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Aerobic dive limit in short-finned pilot whales *Globicephala macrorhynchus*: an assessment of behavioral criteria

Ashley M. Blawas[1,#], Lauren E. Miller[1,#], Jeanne M. Shearer[1], William R. Cioffi[1,2], Daniel L. Webster[3], Zachary T. Swaim[1], Heather J. Foley[1,4], Danielle M. Waples[1], Nicola J. Quick[1,5], Douglas P. Nowacek[1,6], Andrew J. Read[1,*]

[1]Duke University Marine Laboratory, Nicholas School of the Environment, Duke University, Beaufort, North Carolina 28516, USA
[2]Southall Environmental Associates, Aptos, California 95003, USA
[3]Bridger Consulting Group, Bozeman, Montana 59718, USA
[4]Northeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Woods Hole, Massachusetts 02543, USA
[5]School of Biological and Marine Sciences, University of Plymouth, Plymouth PL4 8AA, UK
[6]Pratt School of Engineering, Duke University, Durham, North Carolina 27708, USA

ABSTRACT: Aerobic dive limits (ADLs) are a useful paradigm for assessing marine mammal diving ability. Given the allometry of total body oxygen stores and metabolic rate, larger animals should have increased diving capacities and thus elevated ADLs. The short-finned pilot whale *Globicephala macrorhynchus* is a deep-diving species with pronounced sexual size dimorphism, and individuals are regularly found in size-mixed groups. Therefore, we asked how body size constrains dive durations in this species and whether behavioral ADL (bADL), estimated as the 95th percentile of dive duration, is a useful measure of physiological ADL. We analyzed 30 169 dives from 45 animals tagged with satellite-linked recorders off Cape Hatteras, North Carolina, and Jacksonville, Florida, USA, and determined a species-level bADL of 18.8 min and individual bADLs ranging from 13.9 to 22.1 min. To assess the influence of size on bADL, we estimated the body lengths of 19 whales from dorsal fin measurements. Body length did not fully explain intraspecific bADL variation, but similar dive distributions and lower bADL variance between animals tagged together indicated a potential effect of group membership. Moreover, individuals in Cape Hatteras had a significantly lower median bADL than those in Jacksonville, suggesting location may influence dive durations. These results indicate the potential impact of social and location-specific factors on bADL estimates in a deep-diving, sexually dimorphic species.

KEY WORDS: Allometric scaling · Behavioral aerobic dive limit · Dive duration · Short-finned pilot whale

1. INTRODUCTION

The ability of air-breathing vertebrates to forage at depth is constrained by their need to ventilate at the surface. Diving vertebrates can maximize the time available for foraging by optimizing time spent at the surface versus underwater (Houston & Carbone 1992, Stephens et al. 2008). The aerobic dive limit (ADL) is an important physiological threshold for diving behavior because it indicates the maximal dive duration for

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[#]These authors contributed equally
[*]Corresponding author: aread@duke.edu

which an animal can rely exclusively on aerobic metabolism. If a dive lasts longer than the ADL, a transition to anaerobic respiration must occur, resulting in the accumulation of lactate. This lactate must then be processed, thereby extending the recovery time between foraging dives. Kooyman et al. (1980, 1983) were the first to provide an empirical measurement of an ADL, determined by blood lactate concentration, with their work on Weddell seals *Leptonychotes weddellii*. Several studies have since successfully measured ADLs for other diving vertebrates, including Baikal seals *Pusa sibirica*, emperor penguins *Aptenodytes forsteri*, California sea lions *Zalophus californianus*, common bottlenose dolphins *Tursiops truncatus*, and beluga whales *Delphinapterus leucas* (Ponganis et al. 1997a,b,c, Shaffer et al. 1997, Williams et al. 1999). The ADL concept plays a central role in our understanding of marine mammal diving behavior; although individual dives may exceed the ADL, we expect that most dives should be shorter than this physiological threshold (Kooyman et al. 2021).

The allometry of oxygen storage and utilization suggests that ADL should increase with body size. Total body oxygen stores scale linearly with body mass, but metabolic rate scales to the ¾-power, so larger animals will consume less oxygen per unit mass during a dive, allowing them to remain submerged longer. Due to this allometry, larger animals are predicted to have increased diving capacities (e.g. Weddell seals; Kooyman et al. 1983). In addition to body size, differences in oxygen loading before a dive and variations in diving metabolic rate due to activity level may impact individual dive durations and could therefore affect ADL estimates.

Given the logistical challenge of obtaining the blood samples needed to measure ADL from free-swimming mammals, indirect estimates of ADL can be made using data that are more routinely collected. Two commonly employed approaches are the calculated ADL (cADL) and the behavioral ADL (bADL). Given that true ADL has only been measured in 5 air-breathing marine animal species, cADL and bADL are limited in their validation. Still, these criteria serve as helpful quantities to compare and evaluate diving behavior (Kooyman et al. 2021). The cADL is estimated by dividing total body oxygen stores by the diving metabolic rate (DMR) (Kooyman et al. 1980). This approach assumes that a diving mammal will exclusively utilize aerobic metabolism until there is no more oxygen available, which may not be true in all cases (Purdy 2019). By contrast, the bADL is based on empirical data and is commonly defined as the 95th percentile of dive durations, following Kooyman's finding that 92–97% of the dive durations of Weddell seals fell below the measured ADL (Kooyman et al. 1980, 1983). A particular strength of the bADL approach is that it stems from direct observations of diving behavior and therefore does not require estimates of an animal's oxygen stores and DMR, which are difficult to measure in free-swimming animals. It is possible to collect large samples of dive durations from free-ranging marine mammals from behavioral observations (focal follows) of individuals from accessible populations and/or by using telemetry devices, facilitating estimation of bADL for many species. Importantly, however, bADL may be influenced by factors other than aerobic capacity, including but not limited to behavioral state, time of day, sociality, bathymetry, and prey distribution, all of which may impact individual decisions about dive duration. The potential effects of these factors should be considered when using bADL as an estimate of ADL.

The short-finned pilot whale *Globicephala macrorhynchus* is a deep-diving odontocete (toothed whale) found primarily in tropical and subtropical waters. This species is frequently observed in social units containing individuals of multiple age and sex classes (Heimlich-Boran 1993). Short-finned pilot whales are also one of the most sexually size-dimorphic species of cetaceans (Dines et al. 2015), and substantial variation in body size occurs in most social groups (Bowers 2015). Short-finned pilot whales have long-term social bonds (Alves et al. 2013) and may therefore adjust foraging dives to accommodate social partners. There is evidence from communicative calls made from foraging individuals to suggest that short-finned pilot whales forage independently at depth in the Canary Islands (Jensen et al. 2011), but data from digital acoustic recording tags (DTAGs) deployed on a pair of short-finned pilot whales off Cape Hatteras revealed synchronized diving and concurrent foraging (Bowers 2015). Coordinated foraging dives of differently sized individuals have also been documented through underwater footage of long-finned pilot whales *G. melas* off the coast of Norway (Aoki et al. 2013).

Two previous studies estimated the cADL of short-finned pilot whales by using a species-specific calculation of total oxygen stores and a range of estimates of DMR (Aguilar de Soto 2006, Velten et al. 2013). Aguilar de Soto (2006) calculated a species cADL of 25 min, while Velten et al. (2013) estimated a range of cADL values from under 10 min at a maximum exertion DMR to approximately 50 min at a minimum exertion DMR, extrapolated from data on gliding Weddell seals (Williams et al. 2004, 1999). Their intermediate cADL of 14.2 min resulted from metabolic rates derived from the cost of transport at moderate swim speeds (2.1 m s^{-1}) (Velten et al. 2013). Bowers (2015) estimated bADL for 6 short-finned pilot whales tagged off Cape Hatteras, generating a range from 15.1 to 21.3 min. Importantly, bADL estimates are typically derived from data sets that exclude shallow dives (e.g. dives of <20 m) (Bowers 2015, Quick et al. 2020). It is therefore expected that the bADL will overestimate the ADL, as it excludes some shallow dives that Kooyman et al. (1980) included in their original observations. Despite the small sample size in the Bowers (2015) study, estimates of bADL for the short-finned pilot whales in Cape Hatteras increased with body size. This aligns with findings from Joyce et al. (2017) that indicated a power-law relationship between body size and maximum dive duration of individual short-finned pilot whales.

Our objective was to estimate individual bADLs from a large data set of short-finned pilot whale dive records to understand the influence of body size on this estimate of diving capacity in this highly dimorphic, social species. Furthermore, we aimed to explore whether group membership and location-specific effects influence short-finned pilot whale bADLs. We hypothesized that if bADL is a useful predictor of true physiological ADL, individual bADLs would display positive allometry based on the known allometry of oxygen storage and metabolic rate. If, however, diving patterns are also mediated by group membership, we hypothesized that individuals tagged in groups may have more similar bADLs than predicted by their body sizes (i.e. larger animals may not dive to their true ADL to support group cohesion). We also predicted that bADLs would differ between study locations due to differences in local bathymetry, oceanographic conditions, and, presumably, prey type and availability. By increasing our understanding of the factors that influence bADL values in short-finned pilot whales, this analysis aims to assess the use of bADL as a predictor of the physiological ADL of this species.

2. MATERIALS AND METHODS

2.1. Data collection

Between 2014 and 2019, SPLASH10-292 or SPLASH 10-333 satellite tags (Wildlife Computers) were deployed in the 'low impact minimally percutaneous electronic transmitter' configuration (LIMPET; Andrews et al. 2008) on or at the base of the dorsal fins of 39 short-finned pilot whales off Cape Hatteras, North Carolina, USA, and 6 short-finned pilot whales off Jacksonville, Florida, USA. Tag programming varied across years. The 4 tags deployed in 2014 required a minimum dive depth of 20 m, the 6 tags deployed in 2015 and 2016 required a minimum dive depth of 30 m, and the 35 tags deployed between 2017 and 2019 required a minimum dive depth of 75 m. A pneumatic rifle (DAN-INJECT JM 25; DanWild) was used to deploy the tags remotely, which were attached by 2 surgical-grade titanium darts with backward-facing petals. Immediately after tagging, the tagged dorsal fin of each whale was photographed. If multiple whales that were observed in close proximity (i.e. within 100 m of each other) were engaged in similar and coordinated behavior, those animals were defined as a group. We avoided tagging any animals in groups that contained neonates.

2.2. Tag analysis

Each tag recorded dive duration, maximum dive depth, dive start time, and dive end time to a data log that was transmitted to ARGOS receivers on orbiting satellites and then downloaded for analysis (Wildlife Computers). Three individuals that performed fewer than 20 dives while tagged were dropped from analyses to eliminate biases due to a limited individual sample size. All tag records were examined to identify and eliminate erroneous data using quality control checks (Shearer et al. 2019). Evidence of tag failure and sensor drift was determined by inspecting the records for abnormally large jumps in battery voltage or large deviations from zero in the pressure sensor offset at the surface. Depth and duration were plotted by date to identify sensor drift and message overlap. The biological plausibility of the dives was verified by plotting dive duration against 2 times the maximum depth to check for implausible dive speeds, defined as more than 15 m s^{-1} (Shearer et al. 2019). The consistency of the wet:dry ratio was checked to validate time at the surface. Additionally, dive depths were inspected to confirm that no dives were recorded outside of the programmed dive settings. Only one instance of erroneous data was found. GmTag211 indicated a pressure sensor failure based on unrealistically fast, deep dives with unusually long surface periods. The 4 dives recorded after that tag's failure were omitted from the analyzed data set.

Some tags were deployed as part of behavioral response studies, so we followed Quick et al. (2020) and truncated tag records to exclude periods following experimental exposure to an acoustic stimulus. Following these quality control steps, we calculated the duration and maximum depth of individual dives by averaging the maximum and minimum estimates of each parameter as reported in the dive summary data log. Only dives to a depth of at least 75 m were included in the bADL analysis to standardize data across satellite tags with different programming regimes. Short-finned pilot whales exhibit variable foraging dive patterns (Quick et al. 2017) that range in depth from 57 to over 1000 m (Shearer et al. 2022), so we also explored the effect of varying the dive threshold on estimates of bADLs.

2.3. Body length analysis

To estimate the body length of a tagged whale, we measured the length of the base of the dorsal fin (DBL) from digital images of the dorsal fin after tag deployment. The DBL was measured as the distance between the anterior and posterior insertion of the fin, which we defined as the first deviation from the dorsal fin and body lines, respectively (Fig. 1). We only included photos with clearly visible anterior and posterior insertions in this analysis. Of the 45 tagged whales with sufficient dive data, we retained high-quality images of 19 individuals for body length analysis. These measurements were then converted from pixels to length using a scaling factor determined from the known dimensions of the satellite tag visible in the image. We converted values of DBL to estimates of total body length (TL) using an equation established from a large data set of morphometrics of short-finned pilot whales in the Pacific and Atlantic oceans (Yonekura et al. 1980, NC Marine Mammal Stranding Network unpubl. data, https://collections.nmnh.si.edu/search/mammals/): TL = 4.46(DBL) + 40.37. This method has been applied in other studies of short-finned pilot whales (Bowers 2015). To reduce the influence of measurement error, measurements of DBL were conducted by 6 independent analysts. For each whale, the highest and lowest estimates were eliminated, and we used the mean of the remaining 4 measurements as the DBL.

2.4. Statistical methods

We conducted all statistical analyses in R (v.4.1.2) (R Core Team 2020). Individual bADLs were calculated using the 95th percentile definition for dive durations of dives that were ⩾75 m for each tagged animal (Kooyman et al. 1980, Burns & Castellini 1996), as has been done previously to understand deep-diving odontocete dive behavior (Quick et al. 2020). We pooled dive duration data from all tags to determine a species-level bADL, defined as the 95th percentile dive duration for all dives of ⩾75 m. For comparison, we made supplemental species-level bADL calculations at 15 m incremental depth cutoffs from 75 to 300 m for all tags and from 30 to 300 m for 2014–2016 tags at both the 95th percentile and 97th percentile (Hindle et al. 2011) to examine the robustness of our species-level bADL estimate (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m744p161_supp.pdf). Unless stated otherwise, hereafter, bADL refers to calculations performed on dives of ⩾75 m using the 95th percentile.

We used a linear model to determine the power-law relationship between body length and individual bADL across all tags by $\log_{10}$ transforming body length and bADL. A power analysis of this regression was conducted to quantify the risk of Type II error (Champely et al. 2020) for our model. We also used linear models to examine the effect of deployment date on body length and bADL. We considered the influence of group membership on bADL by using Levene's test for homogeneity of variance in bADLs of animals in the same tagging group compared to animals in any group. We then checked for location-based effects with a Wilcoxon rank sum test, comparing the median bADLs of animals in Cape Hatteras to animals in Jacksonville. To verify that a difference in median bADL of the individuals by location was not a result of the small sample size from Jacksonville, we performed 100 random subsamples of 6 individuals (without replacement within a sample) from Cape Hatteras and determined the percentage of subsam-

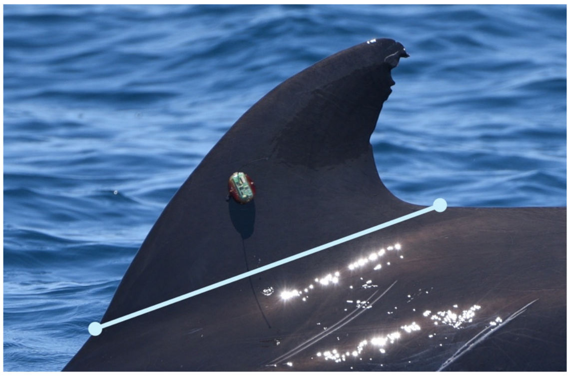

Fig. 1. Example of short-finned pilot whale dorsal fin measurement. The dorsal fin length was measured as the distance between the anterior and posterior insertion, which we defined as the first deviation from the dorsal fin and body line, respectively

pled data sets for which the median bADL was different than that of Jacksonville individuals. We examined Q–Q plots across dive start date and time to verify that dives evenly represented the sampling period as demonstrated by a steady increase in cumulative dives over time. Finally, to ensure that the overall species bADL calculation was not biased by an overrepresentation of dives from individuals whose bADLs were higher or lower than the average, we used a linear model to assess the relationship between individual bADL and number of dives ⩾75 m for that individual.

3. RESULTS

3.1. Tag data

Tags were deployed in 35 sightings (range: 1–4 whales tagged per sighting). A total of 23 whales were tagged either alone (i.e. not in a group) or without another tagged animal in their group, while 22 whales were tagged with other individuals in their group (10 groups, range: 2–4 whales tagged per group). Tags transmitted data up to 423 d (median: 23 d), resulting in 34 954 h of observations. Of the 34 122 dives recorded during these deployments, 30 169 dives were to depths of ⩾75 m. The median number of dives was 646 dives per whale (range: 144–1468 dives per whale). The median duration of dives was 12.3 min (range: 1.4–27.1 min) (Fig. 2A), and the median dive depth was 432 m (range: 76–1360 m). Deployment information is summarized in Table S1.

3.2. Estimates of bADL

Individual bADLs ranged from 13.9 to 22.1 min (median: 17.8 min, n = 45) and the overall species bADL was 18.8 min (Fig. 2A,B). To check the robustness of the bADL calculations, overall bADL for all tags was calculated at dive thresholds from 75 to 300 m in 15 m increments (Fig. S1). The overall bADL using the 95th percentile definition ranged from 18.8 to 19.4 min, while the overall bADL using the 97th percentile definition ranged from 19.6 to 20.1 min. The tags deployed from 2014 to 2016 recorded dives to a depth of at least 30 m, so we calculated the overall bADL for these tagged animals using dive thresholds from 30 to 300 m in 15 m increments. The 95th percentile bADL for 2014–2016 tags ranged from 19.6 to 20.5 min using these depth minima, and the 97th percentile bADL for 2014–2016 tags ranged from 20.2 to 21.2 min.

3.3. Effect of body length on individual bADLs

The median body length of the 19 measured whales was 3.7 m (range: 2.8–5.1 m), with a median of 4.0 m for animals tagged in Cape Hatteras (n = 17) and 3.7 m for animals tagged in Jacksonville (n = 2). Individual bADL increased with body size, although this relationship was not statistically significant (*t*-test, t_{17} = 1.8, p = 0.09, R^2 = 0.11) (Fig. 2C, Table 1).

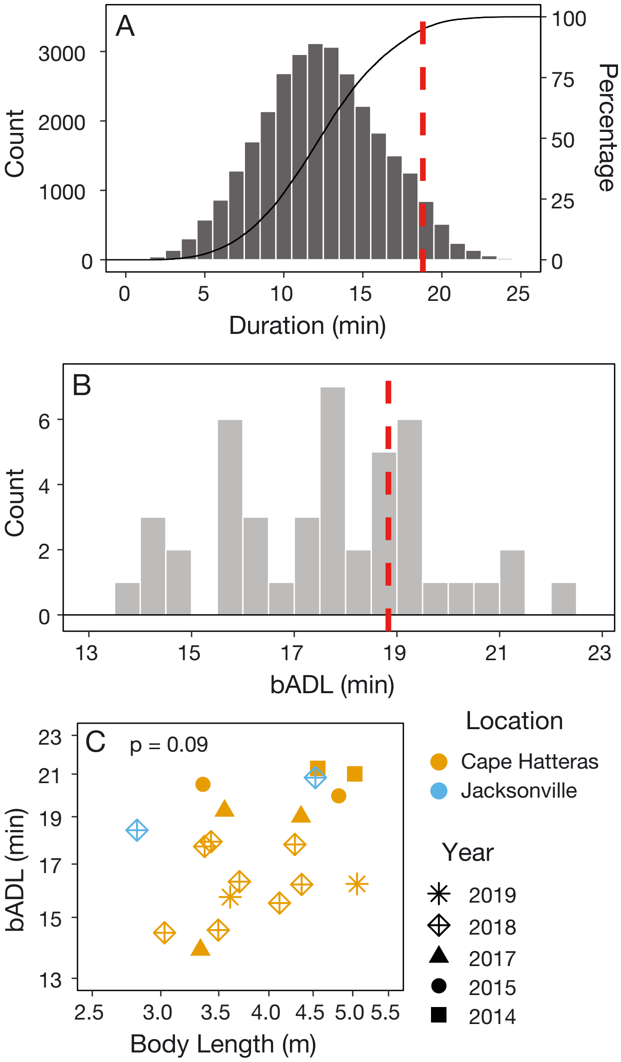

Fig. 2. (A) Binned dive durations of short-finned pilot whales versus count with cumulative distribution function. Red dashed line: the species' behavioral aerobic dive limit (bADL) of 18.8 min, using 95th percentile definition for dives of ⩾75 m. (B) Histogram of the distribution of bADLs (95th percentile dive duration) for all individuals for dives of ⩾75 m. The species' bADL (18.8 min) calculated from pooling all dives is marked by a red dashed line. (C) Body length versus bADL by location and year. The shape of the marker indicates the year of tag deployment, and the color of the marker indicates location with the p-value of a linear model relating the variables. Both axes are $\log_{10}$ transformed

Table 1. Coefficients of the linear model relating body length and behavioral aerobic dive limit (bADL) in short-finned pilot whales

Linear model: $\log_{10}(\text{bADL}) \sim \log_{10}(\text{length})$

Response	Predictor	Coefficient ± SE	t	p
$\log_{10}$(bADL)	$\log_{10}$(length)	0.3 ± 0.16	1.9	0.068
	Intercept	1.1 ± 0.098	10.9	<0.001

Results of the power analysis revealed 41% power for detecting the effect of body length on bADL at the given significance level and sample size, suggesting that our sample size may be limiting in our ability to detect a true effect.

3.4. Effects of group and location on bADLs

There was significantly less variation between bADLs of animals in the same group than among bADLs from any group (Levene's test of homogeneity of variance, $F_{9,12} = 8.7$, p = 0.0005). Qualitatively, group members had markedly similar dive distributions, with consistent minimum and maximum dive durations, modal dive duration, and/or overall distribution shape (Fig. 3).

The median bADL of the whales tagged off Cape Hatteras was 17.7 min, significantly less than that of whales tagged off Jacksonville at 18.8 min (Wilcoxon rank sum test, $W = 56.5$, p = 0.023) (Fig. 4). Using 100 random subsamples of the Cape Hatteras data set to reduce it to the same size as the Jacksonville data set (n = 6) resulted in only 7% of median bADL measurements equal to or greater than the Jacksonville individual median bADL of 18.8 min. When all dives of ⩾75 m were pooled for animals separately in Cape Hatteras and Jacksonville, the overall bADLs calculated as the 95th percentile of dive durations were 18.7 and 19.9 min, respectively.

3.5. Effects of potential biases

To confirm that the data set was drawn from a random sample of individuals, we examined trends in the demographics and diving patterns of tagged individuals. Visualization of dives by depth and duration revealed differences in dive patterns in animals tagged in different years (Fig. S2A). On average, larger whales were tagged earlier in the study, but this effect was not significant (t-test, $t_{17} = -1.4$, p = 0.18, $R^2 = 0.05$) (Fig. S2B). Similarly, though individ-

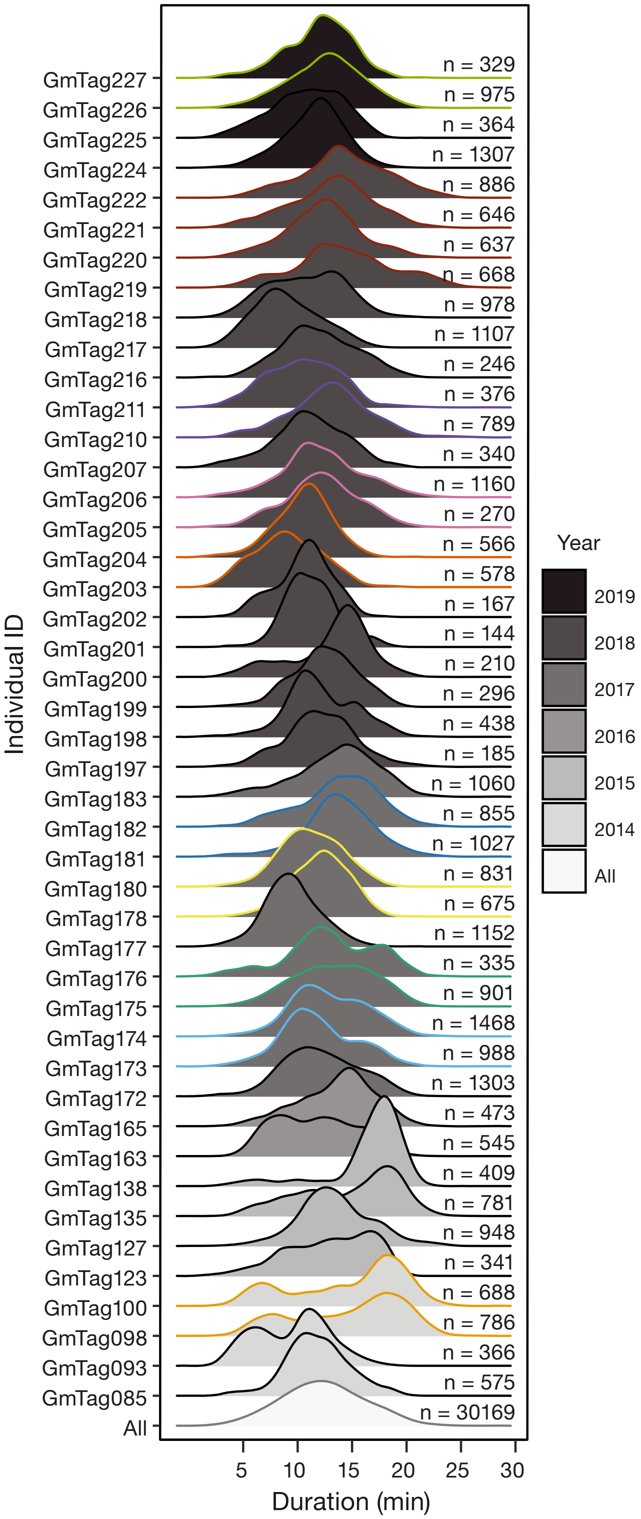

Fig. 3. Distributions of dive durations (dives ⩾ 75 m) for individual short-finned pilot whale tags (n = 45). The ridge fill indicates the year of the tag deployment, and the ridge outline color indicates individuals tagged in the same group, with a black outline indicating whales that were the only tagged member of their group or that were not in a group when tagged. The sample size for each ridge is provided

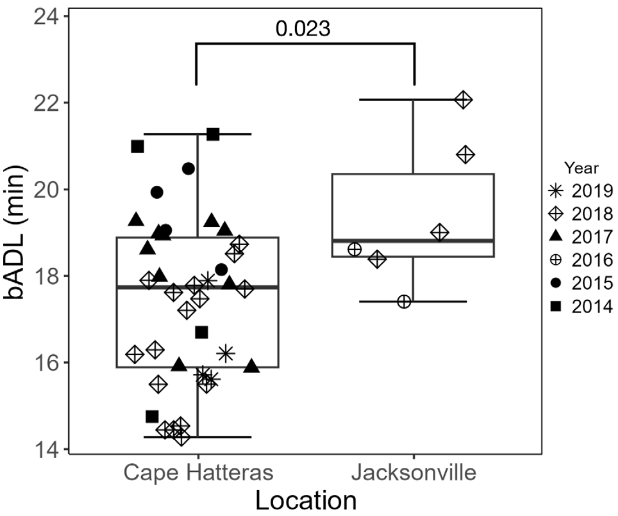

Fig. 4. Individual behavioral aerobic dive limits (bADLs) for short-finned pilot whales in Cape Hatteras and Jacksonville demonstrating significantly lower bADLs for animals in Cape Hatteras (Wilcoxon rank sum test, $W = 56.5$, n = 45). Individual bADLs are plotted as symbols, with symbol shapes indicating the year of tag deployment. Bold horizontal lines: median of each distribution; upper and lower limits of each box: first and third quartiles (the 25th and 75th percentiles); whiskers: the largest and smallest value no further than 1.5 × the inter-quartile range

ual bADL generally decreased throughout the study, this effect was not significant (t-test, $t_{43} = -1.9$, p = 0.06, $R^2 = 0.06$) (Fig. S2C). Q–Q plots (Fig. S3A,B) suggested that the distribution of dives comprising the entire data set and those of ≥75 m represented all dates approximately uniformly, and there was no significant relationship between an individual's bADL and number of dives by that individual (t-test, $t_{43} = 1.1$, p = 0.29, $R^2 = 0.004$), suggesting even representation of individuals in the species bADL calculation (Fig. S3C).

4. DISCUSSION

The estimated bADL of short-finned pilot whales in our sample was 18.8 min. This falls between the cADL estimates of Velten et al. (2013) and Aguilar de Soto (2006) of 14.2 min and 25 min, respectively. Our estimate is also consistent with the previous individual bADL estimates calculated from a smaller sample of short-finned pilot whales tagged off Cape Hatteras of 15.1 to 21.3 min (Bowers 2015). Using a range of dive depth and dive percentile thresholds, bADL estimates in this study ranged from 18.8 min (75 m, 95th percentile) to 21.1 min (300 m, 97th percentile) for all animals. The consistency of our bADL estimate across the various depth thresholds used to define a dive and the different percentiles of dive duration used to calculate bADL supports our choice of using one definition for bADL in our analyses.

Individual bADLs were variable (range: 13.9–22.1 min) around the species bADL of 18.8 min, but body size did not fully explain this variation. Larger animals tended to have elevated bADLs in our subsample of 20 whales with estimates of body length, but this relationship was not statistically significant (Fig. 2C). Assuming that diving capacity scales as the difference between the allometric exponents of total body oxygen stores and metabolic rate, then we expect the exponent of this relationship to be 0.25 (1 − ¾). However, the exponent describing this relationship was 0.32, which does not fully agree with predictions of diving capacity from allometry. If the relationship measured in the study reflects true allometry, this may provide evidence for a metabolic rate allometric exponent closer to ⅔ (i.e. 1 − ⅔ = 0.33). It is important to note that intraspecific patterns of allometry may vary considerably from patterns at the interspecific level (Glazier 2005). However, the high degree of variance around the power law relationship we derived implies that variation in body size does not fully explain the variation we observed in individual values of bADL. This suggests that decisions about dive durations, and therefore estimates of bADL, are influenced by factors beyond aerobic capacity for this species.

We identified group membership and location as 2 potential additional drivers of intraspecific variation in dive duration from the following trends identified in our analyses: (1) reduced variation in bADLs between animals tagged in the same group; and (2) differences in bADL estimates between animals tagged at Cape Hatteras and those tagged at Jacksonville.

The reduced variation of individual bADLs we observed within tagging groups suggests that group membership may influence short-finned pilot whale dive behavior. This is reflected in the distribution of dive durations, which shows that animals tagged in the same group often had consistent minimum and maximum dive durations, modal dive duration, and/or overall shape of the frequency distribution of dive durations (Fig. 3). Social coordination of individual dives could explain the similar dive distributions and bADLs among group members. There are previous accounts of synchronous diving and surfacing in social groups of short-finned pilot whales (Bowers 2015, Quick et al. 2017) and synchronous diving in a pair of long-finned pilot whales (Aoki et al. 2013).

Therefore, differences among the individual ADLs of short-finned pilot whales in a group could constrain the dive durations of larger whales in favor of the more limited breath-holding capacities of smaller individuals, ultimately constraining bADL at the group level. This constraint may be offset by the potential benefits of group living to these larger animals, such as access to mates and protection from predators. Alternatively, individuals may dive in groups with similarly sized individuals to reduce the opportunity cost of group diving over solitary diving, but our small sample size for body length estimates precluded us from testing this hypothesis. The group's age composition may also influence individual diving patterns, especially if the group contains calves or juveniles. Short-finned pilot whale calves and juveniles sometimes remain at the surface while adults dive (Aguilar Soto 2005), so it is possible that group members would shorten their dives to limit the separation period and reduce the risk of calf predation, as has been observed in humpback whales *Megaptera novaeangliae* (Szabo & Duffus 2008). Finally, reproductive state could influence group diving, as pregnant individuals may have a reduced dive capacity, as has been observed in pregnant elephant seals (Hückstädt et al. 2018).

It is important to note that group membership was assigned at tagging, and animals tagged together may not have stayed together throughout the duration of the data set. Previous studies have found that short-finned pilot whales form stable associations of related individuals that last for years, but groups observed in the field may include multiple family groups and transient animals (Alves et al. 2013).

Similar distributions of dive duration among group members may also be attributed to location. Whales tagged in Cape Hatteras had a significantly shorter median individual bADL than those tagged in Jacksonville (17.6 vs. 18.8 min), which was further supported by our resampling analysis, and a shorter group estimate of bADL (18.7 vs. 19.9 min) (Fig. 4). Our data suggest that the differences in bADLs between the 2 locations are not due to differences in body size, given that the 2 animals from Jacksonville for which we estimated body size displayed elevated individual bADLs compared to animals of similar size off Cape Hatteras. We suggest that the differences in bADLs that we observed between locations are due to different bathymetry, oceanographic conditions, and likely prey type(s) and availability that drive patterns of foraging behavior. Short-finned pilot whales off Cape Hatteras frequently forage along the continental shelf break (Thorne et al. 2017) and often feed at or near the sea floor in these environments (Shearer et al. 2022). The 2 tagging sites in our study have very different bathymetries, and the slope of the continental shelf break in Cape Hatteras is much steeper than that in Jacksonville. Previous studies of short-finned pilot whales at these 2 sites show that animals off Jacksonville dive further from the shelf break and away from canyons than animals off Cape Hatteras, perhaps taking advantage of pelagic prey species (Foley 2018). Pelagic foraging, in the absence of physical features to trap prey, may require longer chases and thus longer dive durations. This is supported by findings of higher chasing effort by sperm whales *Physeter macrocephalus* in pelagic zones (Isojunno & Miller 2018), although there is also evidence of sperm whales employing longer buzzes when chasing animals near the seafloor, which could reflect longer chases during benthic foraging (Guerra et al. 2017). Thus, differences in foraging strategies due to bathymetry, oceanography, and prey availability likely have an important influence on the duration of individual dives. Location may therefore contribute to the observed differences in estimates of median individual bADL, group bADL, and overall species bADL.

The trend of reduced individual bADL with increasing date of tag deployment (Fig. S2C) may be a result of our focus on larger whales earlier in the study due to the ease of tagging and identifying these individuals. We expanded our focus to include smaller whales later in the study to counter this initial bias towards larger animals, although we were not able to detect a significant effect with the subset of animals for which body length could be estimated. The data used to estimate species-level bADL represented deployment dates approximately equally, limiting the effect of this bias (Fig. S3A,B). We did not have sufficient genetic sex information on individuals in this study to determine whether there was a sex-related tagging bias. Furthermore, previous work has shown that it is not possible to determine genetic sex from dorsal fin shape, thus limiting our ability to determine the sex of all individuals in the study from dorsal fin photographs, particularly those of similar dorsal fin sizes (i.e. individuals that are not adult males) (Augusto et al. 2013).

We found that body size does not fully predict individual bADLs, implying that there are likely additional drivers of individual dive duration in short-finned pilot whales beyond aerobic capacity. Specifically, we identified group membership and location as 2 potential factors influencing variation in dive duration. ADL is a physiological threshold, but the potential impact of social and location-specific factors must be considered when interpreting the distribution of dive durations. Future work should explicitly test for links between these factors and the diving behavior of short-finned pilot whales to gain further insights into the diving capacity of this species.

5. CONCLUSIONS

Our results indicate that, while bADL tends to increase with body size, aerobic capacity is unlikely to be the only factor driving variation of this parameter in short-finned pilot whales. We suggest that group membership and location are potential additional drivers of dive duration in this species. If group dive capabilities and location do constrain individual members' dives, bADLs based on the distribution of dive durations will underestimate physiological ADL, and some individuals will therefore have a greater dive capacity than predicted by their bADL. Thus, we warn against using bADL to understand the physiological limits of individuals. Further research is needed to elucidate the potential role of these factors in individual dives and their implications for understanding the diving physiology of this species.

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