SHORT COMMUNICATION

Extreme diving in mammals: first estimates of behavioural aerobic dive limits in Cuvier's beaked whales

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ABSTRACT

We analysed 3680 dives from 23 satellite-linked tags deployed on Cuvier's beaked whales to assess the relationship between long duration dives and inter-deep dive intervals and to estimate aerobic dive limit (ADL). The median duration of presumed foraging dives was 59 min and 5% of dives exceeded 77.7 min. We found no relationship between the longest 5% of dive durations and the following inter-deep dive interval nor any relationship with the ventilation period immediately prior to or following a long dive. We suggest that Cuvier's beaked whales have low metabolic rates, high oxygen storage capacities and a high acid-buffering capacity to deal with the by-products of both aerobic and anaerobic metabolism, which enables them to extend dive durations and exploit their bathypelagic foraging habitats.

KEY WORDS: *Ziphius cavirostris*, ADL, Dive duration, Diving behaviour, Metabolic rate

INTRODUCTION

Marine mammals rely on a variety of anatomical and physiological adaptations to perform breath hold dives (Fahlman, 2012; Kooyman et al., 1980; LeBoeuf et al., 1986, 1988; Ponganis, 2011). The aerobic dive limit (ADL) is a useful index of the dive duration that can be supported by aerobic metabolism (Ponganis, 2011, 2015) and was originally defined as the maximum breath hold period without a measurable increase in blood lactate in Weddell seals (Kooyman et al., 1980). In practice, however, measuring ADL experimentally in wild marine mammals is challenging (Ponganis, 2015). More commonly, ADL is approximated as the calculated aerobic dive limit (cADL) by dividing total body oxygen stores by diving metabolic rate and has been estimated in this manner for numerous species (Ponganis, 2015). However, for some marine mammals, the cADL is exceeded frequently by dive durations collected by telemetry. Some species show increased post-dive surface intervals after very long submergences, whilst others do not (Arnould and Costa, 2006; Costa et al., 2001; Costa and Gales, 2003; Hassrick et al., 2010; Weise and Costa, 2007), suggesting that additional physiological and behavioural adaptations may further reduce the energetic cost of diving (Boyd, 1997), or allow efficient use of anaerobic pathways.

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Beaked whales are extreme divers, with deeper and longer foraging dives than any other mammal species (Schorr et al., 2014; Shearer et al., 2019; Tyack et al., 2006). Time-depth recorders have been used to document beaked whale diving behaviour (Schorr et al., 2014; Shearer et al., 2019; Tyack et al., 2006), but direct measurements of metabolic rates or blood lactate levels do not exist. An approximation for the ADL of two beaked whale species was proposed (Tyack et al., 2006) by extrapolating from the estimated total O_2 stores (93 ml O_2 kg^{-1}) and cADL (21 min) for a 330 kg Weddell seal, but these estimated ADLs of 25 min for Blainville's beaked whale (*Mesoplodon densirostris*) and 33 min for Cuvier's beaked whale (*Ziphius cavirostris*) are exceeded, by a factor of approximately two, by the average duration of foraging dives commonly performed by these whales (Tyack et al., 2006). It has been suggested that these whales use prolonged periods at shallower depths between foraging dives to recover from the build-up of anaerobic metabolites (Tyack et al., 2006), akin to other species (Kooyman et al., 1980). Alternatively, beaked whales may have low diving metabolic rates like most other diving species (Williams et al., 2004; Castellini et al., 1992; Maresh et al., 2014), allowing them to remain within their ADL. Velten et al. (2013) estimated cADL for *Mesoplodon* spp. using a range of diving metabolic rates and body composition data from several species to estimate onboard oxygen stores. They demonstrated that the average dive durations reported for *Mesoplodon* species fall within the cADL, if the diving metabolic rate is similar or less than the basal metabolic rate (BMR) predicted by Kleiber's (1987) equation. Resting metabolic rates comparable to BMR have been measured in delphinids (Fahlman et al., 2018a,b; Rosen and Trites, 2013; Worthy et al., 2014), and pinnipeds can lower their diving metabolic rate below resting values (Fahlman et al., 2013; Hurley and Costa, 2001; Williams et al., 2004). In the absence of empirical data on metabolic rates, a behavioural ADL (bADL) can be estimated by examining the distribution of dive durations. This approach has been used with Weddell seals (Burns and Castellini, 1996; Hindle et al., 2011) based on observations that 92–96% of dives were less than measured ADLs, and that longer surface intervals followed dives that exceeded ADL (Kooyman et al., 1980, 1983). Foraging theory predicts that most foraging dives should be shorter than the ADL because utilisation of anaerobic pathways requires extended surface times to manage anaerobic by-products and replenish depleted oxygen stores, leaving less time for foraging (Houston et al., 2003; Houston and Carbone, 1992; Kooyman et al., 1980). We analysed foraging dives of Cuvier's beaked whales (Shearer et al., 2019) to estimate a bADL and assess whether whales extend their inter-deep dive intervals after long duration dives.

MATERIALS AND METHODS
Use of animals in research
All research activities were carried out under NOAA/NMFS Scientific Research Permits 17086 and 20605 issued to Robin

Baird; NOAA/NMFS permit 14809-03, issued to Doug Nowacek; and NOAA General Authorization 16185, issued to Andrew Read, in accordance with the relevant guidelines and regulations on the ethical use of animals as experimental subjects. The research approach was approved by the Institutional Animal Use and Care Committees (IACUC) of Cascadia Research Collective and Duke University.

Data collection

Between 2014 and 2018, 26 SPLASH10-292 satellite-linked location-depth tags (produced by Wildlife Computers, Redmond, WA, USA) were deployed on Cuvier's beaked whales off Cape Hatteras, USA (Table 1), as part of two separate studies (Shearer et al., 2019; Quick et al., 2019). Tags were deployed remotely from a 9 m rigid-hulled aluminium boat (Shearer et al., 2019) using a DAN-INJECT JM 25 pneumatic projector (DanWild LLC, Austin, TX, USA) in the LIMPET configuration (Andrews et al., 2008). Tags were programmed to record and transmit dive data using the behaviour log function in which the beginning and end of each dive was identified by conductivity sensors on the tags. Tags deployed between 2014 and 2016 retained dive events longer than 30 s and deeper than 50 m as well as ventilation periods between dives, and were initially programmed to transmit for 20 h per day for the first 25–28 days and then only every second or third day to maximise duration of contact (Shearer et al., 2019). Tags deployed in 2017 and 2018 were programmed to sample only dives that exceeded 33 min duration and 50 m depth (i.e. likely foraging dives; Shearer et al., 2019) and the intervals between dives of 33 min, with no duty cycling (Quick et al., 2019). Photographs of all tagged individuals were taken to determine sex and age class. Individuals with erupted teeth and heavy body scarring were classed as adult males (Baird, 2016; Coomber et al., 2016; Falcone et al., 2009; McSweeney et al.,

2007). All other animals were assigned as unknown. We did not tag dependent calves. Tags from 2017 to 2018 were deployed as part of a behavioural response study on the effects of US Navy tactical sonar, so we truncated tag records to include only periods before experimental sound exposures (Table S1). For three individuals, this truncation reduced diving records to three or fewer data points, so these individuals were removed from further analysis (Table S1). Incidental exposure to sonar is always possible, but Cape Hatteras is not on a Navy range and is not an area of intensive Navy training activity, so incidental exposure was not considered further (Shearer et al., 2019).

Data analysis

We pooled all foraging dives from both studies, defined for this population as all submergences of 33 min or longer (Shearer et al., 2019), and assigned them to 5-min time bins based on duration. We calculated the percent frequency for each time bin, the cumulative percentage contributed by each bin, and 50th and 95th percentiles of the presumed foraging dive durations. We recorded the inter-deep dive interval (IDDI) that followed each dive, defined as the time between adjacent dives of at least 33 min. This interval was used as a measure of recovery time between the long, presumed foraging dives. Although variable, this IDDI typically included several shorter dives (<33 min, median depth=280 m) interspersed with ventilation periods near the surface (median duration=2.2 min; Shearer et al., 2019). If an IDDI record was missing, we excluded the dive from further analysis. To test for periods of recovery, we fitted a linear mixed effects model using lme4 (Bates et al., 2015) in R software (https://www.r-project.org/) to IDDI with dive duration as a predictor and individual ID as a random effect. We compared dive depths and IDDIs of each dive within the top 5% of dive durations using linear regression. For tags from 2014 to 2016,

Table 1. Summary of dives, inter-deep dive intervals (IDDIs) and surface periods in Cuvier's beaked whales

Individual ID	Age class/sex	Deployment date	Number of dives >33 min (median duration, min)	Number of IDDIs (median duration, min)	Number of dives with before and following ventilation periods
ZcTag029	Unk/Unk	13-May-14	165 (64.1)	92 (83.9)	146
ZcTag030	Ad/M	16-Sep-14	260 (53.8)	208 (81.7)	235
ZcTag038	Ad/M	14-Jun-15	327 (60.4)	293 (89.4)	318
ZcTag040	Ad/M	14-Jun-15	9 (55.9)	8 (58.5)	8
ZcTag041	Ad/M	15-Oct-15	275 (60.8)	247 (55.7)	261
ZcTag042	Ad/M	21-Oct-15	97 (59.7)	62 (74.0)	83
ZcTag046	Ad/M	25-May-16	58 (51.7)	38 (38.6)	55
ZcTag048	Unk/Unk	27-May-16	140 (53.4)	95 (59.1)	128
ZcTag051	Ad/M	22-Aug-16	66 (59.7)	54 (56.1)	56
ZcTag054	Ad/M	10-May-17	193 (57.7)	193 (74.5)	N/A
ZcTag055	Ad/M	10-May-17	144 (58.9)	144 (68.5)	N/A
ZcTag056	Ad/M	10-May-17	524 (57.5)	524 (71.9)	N/A
ZcTag057	Unk/Unk	16-May-17	303 (58.7)	303 (102.2)	N/A
ZcTag058	Unk/Unk	16-May-17	352 (58.4)	352 (97.9)	N/A
ZcTag060	Ad/M	17-Aug-17	45 (69.8)	45 (74.4)	N/A
ZcTag061	Unk/Unk	17-Aug-17	62 (51.8)	62 (49.1)	N/A
ZcTag062	Unk/Unk	17-Aug-17	40 (68.0)	40 (92.7)	N/A
ZcTag063	Ad/M	20-Aug-17	20 (51.3)	20 (67.7)	N/A
ZcTag064	Unk/Unk	20-Aug-17	19 (54.3)	19 (93.9)	N/A
ZcTag065	Ad/M	22-Aug-17	1*	1*	N/A
ZcTag066	Ad/M	04-Sep-17	75 (57.4)	75 (86.5)	N/A
ZcTag067	Ad/M	04-Sep-17	2*	2*	N/A
ZcTag068	Ad/M	04-Sep-17	78 (52.3)	78 (77.6)	N/A
ZcTag070	Unk/Unk	25-May-18	3*	3*	N/A
ZcTag076	Ad/M	06-Aug-18	228 (64.4)	228 (65.6)	N/A
ZcTag078	Ad/M	06-Aug-18	200 (65.2)	200 (78.7)	N/A
			3686	3386	1290

Ad, adult; M, male; Unk, unknown. Asterisks indicate tags excluded from analysis owing to low sample size. N/A, data not available.

we compared all dive durations with periods of ventilation (Table 1) both before (time actively breathing at the surface directly before a 33-min dive and after a dive of any length) and following (time actively breathing at the surface directly after a 33-min dive and before a dive of any length) dives using linear models.

RESULTS AND DISCUSSION

We analysed 3680 foraging dives from 23 individuals (Table 1). Dives were not evenly distributed across individuals owing to variation in deployment durations and data truncation (Table S1). In total, 3380 dives had IDDIs available for analysis and 1290 dives had before and after ventilation periods (Table 1, Table S1). Of the 26 tagged individuals, 18 whales were adult males and eight were of unknown age and sex class (Table 1). The median duration of the 3680 recorded dives was 59.0 min, with a maximum duration of 132 min, and 5% of the dives exceeded 77.7 min (Fig. 1, Table S1). IDDI following a dive was significantly correlated with dive duration ($P=0.006$; Fig. 2A) with an effect size of 0.79 min. Individual ID explained only a small amount of the variance (537.8, s.d.=23.19, residual variance=34,002.2, s.d.=184.40; Table S2). In an analysis of the longest 5% of dives, a linear model showed no significant relationship between dive duration and subsequent IDDI ($R^2=-0.003$, $F_{1,173}=1.595$, $P=0.208$; Fig. 2B, Table S2). There was also no relationship between the duration of these longest dives and depth ($P=0.916$; Table S2). Linear regression of dive duration against ventilation period immediately before a dive showed no significant relationship ($R^2=0.0001$, $F_{1,1288}=0.179$, $P=0.673$; Fig. 2C, Table S2), nor did the dive duration against the ventilation period immediately following the dive ($R^2=0.002$, $F_{1,1288}=3.126$, $P=0.077$; Fig. 2D, Table S2). Seventeen of the 23

whales exhibited dive durations in the top 5%, including five of the eight animals that were not adult males (Fig. 2B).

Our study demonstrated a significant relationship between dive duration and IDDI for presumed foraging dives. For every extra minute submerged, there was a 0.79 min increase in IDDI, suggesting that recovery takes more time as dive duration increases. However, this relationship does not hold for the top 5% of dive durations, suggesting that there is no apparent requirement for additional surface rest immediately after long dives that exceeded 77.7 min. If Cuvier's beaked whales exceed their ADL during foraging dives with a frequency (5%) similar to that of Weddell seals, then the bADL for this species is 77.7 min. However, the lack of association between the duration of the longest dives and IDDI and that very short IDDIs occur before and after the 95th percentile of dive durations suggests that Cuvier's beaked whales may dive again before lactate levels have returned to baseline, if they are surpassing ADL on these very long dives. Such behaviour would require the ability to buffer disturbances to acid–base balance from anaerobic metabolism, allowing lactate to accumulate over a series of deep dives to be metabolised either during later extended surface periods, or during the sequences of shallow dives that follow a deep dive (Tyack et al., 2006).

The cADL for Cuvier's beaked whales of 33 min (Tyack et al., 2006) corresponds to the minimum duration of foraging dives used in our study. However, many diving species exceed cADL with morphological, physiological and behavioural adaptations that increase the duration of aerobic diving (Arnould and Costa, 2006; Costa et al., 2001; Halsey et al., 2006; Nakai, 1959; Villegas-Amtmann and Costa, 2010; Villegas-Amtmann et al., 2012; Velten, 2012). Pabst et al. (2016) demonstrated that some beaked whales of the genus *Mesoplodon* invest a much smaller percentage of their
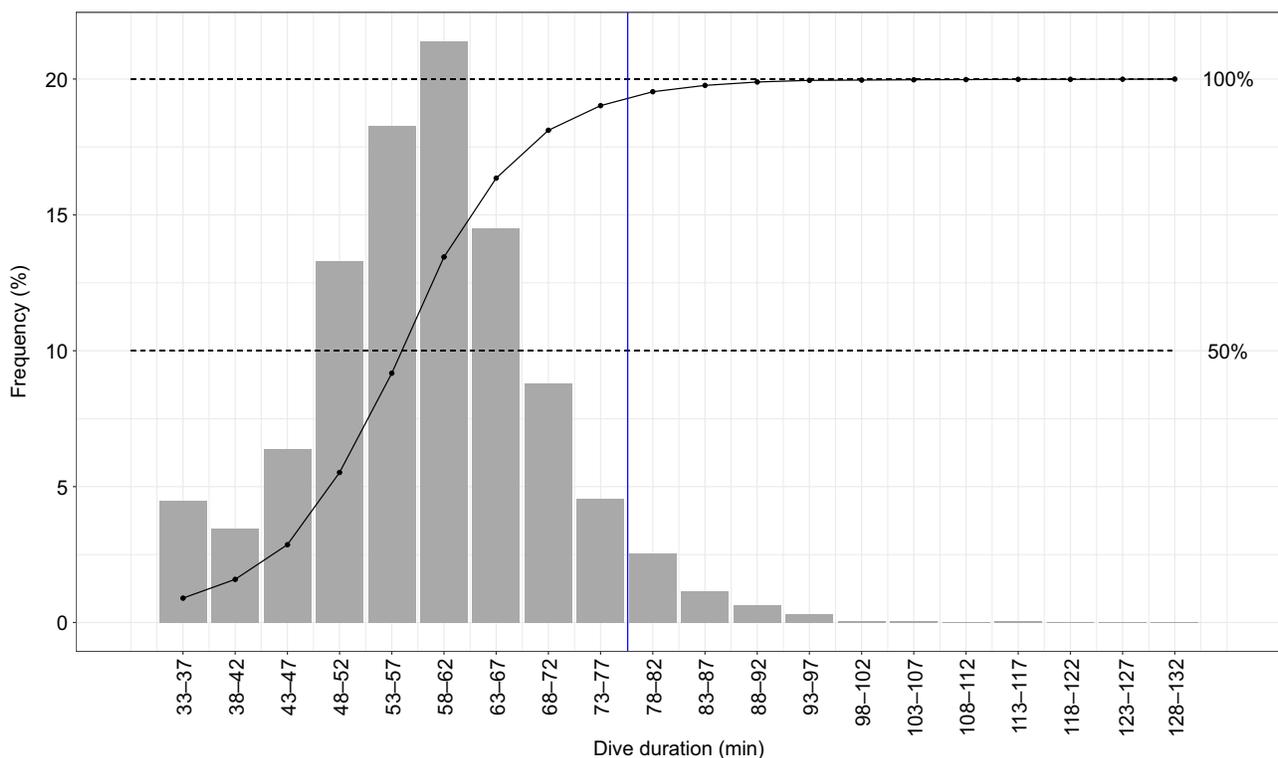
Fig. 1. Binned dive duration ($N=3680$ dives) against frequency contribution to overall distribution (primary y-axis) in Cuvier's beaked whales. Solid line shows cumulative frequency (5:1 scale), dashed horizontal lines show 50 and 100% of cumulative frequency. Blue vertical line indicates the 95th percentile.
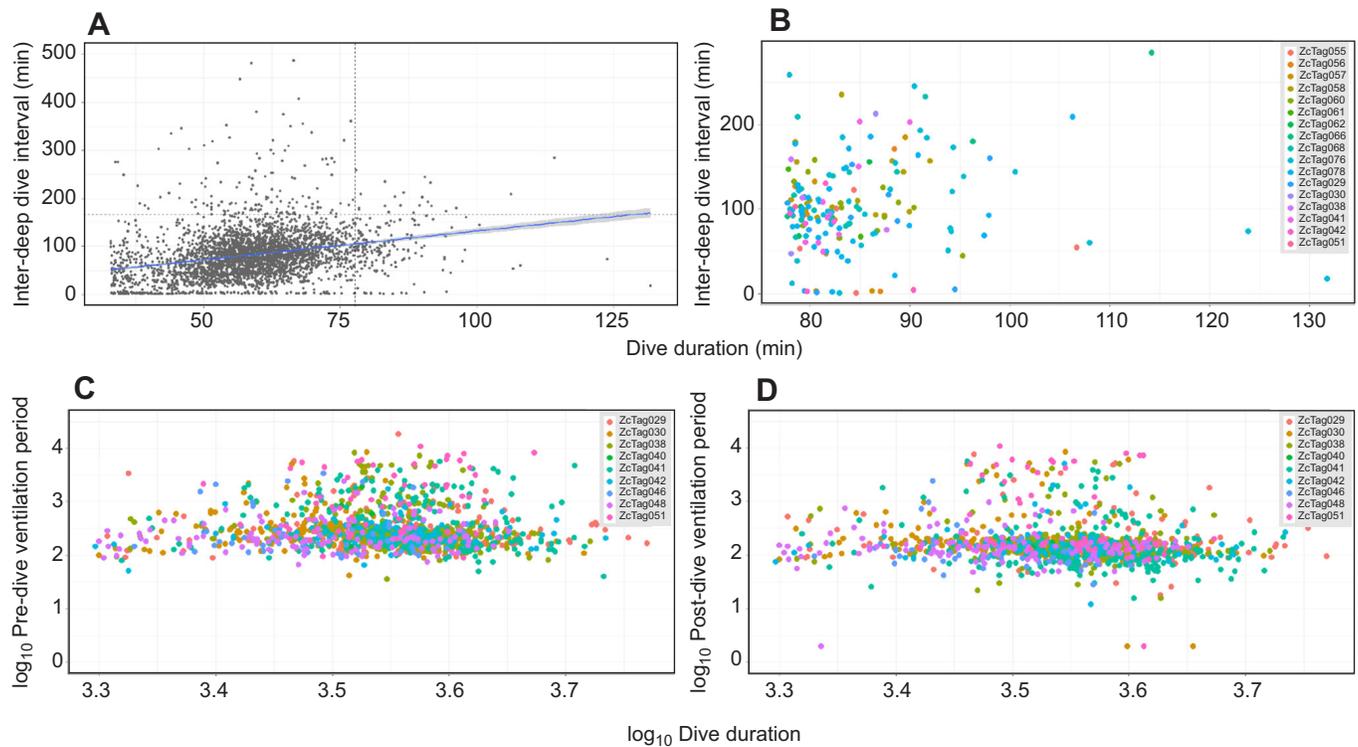
Fig. 2. Dive duration against inter-deep dive interval and pre- and post-ventilation period. (A) Dive duration against inter-deep dive interval (IDDI) with regression from linear mixed model (seven outliers with IDDIs over 500 min are not plotted). Black dashed lines show 95% values of duration and IDDI. (B) Top 5% of durations with IDDIs, by individual. (C) Log of dive duration against log before ventilation period, by individual. (D) Log of dive durations against log following ventilation period, by individual.

body mass in metabolically expensive tissues such as brain and viscera, and a much higher proportion in locomotor muscle with low tissue metabolic rates, high oxygen storage (Velten et al., 2013) and muscle fibre types that may protect against ischemia/reperfusion injury (Moore et al., 2014). Beaked whale locomotor muscle exhibits elevated myoglobin concentrations, low mitochondrial volume densities, higher lean mass, large fibre diameters and fast glycolytic fibres. Cuvier's beaked whales are larger than *Mesoplodon* species, and their adaptations may be even more extreme. Noren (2004) demonstrated that Cuvier's beaked whale muscle is capable of prolonged, low-level anaerobic function, as it has one of the highest acid buffering capacities among cetaceans. These adaptations, coupled with a dive response that includes bradycardia and peripheral vasoconstriction (Ponganis, 2011), reduced kidney and liver function, and delayed digestion (Sparling et al., 2007; Svärd et al., 2009; Thouzeau et al., 2003), together with behavioural modifications including swimming strategies to minimise metabolism (Williams, 2001; Martín López et al., 2015), have enabled beaked whales to extend dive durations.

Elephant seals (*Mirounga* spp.) conduct many extended dives that exceed cADL and are not followed by extended surface periods (LeBoeuf et al., 1988; Hassrick et al., 2010; Hindell et al., 1992). The lack of observed recovery time in these species has led to the conclusion that they modulate their diving metabolic rates, essentially allowing ADL to vary per dive (LeBoeuf et al., 1988; Hindell et al., 1992). Diving metabolic rates do not exist for Cuvier's beaked whales, but Velten et al. (2013) calculated a diving metabolic rate for a 1000 kg *Mesoplodon* using a value for total body oxygen stores of 86.9 ml O_2 kg^{-1}. Scaling this value for a 2000 kg *Ziphius*, and using our 95% bADL value of 77.7 min, we estimate a diving metabolic rate of 1.12 ml O^2 kg^{-1} min^{-1} for

Cuvier's beaked whales. This value is 25% lower than an estimated BMR for a generic 2000 kg terrestrial mammal of 1.48 ml O_2 kg^{-1} min^{-1}, calculated using Kleiber's equation (BMR= $0.00993 \times M_b^{0.75}$, in 1 O_2 min^{-1}, where M_b is body mass) (Kleiber, 1987). Body oxygen stores may be underestimated as samples from Velten et al. (2013) were taken some hours after death, and the BMR for a beaked whale may be lower than that predicted by Kleiber (1987). Studies have shown differences in metabolic rates among marine mammals, including reductions in diving metabolic rates below resting metabolic rate in large phocid seals during long dives (Williams et al., 2004; Castellini et al., 1992; Maresh et al., 2014) and the influence of offspring age and environment in fur seals (Trillmich and Kooyman, 2001). Weddell seals have large oxygen stores per unit of body mass and are capable of very low diving metabolic rates (Ponganis, 2015; Velten et al., 2013; Williams et al., 2004). Cuvier's beaked whales have a much larger average adult body mass than Weddell seals, so we assume that the ADLs of beaked whales exceed that of Weddell seals and also that the adaptations documented in *Mesoplodon* (Velten et al., 2013) are present in Cuvier's beaked whales. Therefore, we propose that the ADL in Cuvier's beaked whales may be much greater than suggested by previous estimates and more akin to the value of 77.7 min calculated from our data.

The durations of ventilation periods before and after dives in our study were not correlated with dive duration, possibly because the time to oxygen load tissues before diving and replenish oxygen stores after diving is similar regardless of dive duration. This absence of an increased ventilation period after long duration dives suggests that the remaining body oxygen stores following shorter dives may not be substantially higher than following long dives and could help explain the levelling off of the correlation between IDDI and dive duration at dive times above our calculated bADL. The

ventilation period before a foraging dive is consistently longer than that following a foraging dive (Shearer et al., 2019) and is perhaps necessary for another function, such as the anticipatory adjustments for diving observed in seals and penguins (Boutilier et al., 2001; Fahlman et al., 2008; McKnight et al., 2019; Wilson et al., 2003), or social coordination before a group dive.

Blood lactate accumulation (Ponganis, 2011) and myoglobin levels (Noren and Williams, 2000) are known to vary with age and size in cetaceans. We were not able to quantify the absolute size of our whales, but five individuals of unknown age and sex (assumed not to be adult males) recorded dive durations within the top 5% of all dives observed. We did observe some very long IDDIs that may reflect processes other than recovery, such as increased time to digest food from long dives, or periods of social coordination, but we are unable to explore this fully in our data owing to differences in tag durations. Nevertheless, we observed extended IDDIs and long duration dives in the diving records of most individuals.

Our value of bADL is calculated from a large sample of presumed foraging dives in our population. It is possible that the 5% value calculated from our data does not accurately estimate cADL for beaked whales given their extreme anaerobic capacity, and we assumed that all long dives (over 33 min) are primarily for foraging, consistent with previous authors (Tyack et al., 2006). If shorter dives function to process metabolic by-products from anaerobic metabolism, then the period during which this metabolism occurs should increase as the foraging dive duration increases. However, if all dives are considered equal, we could calculate a bADL using each dive from a tag record. We explored this approach and calculated a 95% value of 65.9 min (Fig. S1). This value is lower than the bADL calculated using only foraging dives, owing to the large number of shallow non-foraging dives, but is still considerably higher than the cADL from Tyack et al. (2006).

Finally, in our extended dataset, we recorded two extremely long dives from one individual (ZcTag066) of 173 and 222 min, followed by IDDIs of 236 and 268 min, respectively. These records were censored from our primary data set because they were recorded 17 and 24 days after a known 1-h exposure to a Navy mid-frequency active sonar signal. These extreme dive durations and IDDIs are perhaps more indicative of the true limits of the diving behaviour of this species. These extreme records demonstrate that Cuvier's beaked whales have evolved an unparalleled ability to deal with the by-products of aerobic and anaerobic metabolism, which allows them to exploit their bathypelagic foraging habitats. We hope that our study provides an impetus to explore these adaptations; further information on oxygen loading between dives, blood perfusion during diving, and metabolic rates would greatly help to interpret the remarkable diving behaviour of this species.

Author contributions
Conceptualization: N.J.Q., W.R.C., A.F., A.J.R.; Methodology: N.J.Q., A.F.; Formal analysis: N.J.Q., W.R.C., J.M.S.; Writing - original draft: N.J.Q.; Writing - review & editing: W.R.C., J.M.S., A.F., A.J.R.; Project administration: A.J.R.; Funding acquisition: A.J.R.

Data availability
Data are available at
https://github.com/williamcioffi/quick_zc_adl (doi:10.5281/zenodo.3880177)

Supplementary information
Supplementary information available online at
https://jeb.biologists.org/lookup/doi/10.1242/jeb.222109.supplemental

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