

Daytime dive characteristics from six short-finned pilot whales *Globicephala macrorhynchus* off Madeira Island

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Six time-depth recorders attached with suction-cups were deployed in resident and transient adult short-finned pilot whales to evaluate their daytime diving characteristics in their preferred habitat area off Madeira Island. Here, data on the proportion of time spent at the surface and at different dive phases (descent, bottom and ascent), dive depths and dive rates are presented. With mean attachment durations of 2 h 31 min (SD=2 h), the whales spent a considerable amount of time at the surface (mean=76.3%, SD=18.6) and presented a low diving rate (mean=6.8 dives h⁻¹, SD=6.1; considering dive as submergence deeper than 10 m). The maximum dive depth recorded in this study was 988 m, and dives deeper than 500 m, which were recorded from resident and transient whales, suggest foraging activity along their preferred habitat area. The analysis of dives deeper than 100 m shows that the percentage of time spent on descent, bottom or ascent varied between dives, with means of ~40, 30 and 30%, respectively.

Key words: biologgers, dive profile, marine mammal, NE Atlantic, TDRs

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INTRODUCTION

Obtaining information on the diving behaviour of marine mammals is of major interest for management purposes (Hooker & Baird 2001). When combined with knowledge on group behaviour, the percentage of time a species spends at the surface can help converting the at-surface abundance to total estimates of abundance, as this adjusts for whales that are not detected at the surface during visual surveys (Lake & Borchers 2004). On the other hand, information on the subsurface dive profile is important in the study of feeding ecology (Panigada et al.

1999) or in assessment of depth-specific impacts (e.g. acoustic; Hooker & Baird 2001).

Short-finned pilot whales, *Globicephala macrorhynchus* Gray, 1846, are top predators inhabiting circum-tropical and warm temperate waters. Several aspects of this species diving behaviour have been documented, such that foraging dives seem to adapt to circadian rhythms, with deeper dives and longer periods of time shallow diving or surface resting occurring during the day (Baird et al. 2003; Soto et al. 2008). Yet, time-per-depth data for this species has only been addressed by Wells et al. (2013), based on post-release monitoring via satellite-

linked telemetry of two adult males released directly from a mass stranding. Moreover, the proportion of each dive spent at the bottom has only been described for the related long-finned pilot whale *G. melas* (Baird et al. 2002; Heide-Jørgensen et al. 2002).

In Madeira Archipelago (NE Atlantic) short-finned pilot whales demonstrate a large degree of variability in site fidelity (Alves et al. 2013). It is suggested that transient and resident whales interact for mating purposes when they meet (Alves et al. 2013), and that there is a preference for these whales to use the southern and eastern waters of Madeira Island (Filipe Alves, unpublished data from the Madeira Whale Museum). In this study, and for the first time in Madeira, biologgers were used in short-finned pilot whales to evaluate their daytime diving characteristics. Six time-depth recorders (TDRs) attached with suction-cups were deployed in resident and transient adult whales in their preferred habitat area. Here, we present data on the proportion of time spent at the surface and at different dive phases (descent, bottom and ascent), dive depths and dive rates.

MATERIAL AND METHODS

Fieldwork was undertaken from the 18 m research yacht *ZIPHIUS* or from the 6.5 m inflatable boat *ROAZ*, from 2005 to 2011, along the south and east coast of Madeira Island (Fig. 1). Tags technical specificities, deployment procedures, and data download are described in Alves et al. (2010). TDRs were set to sample depth once per second, to a maximum of 2000 m. At each tag deployment, the reaction of the animal was recorded, as well as the presence of calves, group size, animal's behaviour, GPS position and travel direction. To minimize disturbance and record more natural behaviours, the boat left the group approximately 10 min after each deployment. During tag deployment, each tagged whale was digitally photographed for dorsal fin comparison to 683 individuals recorded between 2001 and 2011 and catalogued in a photo-identification database held at the Madeira Whale Museum.

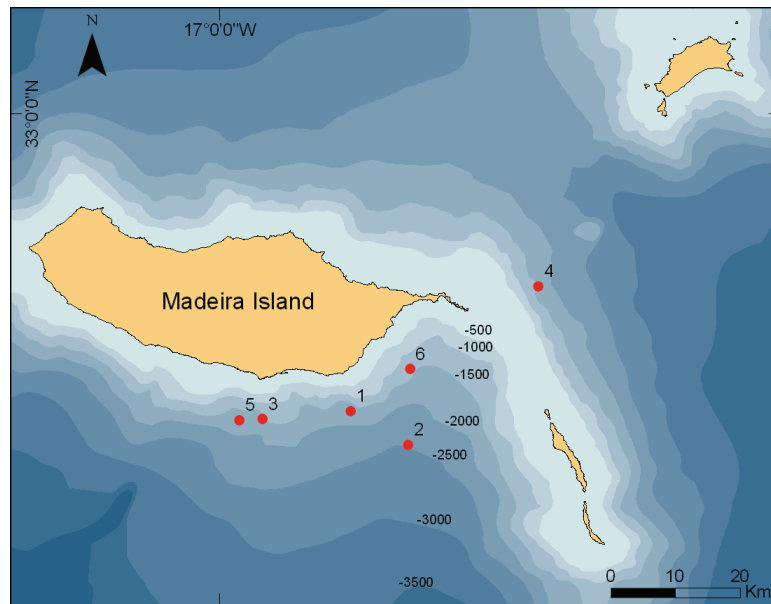


Fig. 1. Bathymetric map showing the location of the six deployments used in this study, archipelago of Madeira, Portugal. Numbers 1-6 correspond to whales ID. Depth in metres.

This allowed assignment of a residency pattern and a pod affiliation (in the case of resident whales) according to Alves et al. (2013). The photographs, together with field observations, allowed categorising all tagged whales as adults, and classifying their sex according to descriptions by Yonekura et al. (1980) and Kasuya & Marsh (1984).

A dive was defined as submergence deeper than 10 m (about two body lengths) to exclude brief shallow submersions between respirations. The proportion of time spent at the top 10 m layer and the diving rate (number of dives h⁻¹) were determined for each whale. The mean proportion of time spent at the top 10 m and the mean diving rate were calculated per component (sex, residency pattern and resident pod); however the limited number of samples did not allow a robust analysis. Additionally, the total proportion of time spent at different depth bins was determined.

To characterise the proportion of time spent at each phase in dives deeper than 100 m, we defined: ‘descent’ as the time between the beginning of the dive, from the surface, to the bottom; ‘bottom’ as the time between the point characterised by an inversion of the vertical direction in the last 2/3 of maximum depth and/or followed by a stabilisation of depth, and the point when ascent

begins at constant rate; and ‘ascent’ as the time between the end of bottom and surface.

A variety of depths (e.g. >100, >300, >500 m) are described in literature for establishing deep foraging dives in short-finned pilot whales (Baird et al. 2003; Soto et al. 2008; Jensen et al. 2011). We tried to establish it by searching for a bimodal distribution on a plot of the duration and maximum depth of dives (following Hooker & Baird 2001). Two sets of dives longer and deeper than the majority of dives were found: one between 100 and 200 m, and other deeper than 500 m (Fig. 2). Therefore, instead of establishing one depth defining deep dives, the dive statistics were analysed for these categories.

RESULTS

Six tag deployments (out of 18 attempts) yielded 15 h 06 min of data, and attachment durations ranged from 22 min to 5 h 08 min, with a mean of 2 h 31 min (SD=2 h) (Table 1). Tag recordings occurred between 11:44 and 18:49 local time, i.e. before sunset independently of the sampling season. Tags were applied to four residents (three females from the same pod and one male from a different pod) and two male transients (Table 1).

Table 1. Summary of the tags deployed on adult short-finned pilot whales, including diving behaviour; MWM - Madeira Whale Museum; *With calf; †Sex confirmed by genetic analysis from a biopsy collected in another encounter (Alves et al. 2013). Residency pattern and pod ID according to Alves et al. (2013).

Whale				Deployment		Diving behaviour				
ID	# MWM photo-id catalogue	Sex	Residency pattern	Date	Time to sunset when detached	Duration	% Time top 10 m	Dive rate (dives h ⁻¹) deeper than		
								10 m	100 m	500 m
1	089	♂	Resident - Pod R4	13-06-2005	>2 h	2 h 57 min	78.0	5.8	0.7	0
2	149	♂	Transient	20-10-2005	>2 h	22 min	73.7	18.8	0	0
3	137	♀	Resident - Pod R5	19-07-2006	>6 h	37 min	41.2	6.5	1.6	1.6
4	373	♂	Transient	06-05-2008	4 h	5 h 08 min	84.3	2.5	0.4	0.4
5	133	♀*	Resident - Pod R5	18-10-2011	3 h	1h 33 min	85.3	3.9	0.6	0
6	135	♀†	Resident - Pod R5	30-11-2011	12 min	4 h 29 min	95.0	3.1	0	0
						Mean (SD)	2 h 31 min (2 h)	76.3 (18.6)	6.8 (6.1)	0.6 (0.6)
						Total	15 h 06 min			

The water depth during deployments ranged from 1000 to 2500 m (Fig. 1). Tagging caused only short-term (few seconds) reactions to tagged animals, such as sudden shallow dive or tail slapping. These animals then rejoined the group and regained their natural behaviour. A visual inspection of the dive profiles showed no discrepancies during the first minutes (Fig. 3 and 4), thus these were not excluded from the data analysis.

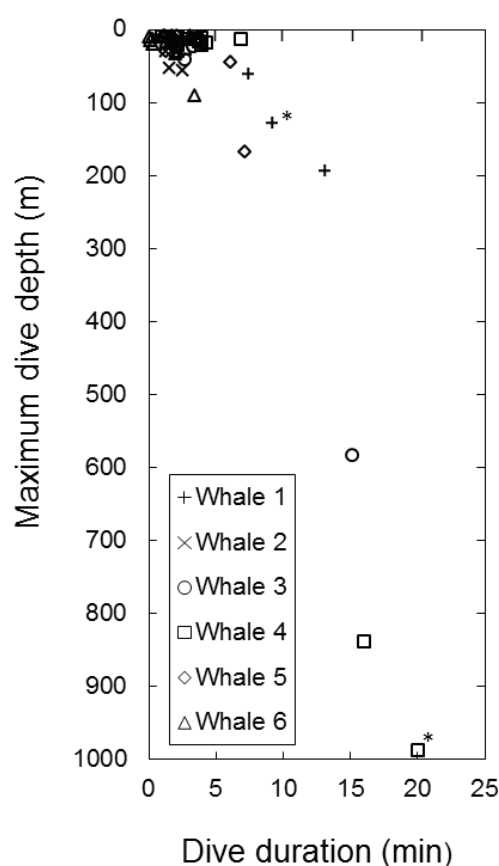


Fig. 2. Dive duration and maximum dive depth for 59 dives deeper than 10 m recorded from six adult short-finned pilot whales. * Estimated values since tag detached during beginning of ascent; using the mean ascent rate of the previous (similar) dive of the same whale. Two dives were not considered since tag detached during descent. Three dives between 100 and 200 m and three deeper than 500 m differentiate from the majority of dives, which were shallower than 100 m and shorter than 5 min.

The dive profiles in relation to time of day showed periods of surfacing and shallow diving (shallower than 100 m) intercalated with periods of dives between 100 and 200 m (whales 1, 2, 5 and 6; Fig. 3), and with periods of dives between 500 and 1000 m (whales 3 and 4; Fig. 4). With the exception of one animal (whale 3), the percentage of time each tagged whale spent in the top 10 m was >73%, with an overall mean of 76.3% (SD=18.6) (Table 1). Similar values were obtained between all components (sex, residency pattern and pod affiliation; Table 2).

Table 2. Mean of the percentage of time spent in the top 10 m and of the dive rate deeper than 10 m per sex, per residency pattern and per resident pod.

Component	% Time top 10 m	Dive rate (dives h ⁻¹)
Male	78.7 (SD=5.3, n=3)	9.0 (SD=8.3, n=3)
Female	73.8 (SD=28.7, n=3)	4.5 (SD=1.8, n=3)
Resident	74.9 (SD=23.5, n=4)	4.8 (SD=1.6, n=4)
Transient	79.0 (SD=7.5, n=2)	10.7 (SD=11.5, n=2)
Male-Resident	78.0 (n=1)	5.8 (n=1)
Male-Transient	79.0 (SD=7.5, n=2)	10.7 (SD=11.5, n=2)
Female-Resident	73.8 (SD=28.7, n=3)	4.5 (SD=1.8, n=3)
Pod R4	78.0 (n=1)	5.8 (n=1)
Pod R5	73.8 (SD=28.7, n=3)	4.5 (SD=1.8, n=3)

Whales performed a total of 61 dives deeper than 10 m, of which three were between 100 and 200 m, and three were deeper than 500 m, presenting mean dive rates of 6.8 (SD=6.1), 0.6 (SD=0.6) and 0.3 (SD=0.6) dives h⁻¹, respectively (Table 1). Transient males presented a considerably higher number of dives (Table 2). The analysis of the total proportion of time from the six tagged whales per depth bin shows that 94.1% of the time was spent in the 100 m bin, of which most was spent in the shallower bins (84.3% in the top 10 m, Table 3). The whales then spent 1.89% of their time in the 200 m bin (i.e. between 101 and 200 m), followed by the 600 m bin (0.80%) and the 800 m bin (0.63%) (Table 3).

G. macrorhynchus dive patterns off Madeira

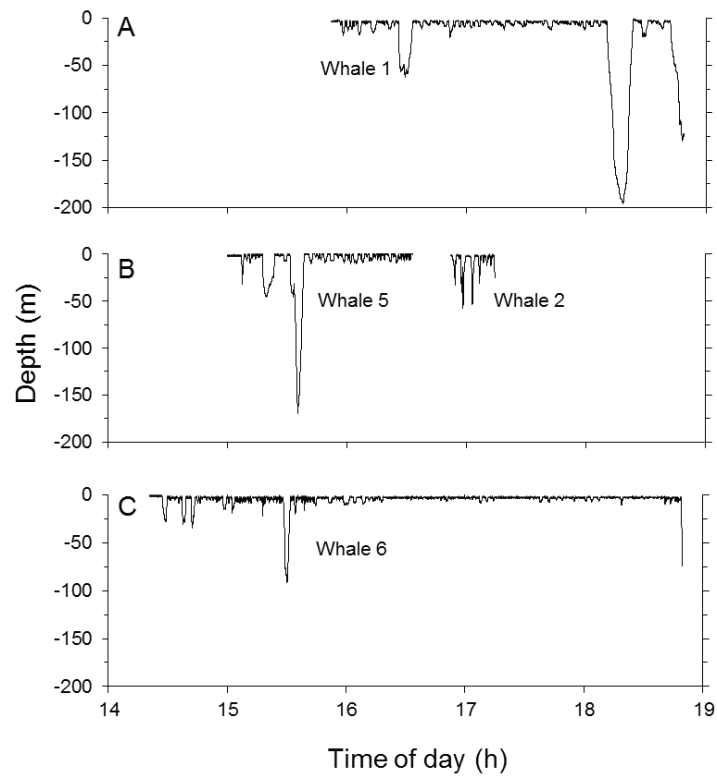


Fig. 3. Dive profiles in relation to local time of day for whales 1 (A), 2, 5 (B) and 6 (C). The last dive of whales 1, 2 and 6 is incomplete due to tag detachment at depth. Dive profiles show periods of surfacing and shallow diving intercalated with dives to almost 200 m.

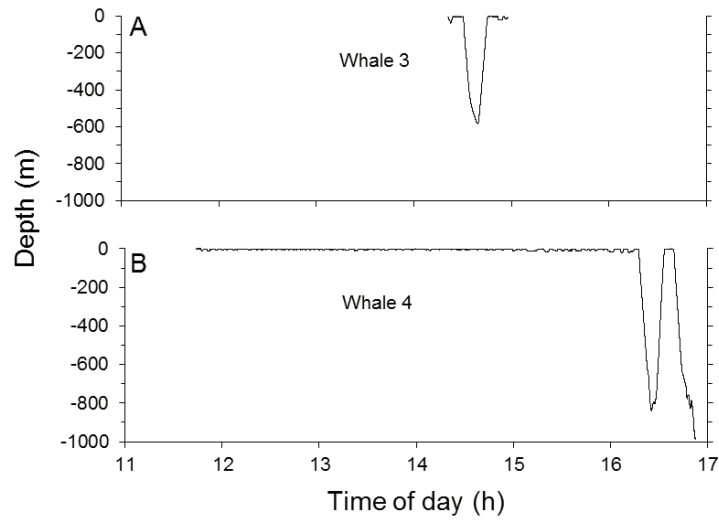


Fig. 4. Dive profiles in relation to local time of day for whales 3 (A) and 4 (B). The last dive of whale 4 is incomplete due to tag detachment at depth. Dive profiles show periods of surfacing and shallow diving intercalated with dives to almost 1000 m.

Table 3. Total percentage of time spent by six tagged whales at each depth bin. The depth bin '10' covers the top 10 m, the bin '20' covers depths between 11 and 20 m, etc. The depth bin '200' covers depths between 101 and 200 m, etc. The whales spent 94.1% of time in the 100 m depth bin.

10 m depth bin	% Time	100 m depth bin	% Time
10	84.32		
20	5.26	200	1.89
30	1.31	300	0.46
40	0.94	400	0.46
50	0.72	500	0.55
60	0.76	600	0.80
70	0.23	700	0.49
80	0.23	800	0.63
90	0.22	900	0.47
100	0.15	1000	0.12
<i>Sum</i>			100

Apart from three dives, all dives shallower than 100 m lasted less than 5 min and, as a general trend, deeper dives tended to be longer (Fig. 2). The maximum dive depth recorded was 988 m, based on an incomplete dive (Table 4). The maximum dive depth and duration recorded from a complete dive were 839 m and 16.08 min

(Table 4). The analysis of dives deeper than 100 m shows that the percentage of time spent on descent, bottom or ascent varied between dives, and presented means of ~40, 30 and 30%, respectively (Table 4). Higher mean rates of descent and ascent were recorded in the dives deeper than 500 m (Table 4).

DISCUSSION

This study shows that six adult short-finned pilot whales tagged during daytime in Madeira spent a considerable amount of time at the surface with a low diving rate. Even not being directly comparable due to using different depth bins, Wells et al. (2013) have shown that two adult short-finned pilot whales tagged in the west Atlantic also spent most of the time at the surface and at shallower depths. Similar findings have also been described for the long-finned pilot whale (Heide-Jørgensen et al. 2002; Nawojchik et al. 2003).

However, and despite the consistency in the results found among whales of different components in our study, a higher number of deployments or of hours of data is required to address the many different parameters that might influence diving behaviour.

Table 4. Dive statistics of daytime dives deeper than 100 m. Dives ranked by maximum depth. ^aMinimum value since tag detached during beginning of ascent, but the whale could have descended again. ^bEstimated value (due to incomplete dive) using the mean ascent rate of the previous (similar type and depth) dive of that whale. ^cApproximate value due to incomplete dive. ^dV-shaped dive with no defined bottom. ^eSee definition in M&M.

Whale	Maximum	Duration	% Time at			Mean rate (m s ⁻¹) of	
ID	depth (m)	(min)	descent	bottom ^e	ascent	descent	ascent
1	130 ^a	9.32 ^b	50 ^c	25 ^c	-	0.4	-
5	170	7.22	56.9	- ^d	43.1	1.2	1.0
1	196	13.20	30.2	42.5	27.3	0.7	0.8
3	584	15.15	24.2	41.3	34.6	1.9	1.8
4	839	16.08	49.4	18.7	32.0	1.8	2.4
4	988 ^a	20.09 ^b	43 ^c	27 ^c	-	1.6	-
<i>Mean (SD)</i>							
<i>dives deeper than 100 m</i>	485 (373)	13.51 (4.69)	42.3 (12.6)	30.9 (10.5)	34.2 (6.6)	1.3 (0.6)	1.5 (0.7)
<i>dives deeper than 500 m</i>	804 (204)	17.11 (2.62)	38.8 (13.1)	29 (11.4)	33.3 (1.9)	1.8 (0.2)	2.1 (0.4)

Information on the time the animals spent at surface can be very helpful in the analysis of visual line-transect surveys assuming the contribution to convert the at-surface abundance to total estimates of abundance (Laake & Borchers 2004). However, individual dive behaviour can differ from group diving behaviour, so that information is biased if not combined with information on dive synchrony. While Shane (1995) and we (unpublished data) have observed entire pods of short-finned pilot whales submerging during several minutes, acoustic studies have shown an apparent lack of dive synchrony (Jensen et al. 2011; Soto 2006; Soto et al. 2008). Therefore, further information on dive synchrony is needed in order to determine with accuracy the proportion of time whales are 'detectable', thus accounting more adequately for the 'availability bias' (Laake & Borchers 2004). That information can be acquired with visual behavioural studies, acoustic studies or possibly through tagging of all individuals in a small (3-5 individuals) pod.

The dives recorded in this study are likely to represent maximum diving performance for the species given that dive capability is known to generally increase with body size (Schreer & Kovacs 1997) and all the tagged whales were identified as adults, and given that dives were not depth limited. The depths reported here are in agreement with depth ranges described for daytime deep dives of short-finned pilot whales off Tenerife (Soto et al. 2008). Dives deeper than 500 m recorded in this study suggest foraging activity, especially as they are comparable to results in Baird et al. (2002) and Soto et al. (2008). Such deep dives have a high energetic cost and likely enable the animals to get a high-gain in return (Thompson & Fedak 2001), for example feeding on high-caloric prey such as squid which have been described as the primary diet of pilot whales (Desportes & Mouritsen 1993; Mintzer et al. 2008). Therefore, at least three dives, one from a resident (whale 3) in the south and two from a transient (whale 4) in the east of Madeira Island, are assumed to be foraging dives.

The duration of dives in this study is in accordance with values obtained for this species in the western Atlantic (Wells et al. 2013) and long-finned pilot whales (Baird et al. 2002; Heide-Jørgensen et al. 2002). The mean rate of

descent and ascent recorded for dives deeper than 500 m are comparable to the values obtained for similar dives of short-finned pilot whales off Tenerife (Soto et al. 2008). Concerning the percentage of time at bottom, the ~30% obtained during five dives deeper than 100 m in this study are within the range of the means presented for its related species (Baird et al. 2002).

The limited number of successful TDR tag deployments during this study may have been caused by difficulties in approaching animals and by a limited number of animals available for tagging. This limited amount of data per disturbance discourages further use of these tags, in substitution of the technologically improved satellite-linked TDRs. Yet, attachment durations in this study did not differ much from those described in Baird et al. (2002) and Soto et al. (2008).

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