
| Hamilton | 60.0 ± 16.6 | 0.14 ± 0.09 | 1.15 ± 0.10 | 270 ± 11 | 0.80 |
| Pembroke | 26.5 ± 11.0 | 0.37 ± 0.05 | 0.84 ± 0.06 | 317 ± 11 | 0.74 |
| Paget | 31.8 ± 32.3 | 0.30 ± 0.21 | 0.75 ± 0.21 | 220 ± 30 | 0.78 |

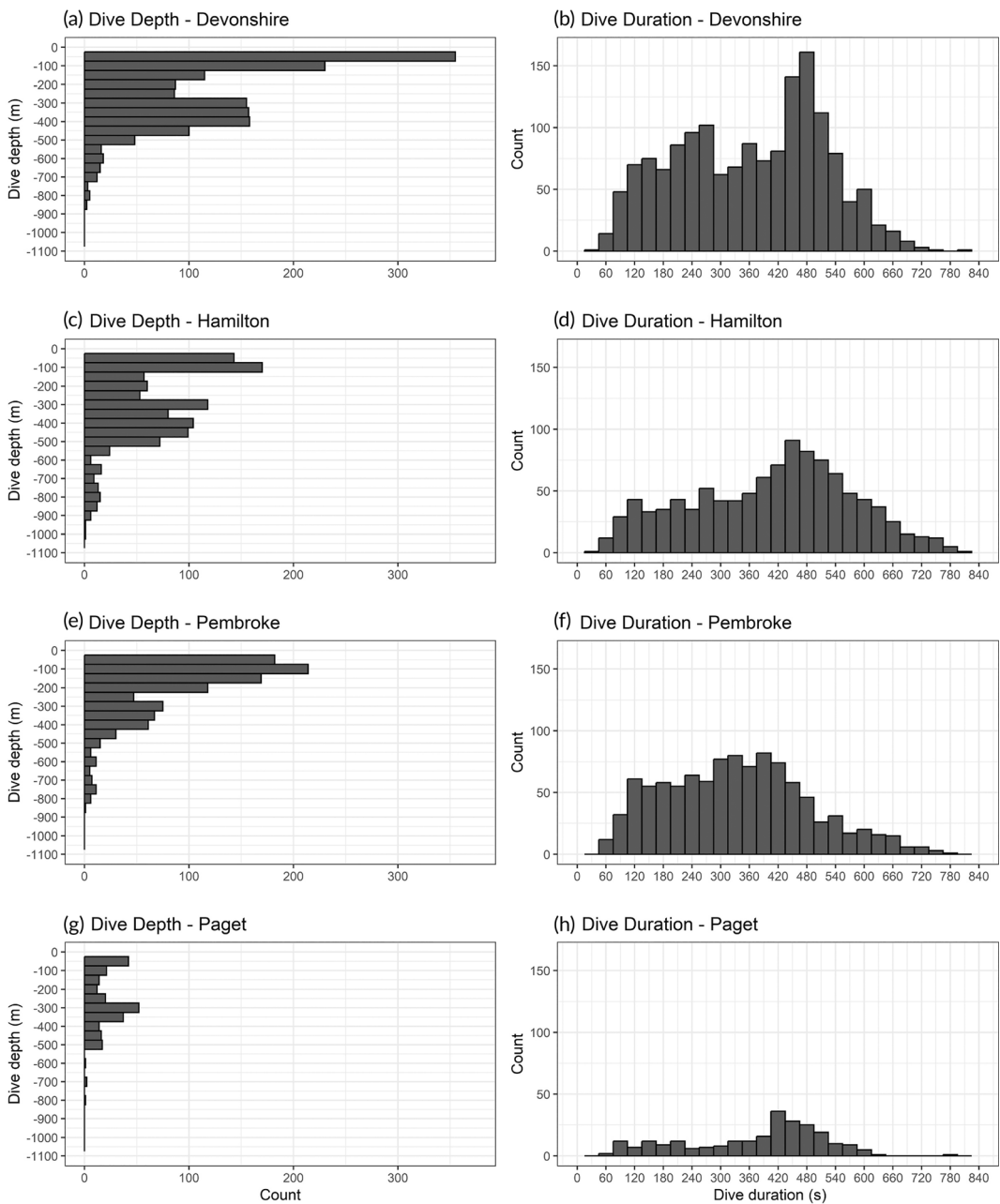


FIGURE 3 Frequency distribution of dive depths (m) and durations (s) for all tagged dolphins.

longest dives recorded were executed by Hamilton: the deepest dive this animal made was to 1,000 m (which had a dive duration of 804 s). The longest dive this animal made lasted 826 s (13.8 min) to 744 m depth.

Deeper dives typically had longer dive durations (Figure 2); however, a segmented linear regression analysis showed that the relationship between dive duration and maximum dive depth changed significantly when dive durations reached 220–317 s ($272(274) \pm 40$ s; Table 3, Figure 2), where the rate of change in depth began to increase more rapidly, i.e., there was a steeper slope between depth and time (Table 3, Figure 2).

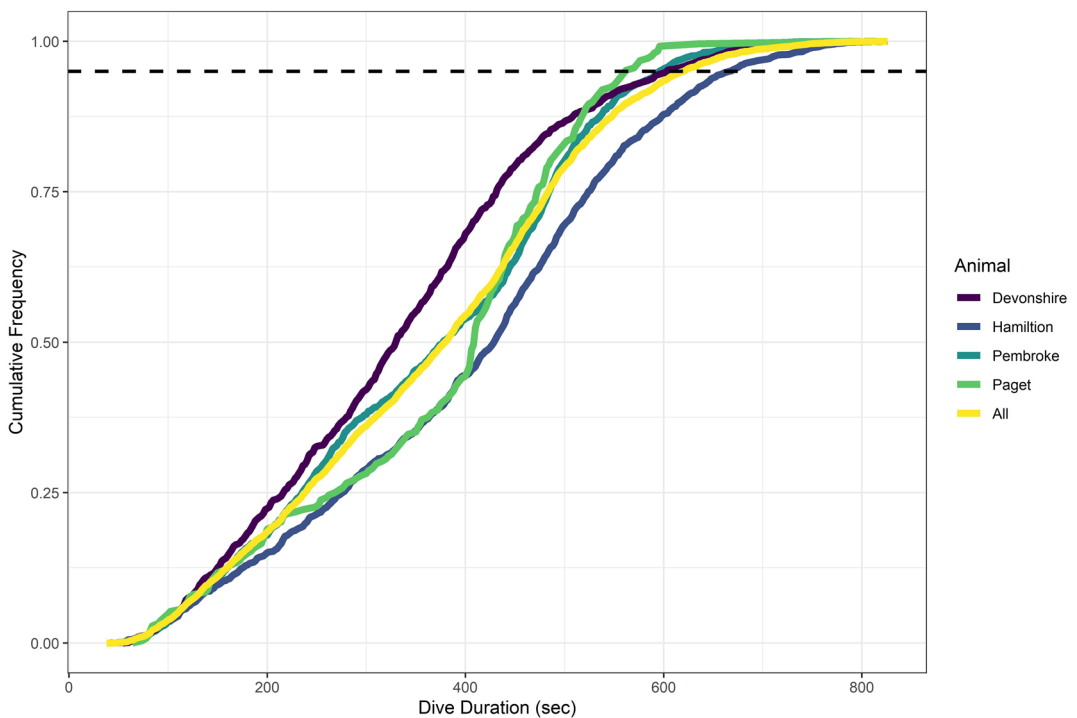


FIGURE 4 Cumulative frequencies of dive durations for each tagged individual dolphin as well as all of them combined (yellow). The horizontal dashed line represents 95% of the cumulative frequencies, or the behavioral aerobic dive limit (bADL).

Similarly, the relationship between maximum dive depth and dive duration changed when a maximal depth reached 184–223 m ($199 (194) \pm 18$ m, Table 3, Figure 2). As the breakpoints identified changes in dive behavior, i.e., the slope between dive depth and duration by the segmented linear regression analysis (Table 3), we defined dives <272 s and <199 m as short and shallow dives, and dives ≥ 272 s and ≥ 199 m as long dives and deep dives. Individuals performed 39%–66% and 64%–76% of their dives deeper and longer, respectively, than their respective breakpoints.

There was a bimodal distribution of dive depths with peaks generally between 50 m and 100 m, and between 300 m and 550 m for all dolphins (Figure 3). For all dolphins, 50% of dives were deeper than 220 m, 296 m, 156 m, and 288 m, respectively (Figure 3A, C, E, and G). A bimodal distribution for dive duration was observed for Devonshire, with peaks around 270 s and 480 s (Figure 3B), but this pattern was not observed in the other dolphins. The bADL, defined here as 95% of the cumulative distribution of dive durations (Quick et al., 2020), of all dolphins was 620 s (Figure 4), and individual bADLs ranged from 560 to 666 s (Table 2).

Postdive shallow intervals following dives exceeding each dolphin's bADL were 59% longer as compared with shallow intervals following dives shorter than each dolphin's bADL (Table 2, linear mixed effects using animal as random effect: $\chi^2 = 5.93$, $df = 1$, $p < .05$).

There were clear diurnal changes in dive behavior, with most dives occurring at night, and the dolphins exhibiting longer periods of time in the upper 50 m during the day (Figure 5). At 19:00 local time all four dolphins' median dive depths increased to more than 380 m, and the animals continued to dive to depth throughout the night until approximately 08:00 local time, when the dolphins focused more time in the upper water column (Figure 5). Median postdive shallow durations, similarly, decreased (Figure 5).

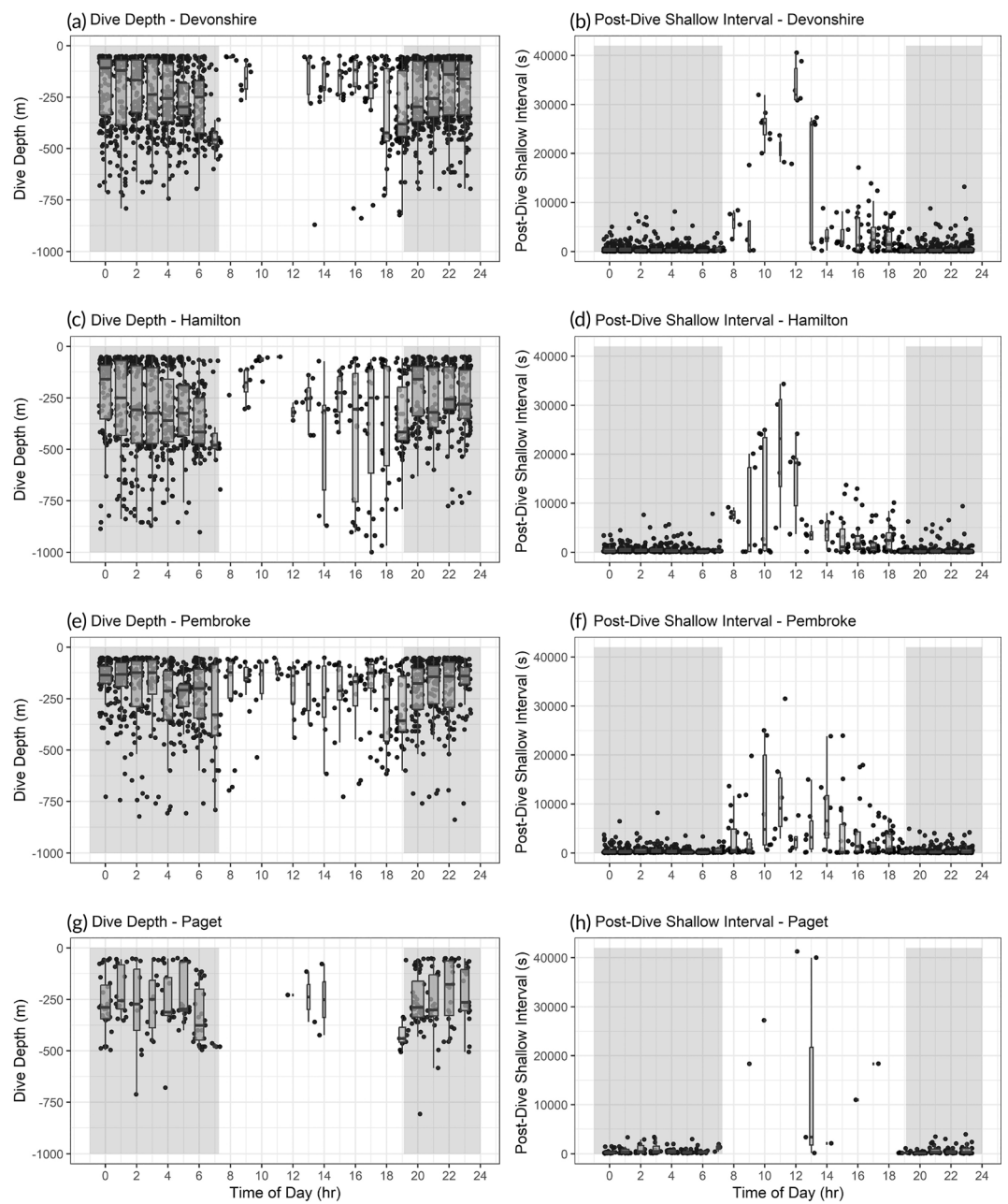


FIGURE 5 Dive depth (m) and postdive shallow intervals (s) versus time of day for all tagged individual dolphins. Time of day is in local time (i.e., it accounts for GMT). Boxes span the inter-quartile range, and box widths are proportional to the square root of n . Thick horizontal lines show medians, and box whiskers extend no greater or less than $1.5\times$ the interquartile range. Area shaded in gray represents nighttime based on local sunset and sunrise.

4 | DISCUSSION

We present dive depth and duration data from satellite-linked, time-depth recording tags attached to bottlenose dolphins moving through waters off Bermuda. To our knowledge, we report the longest (826 s [13.8 min]) and deepest

(1,000 m) dives recorded in free-ranging bottlenose dolphins and show that these dolphins regularly perform deep (>199 m) and long (>272 s) dives (Figure 3). Most dives below 50 m are performed at night with relatively short periods of time spent in the upper 50 m of the water column (Fig. 5). The estimated bADL ranged from 560 s to 666 s, and was 620 s when considering dives from all four dolphins (Table 2). The data reported here provide evidence that the offshore ecotype (or species, see Costa et al., 2021) of bottlenose dolphins has the capacity, and regularly performs deep and long dives. Programming trade-offs limited our ability to obtain high temporal resolution of dive and surfacing behaviors. Despite these limitations with our study, these data provide a novel and interesting view into the physiological capacity and plasticity within a species.

Diurnal variation in dive behavior was observed in the current study, where the dolphins dove deeper at night as compared to during the day (Figure 3). In all dolphins, the diving behavior changed around 18:00 local time, when the average dive depths appeared to track prey of the deep scattering layer, and continued throughout the evening until around 07:00 local time (Figure 5; August 31—sunrise 06:53, sunset 19:46; November 5—sunrise 07:39, sunset 18:26; averages = 07:16 and 19:06). Thus, the dolphins changed dive behavior approximately 1 hr after local sunset and sunrise, respectively. This is similar to the findings of Klatsky et al., (2007), who also documented diel trends in the diving behavior of one of the three dolphins they tagged off Bermuda. The diet of the bottlenose dolphins in Bermuda is not known, but the suction-cup-like marks they have near their mouth suggest that they likely prey on deep scattering layer organisms such as squid, and probably fish. Thus, the temporal variation in dive behavior is likely reflecting changes in the deep scattering layer and shallower access to prey at night (Figure 5). Similar diurnal changes in activity, although not as extreme, have been reported in near-shore bottlenose dolphins from Argentina, South Africa, and Florida (Goodwin, 1985; Saayman et al., 1973; Shane, 1990; Würsig & Würsig, 1979), where the dolphins were more active in the late afternoon as compared to the morning. In Sarasota Bay, Florida, on the other hand, these diurnal changes were not observed, although dolphins have been reported to spend considerable time at the surface, with less activity at night (Irvine et al., 1981; Scott et al., 1990). More recently, Wells et al. (2013) reported continuous movement throughout the day and night for Sarasota Bay dolphins, although with decreased travel rate at night. Diurnal variation in diving behavior has also been reported in both toothed and baleen whales; e.g., rough toothed dolphins (*Steno bredanensis*), pantropical spotted dolphins (*Stenella attenuata*), spinner dolphins (*Stenella longirostris*), pygmy killer whales (*Feresa attenuata*), Risso's dolphins (*Grampus griseus*), short-finned pilot whales, southern resident killer whales (*Orcinus orca*), melon-headed whales (*Peponocephala electra*), and also humpback whales (*Megaptera novaeangliae*) (Aoki et al., 2017; Baird et al., 2001, 2005; Friedlaender et al., 2013; Norris et al., 1994; Owen et al., 2019; Pulis et al., 2018; Rone et al., 2022; Shaff & Baird, 2021; Tyson Moore et al., 2020; Visser et al., 2021; West et al., 2018). In most of these species, most dives occur at night, but deep dives during the day were to greater depths as compared to at night. However, in the rough-toothed dolphin the deepest and longest dives occurred at dusk, a possible strategy to push physiology to the limit and take advantage of the prey rising to the surface at night (Shaff & Baird, 2021). In one study in the short-finned pilot whale, deep dives (depth >200 m) during the day were longer and deeper but most deep dives occurred at night (Owen et al., 2019). However, this was not observed in another study involving a rehabilitated pilot whale where deeper and longer dives at night were reported (Tyson Moore et al., 2020). Similarly, Cuvier's beaked whales show diurnal changes in dive behavior, although the specific changes appear to vary slightly between locations (Baird et al., 2008; Barlow et al., 2020). Thus, as suggested previously by others (e.g., Norris et al., 1994), diurnal changes in diving behavior seem to provide a link between physiology and optimal foraging, where prey rising at night reduces transit time and provides a greater proportion of the dive duration at the prey patch.

The relationship between maximum dive depth and dive duration consisted of two distinct relationships. For dives shorter than about 272 s (Table 3, all dolphins except Paget with only 9 days of data transmission, Table 1), there was large variation in the dive depth, but for deeper dives the dive duration was more consistently related to the dive depth (Figure 2, Table 3). Thus, the dolphins appeared to change diving behavior during dives deeper than 184–223 m (Table 3), possibly because of changes in foraging effort. Optimal foraging theory suggests that behavioral decisions change during deeper dives or when encountering denser prey fields, and existing dive data agree

with this suggestion (Arranz et al., 2018; Friedlaender et al., 2016; Tyson et al., 2016). These behavioral decisions help maximize the cost–benefit as long as the dive does not exceed the ADL. Empirical data from the Steller sea lion (*Eumetopias jubatus*) support that the dive duration increases as both prey depth and density increase (Cornick & Horning, 2003; Fahlman et al., 2008).

The distribution of dive durations was used to estimate the bADL. In the current study, the bADL was estimated to be around 560–666 s (Figure 4). In total, 173 dives, or between 5.1%–6.5% of all dives, exceeded the bADL of the tagged dolphins, and the postdive shallow intervals spent at depths shallower than 50 m following these dives were significantly longer as compared with those dives shorter than the bADL (Table 2). Thus, for dives longer than the observed bADL it appears that the dolphins at times required a longer duration close to the surface before the next dive. This agrees with data from past studies showing that prolonged dives result in an O₂ debt, and the switch to anaerobic metabolism results in accumulation of lactate, which requires an extended duration at the surface. It is likely that some of these postdive shallow intervals are affected by the limited resolution of the satellite-linked tag due to our programming specifications and that the dolphins do perform shorter and shallower dives during this period. It is also possible that these durations closer to the surface help to reduce the inert gas burden to prevent diving related problems, like the bends (Fahlman et al., 2021). Thus, although there was a clear difference in the time spent in waters <50 m deep following dives shorter than or exceeding the bADL, the low-resolution data set presented in the current study does not allow a more detailed investigation of this hypothesis.

The cADL provides an alternative estimate of the diving capacity, and a previous study estimated the cADL to be 666–1,122 s in the Bermuda bottlenose dolphins (Fahlman et al., 2018b). In the past study, the cADL was based on an assumption that the oxygen stores were similar to those estimated for beaked whales, and a diving metabolic rate similar to that of inactive dolphins (Fahlman et al., 2018a, 2018c, 2023). In a more recent study, the dynamic ADL (dADL) was introduced, which is calculated from the diving metabolic rate, including the locomotor metabolic rate (LMR, L O₂/min), and the O₂ stores as the animal begins the dive (Fahlman et al., 2023). Thereby, the dADL accounts for variation in the dive behavior, where the diving metabolic rate and the total O₂ vary depending on the activity during the dive, and utilization and recovery of the O₂ stores during the previous dive and surface interval (Fahlman et al., 2023). The dADL ranged between 648 s and 684 s during deep dives in the offshore Bermuda dolphins (Fahlman et al., 2023), which is a bit higher than the estimated bADL in the current study for all dolphins except Hamilton.

It is known that the offshore ecotype has higher blood O₂ capacity as compared to the nearshore ecotype (Duffield et al., 1983; Fahlman et al., 2018c; Klatsky et al., 2007), and also likely that the offshore ecotype has a higher relative muscle mass (Pabst et al., 2016). Thus, the overall O₂ stores are likely higher in the offshore ecotype as compared with the nearshore ecotype, but data on overall muscle mass, myoglobin concentration and blood volume are still not available and would be useful to improve these estimates of ADL. The offshore Bermuda dolphins' resting metabolic rate while inactive on a foam mat was similar to that of the inshore Sarasota Bay dolphins under the same circumstances (Fahlman et al., 2018a, 2018c), but additional information about the metabolic requirements for different activities are warranted. Although the diving metabolic rates in Steller sea lions have been shown to be similar to, or even slightly lower than, the metabolic rate at the surface (Fahlman et al., 2008, 2013), it is likely that deep diving is more metabolically costly as the transit to and/or from depth in part requires active movement (Aoki et al., 2017; Miller et al., 2004; Skrovan et al., 1999). In a recent study where activity was used to estimate the LMR, it was shown that the LMR did not vary with depth, and that the dolphins transitioned between behaviors for dives to different depths (Fahlman et al., 2023). Therefore, more information is required about the energy use in these populations to better estimate the true diving capacity of this species.

We have shown that bottlenose dolphins have the capacity for extreme deep diving with dives reaching 1,000 m and exceeding 789 s. The data show consistent behavioral changes, where deep dives exceed 272 s, possibly due to extended time at depth to catch prey. Based on the dive behavior and distribution of dive durations, we propose a conservative estimate of the bADL to be 560–666 s, much longer than previously estimated in this species. A better understanding about the physiological capacity and plasticity of marine mammals is important to better

understand their physiological limits for survival. Conservation efforts for marine mammals will be aided by improved understanding about their ecophysiology and their capacity to respond to environmental changes.

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AUTHOR CONTRIBUTIONS

Andreas Fahlman: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; validation; writing original draft. **Reny B. Tyson Moore:** Conceptualization; formal analysis; methodology; visualization; writing – original draft. **Rae Stone:** Funding acquisition; investigation; project administration; writing – review and editing. **Jay Sweeney:** Funding acquisition; investigation; project administration; writing – review and editing. **Robyn Faulkner Trainor:** Investigation; project administration; writing – review and editing. **Aaron A. Barleycorn:** Investigation; methodology; writing – review and editing. **Katherine McHugh:** Investigation; methodology; writing – review and editing. **Jason B. Allen:** Investigation; methodology; writing – review and editing. **Randall S. Wells:** Conceptualization; data curation; investigation; methodology; project administration; supervision; writing – review and editing.

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SUPPORTING INFORMATION

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

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