Journal of Animal Ecology 2008 doi: 10.1111/j.1365-2656.2008.01393.x

Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands)

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Summary

1. Empirical testing of optimal foraging models for breath-hold divers has been difficult. Here we report data from sound and movement recording DTags placed on 23 short-finned pilot whales off Tenerife to study the foraging strategies used to catch deep-water prey.

2. Day and night foraging dives had a maximum depth and duration of 1018 m and 21 min. Vocal behaviour during dives was consistent with biosonar-based foraging, with long series of echolocation clicks interspersed with buzzes. Similar buzzes have been associated with prey capture attempts in other echolocating species.

3. Foraging dives seemed to adapt to circadian rhythms. Deep dives during the day were deeper, but contained fewer buzzes (median 1), than night-time deep dives (median 5 buzzes).

4. In most deep (540–1019 m) daytime dives with buzzes, a downward directed sprint reaching up to 9 m s^{-1} occurred just prior to a buzz and coincided with the deepest point in the dive, suggestive of a chase after escaping prey.

5. A large percentage (10–36%) of the drag-related locomotion cost of these dives (15 min long) is spent in sprinting (19–79 s). This energetic foraging tactic focused on a single or few prey items has not been observed previously in deep-diving mammals but resembles the high-risk/high-gain strategy of some terrestrial hunters such as cheetahs.

6. Deep sprints contrast with the expectation that deep-diving mammals will swim at moderate speeds optimized to reduce oxygen consumption and maximize foraging time at depth. Pilot whales may have developed this tactic to target a deep-water niche formed by large/calorific/fast moving prey such as giant squid.

Key-words: deep water ecosystem, foraging ecology, marine mammal, pilot whale, swimming speed

Introduction

While foraging plays a central part in the ecology of all animals, a preponderance of studies have targeted terrestrial animals as these are often more tractable than marine animals for studying predator–prey interactions (e.g. Scheel 1993; Palomares *et al.* 2001; Hopcraft, Sinclair & Packer 2005). However, the recent advent of multisensor data-loggers means that it is now possible to study the foraging behaviour of a range of marine species, including reptiles, birds and mammals (e.g. Chappell *et al.* 1993; Bost *et al.* 2002; Madsen *et al.* 2005; Ropert-Coudert & Wilson 2005; Myers & Hays 2006; Tyack *et al.* 2006).

Marine animals that undertake breath-hold dives to access underwater niches must balance their access to two vital, but spatially separated resources: oxygen at the surface and food at depth (Kramer 1988). Data from tagging studies on several species of diving birds and pinnipeds (Kooyman 1989; Wilson, Ropert-Coudert & Kato 2002) have led to the development of optimal foraging models, which predict behavioural strategies enabling the animals to get the highest net energy returns in the available foraging patches (Thompson & Fedak 2001). These models emphasize the importance of minimizing the cost of transport between the surface and the prey at depth, using efficient locomotion and a low metabolic rate while diving to ration the limited oxygen stores available (Thompson, Hiby & Fedak 1993; Williams *et al.* 1999; Reina *et al.* 2005;

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Wallace *et al.* 2005). Most marine birds, reptiles and mammals studied employ oxygen conserving strategies while diving by swimming at moderate speeds with extensive gliding and adjusting stroke frequency and/or amplitude to changes in buoyancy (van Dam *et al.* 2002; Lovvorn *et al.* 2004; Miller *et al.* 2004a; Williams *et al.* 2004; Watanuki *et al.* 2005; Hays, Marshall & Seminoff 2007). The optimal swimming speeds during dives for a range of marine mammals have been found to centre around 2 m s^{-1} (Videler & Nolet 1990) and the scarce data available suggest that deep diving birds, pinnipeds and cetaceans seldom exceed that speed (Costa, Croxall & Duck 1989; Fish & Hui 1991; Le Boeuf *et al.* 1992; Davis *et al.* 1999; Watanuki *et al.* 2003, 2005; Miller *et al.* 2004a; Williams *et al.* 2004; Tyack *et al.* 2006).

The problems of resource separation and cost of transport are especially acute for air-breathing animals that make deep foraging dives. The strategies adopted by these animals to maximize efficiency in prey capture might be expected to differ from those of animals that feed near the surface. Foraging strategies during deep breath-hold dives have been studied in some pinnipeds, such as Weddell seals *Leptonychotes weddellii* (Lesson) or elephant seals *Mirounga leonina* (Linnaeus), and large toothed whales such as sperm whales *Physeter macrocephalus* (Linnaeus) (Le Boeuf *et al.* 1992; Hindell *et al.* 1992; Kooyman & Ponganis 1998; Miller, Johnson & Tyack 2004b; Watwood *et al.* 2006). However, little is known about the foraging behaviour and swimming strategies of medium-sized deep-diving delphinids such as pilot whales (long-finned *Globicephala melas* Traill, and short-finned *G. macrorhynchus*, Gray). The diving patterns and vertical swimming speeds of beaked whales *Ziphius cavirostris* (Cuvier) and *Mesoplodon densirostris* (de Blainville) have been described recently (Tyack *et al.* 2006) and their size, comparable with pilot whales, suggests a potential similarity in diving capability. Both beaked whale species dive to great depths to forage, averaging 1070 and 835 m for Cuvier's and Blainville's beaked whales, respectively (Tyack *et al. op. cit.*). The scarce data available for long-finned pilot whales, the only pilot whale species for which data are available, show that they can dive to broadly comparable depths of 650 m (Baird *et al.* 2002), with a mean maximum dive depth of 600 m and maximum of 830 m (Heide-Jørgensen *et al.* 2002). However, the average foraging dive durations recorded from beaked whales, 58 min (Cuvier's) and 47 min (Blainville's) (Tyack *et al.* 2006), are much longer than the 15–21-min deep dives performed by long-finned pilot whales (Baird *et al.* 2002; Heide-Jørgensen *et al.* 2002; Nawojchik, Aubin & Johnson 2003). The diving behaviour of long-finned pilot whales led Heide-Jørgensen *et al.* (*op. cit.*) to suggest that this species has lower diving capabilities than other odontocetes of similar size or utilize a niche that requires less diving activity.

Extant tagging studies on pilot whales have used time-depth-recording tags (TDRs, Heide-Jørgensen *et al. op. cit.*, Baird *et al. op. cit.*) and so little is known about the sounds produced or three-dimensional movements made by this species while foraging at depth. The biosonar-based foraging behaviour of other free-ranging toothed whales has been shown recently (Johnson *et al.* 2004; Madsen *et al.* 2005; Johnson *et al.* 2008) to resemble that of echolocating bats (Griffin 1958). As in bats, the echolocation process in sperm whales (Gordon 1987; Madsen, Wahlberg & Møhl 2002a; Madsen *et al.* 2002b; Miller *et al.* 2004b), and Cuvier's and Blainville's beaked whales (Johnson *et al.* 2004; Madsen *et al.* 2005) comprises the emission of click trains used to search for, select and approach prey targets with rapid sequences of clicks, called buzzes, marking prey capture attempts. Echolocation has also been demonstrated in blindfolded pilot whales in captivity (Evans 1994), but nothing is known about how, or if, they may use biosonar to locate and capture prey in the wild.

Here we report data from acoustic and movement recording DTags (Johnson & Tyack 2003) deployed on short-finned pilot whales off Tenerife in the Canary Islands. Combining sound and motion data we show that, while the acoustic behaviour of deep foraging pilot whales is similar to that of other echolocating deep-divers, the tactics apparently used to capture prey at depth differ widely and include a surprisingly energetic behaviour for a breath-holding deep diving animal. We explore the ecological implications of these tactics for prey selection and energy investment in foraging.

Methods

A resident population of some 350 short-finned pilot whales along with transient visitors can be found off the south-west coast of Tenerife (Canary Islands) mainly in water depths from 800 to 2000 m (Heimlich-Boran 1993) and 1–8 km from the coast. Two tagging cruises were undertaken to study this population in the spring and autumn of 2003 using a 12-m motor-vessel, the Punta Umbría, with a total of nine good weather days for tagging.

Data were collected with multisensor DTags (Johnson & Tyack 2003) attached with suction cups, that recorded: (i) sound with 12–16-bit resolution and at sampling rates between 32 and 96 kHz, (ii) depth and (iii) orientation from triaxial accelerometers and magnetometers providing data on the pitch, roll and heading of the whale. Orientation and depth were sampled at 50 Hz and decimated to 5 Hz for analysis. Tracking and recovery of the tags were aided by a radio beacon embedded in the tag.

Sound recordings were analysed using *Matlab 6·5* (Mathworks) to determine the time and depth of vocalizations from the tagged whale. These were generally distinguishable from those produced by other whales on the basis of an increased low frequency content in the former and variations in the received level in the latter (Zimmer *et al.* 2005; Johnson *et al.* 2006). Pilot whale vocalizations during dives were broadly classified into tonal and pulsed sounds. The latter category includes long series of clicks with occasional buzzes, similar to those related to echolocation of prey in deep diving sperm whales and beaked whales (Johnson *et al.* 2004; Miller *et al.* 2004b; Madsen *et al.* 2005). Buzzes were easily distinguishable from regular clicks by their drastically reduced interclick-interval (ICI) and lower received level on the tag. To describe variation in the ICI, a supervised detection algorithm was used to locate 31 629 regular clicks from a subset of 21 of 59 deep (> 500 m) dives recorded from 12 whales.

The vertical component of swim velocity was computed by differentiating the depth signal and then applying a low-pass filter at 1 Hz to reduce sensor noise. Although swim speed can be estimated from the depth rate and the pitch angle of the whale, the reliability of the estimate decreases with declining pitch angles. Here we use the depth rate without pitch angle correction as a robust proxy for speed, accepting that this will lead to an underestimation of the swimming speed in most cases. Fluking motion appears in the sensor recordings as cyclic variations in the accelerometer signal. In order to extract fluking rate, the ventral-dorsal acceleration was differentiated and low pass filtered at 2 Hz to estimate the jerk. Individual fluke strokes were then identified in the estimated jerk as cyclic variations with peak-to-peak magnitude greater than 4 m s^{-3}, a threshold chosen by visual inspection of the signal. Fluking rate was estimated as the number of fluke strokes per 10 s bin. All data analyses and statistical tests were performed using *Matlab 6·5*.

Results

Tags were applied to 23 adult and subadult short-finned pilot whales yielding 90 h of tag recordings (29 h/10 whales in the spring, 61 h/13 whales in the autumn, maximum tag duration of 9 h). The tag recordings covered a time period from 8 h before sunset to 4 h after sunset (at 19.25 h in spring and 18.33 h in autumn, local time). Three additional deployments with attachments shorter than half an hour were not analysed.

Tagged whales performed a total of 192 dives reaching a maximum depth of 1019 m and with durations from 0·4 to 21 min. A dive was scored every time the depth record went deeper than 20 m (i.e. about four to six body lengths) to exclude brief shallow submersions between respirations. A sample dive profile is given in Fig. 1 and the durations of the 192 recorded dives are plotted against maximum depth in Fig. 2c. The dive-depth histogram in Fig. 2a is bimodal, with only three dives with depths between 375 and 525 m. Based on this gap in the distribution, we defined shallow and deep dives as those with maximum depth less than or greater than 500 m, respectively. The depth of the 59 deep dives fits a normal distribution (Lilliefords modification of K-S, $P >> 0·05$) centred at 738 m depth (SD 110 m). A similar result (L-K-S, $P >> 0·05$) holds if the three dives with intermediate depths are also included (for all dives > 370 m, the mean depth is 723 m, SD 126 m) indicating that the subsequent statistical results are robust to the precise definition of a deep dive.

Some dives contained short episodes of elevated vertical speed of up to 9 m s^{-1} that were accompanied by increases in the fluking rate and flow noise over the tag (Fig. 3). In order to identify these events in an objective manner, we examined the distribution of vertical speed during dives. Transients due to individual fluke strokes were smoothed by averaging the vertical speed over consecutive 10 s intervals (i.e. about five fluke strokes) starting at the beginning of each dive. The highest sustained vertical speeds were found to occur during minutes 2–4 of the descent and in the last 2–4 min of the ascent of deep dives (mean 2 m s^{-1}, SD 0·2), excluding the brief episodes of high vertical speed evident in Fig. 4 as isolated peaks. We therefore defined sprints as any interval of 10 s or more with a mean vertical speed greater than 3 m s^{-1}, i.e. 5 SDs greater than the mean sustained speed of 2 m s^{-1}. Applying this criteria to all dives, 49 sprints were located. We also noted three possible low-pitch-angle sprints identified on the basis of high fluking rates and flow noise but not vertical speed. These were not included in the analyses because of the inaccuracy of vertical speed as a proxy for swim speed at low pitch angles.

The presence or absence of sprints and buzzes in dives seems to be well predicted by two parameters as shown in Fig. 5: dive time with respect to sunset and maximum dive depth. During the day, deep dives contained few buzzes per dive (median of 1) but most of the sprints [39 of the 49 sprints occurred in 28 of the 40 daytime deep (DD) dives]. Sprints were performed by all but one of the tagged whales that performed deep dives during the day. In contrast, very few of the 71 shallow daytime dives contained buzzes ($n = 3$) or sprints ($n = 2$). Night-time dives contained markedly more buzzes, but sprints only occurred in three of 62 shallow dives

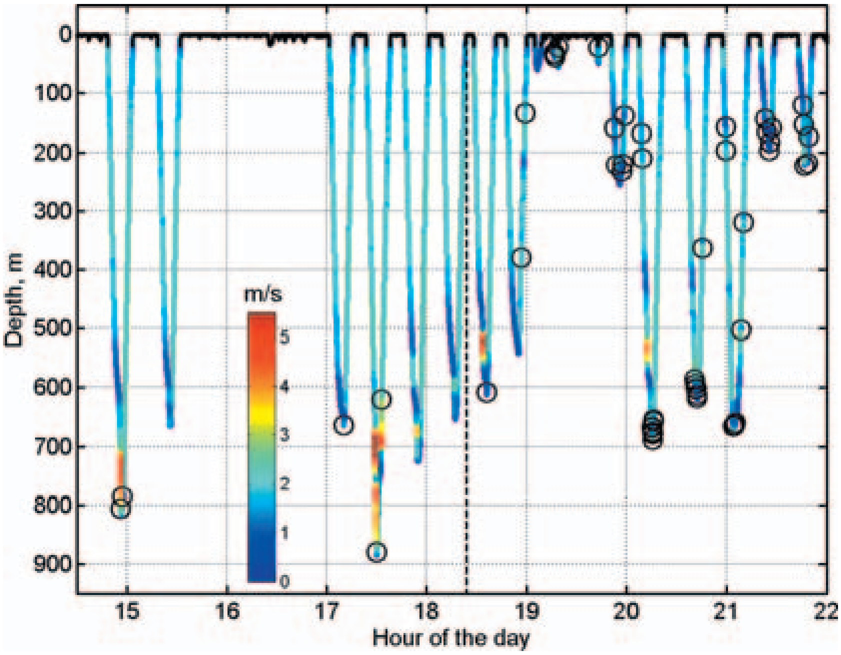

Fig. 1. Dive profile of a short-finned pilot whale (pw306b) tagged off Tenerife in the autumn of 2003. The colour of the line indicates the vertical speed (1 Hz averages), with a black line denoting depths < 20 m where vertical speed was not calculated. The vertical dotted line indicates sunset, which was at 18.20 h local time. A search phase with reduced descent rate at about 400–650 m depth is evident in most dives. Some of the deepest dives contained a burst of high speed swimming (a sprint) culminating in 0–2 buzzes (black circles) often marking the turning point of the dive.

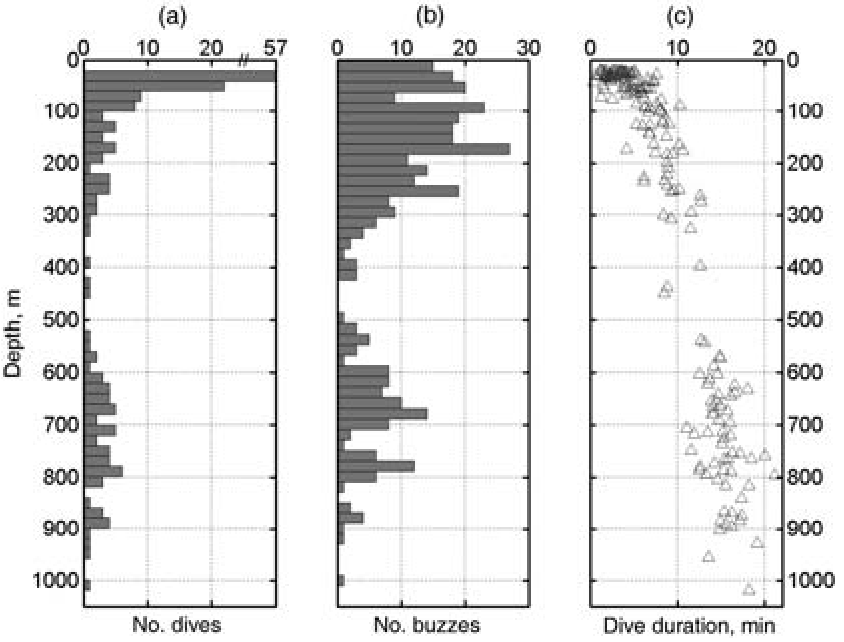

Fig. 2. Dive parameters for 192 dives > 20 m recorded from 23 short-finned pilot whales off Tenerife. (a) Maximum depth: the bars show the number of dives with maximum depth in each 20 m depth bin. (b) Number of buzzes recorded per 20 m depth bin. (c) Dive duration vs. maximum dive depth. Dives appeared to fall into two clusters according to their maximum depth with a notional boundary between shallow and deep dives at about 500 m depth.

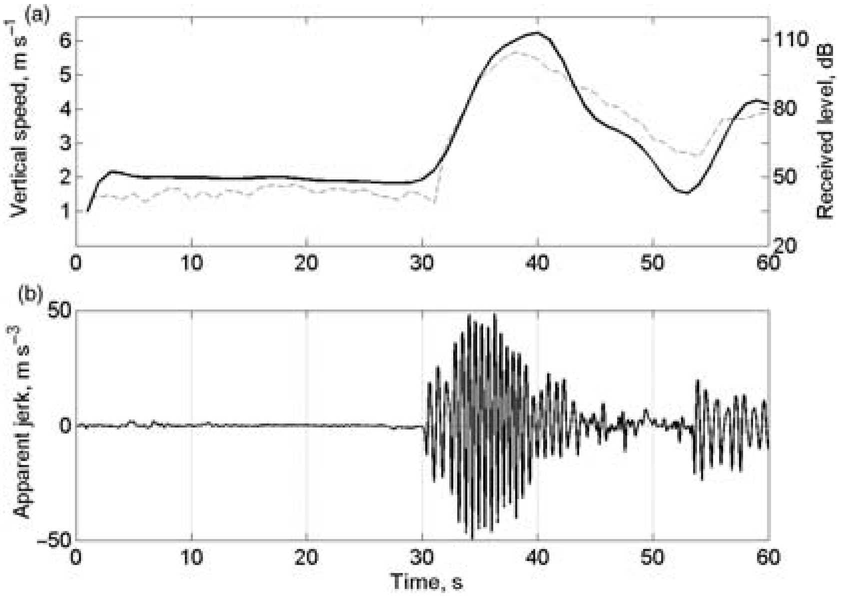

Fig. 3. Example of the relation between (a) vertical speed (continuous line) and flow noise over the tag (dashed line) during 60 s of data starting 30 s before the whale initiates an episode of high speed swimming, and (b) apparent dorsal–ventral jerk (i.e. the differential of the acceleration signal in the dorsal–ventral axis), which is related to the fluking rate and amplitude. The dramatic increase in vertical speed creates more flow noise around the tag and is achieved by a burst of high speed (1·8 flukes s^{-1}) fluking.

and five of 19 deep dives at night. Sprints were thus mostly restricted to deep dives with the majority being performed during the day (Table 1). DD dives with sprints had more buzzes than those without (Wilcoxon rank-sum, $P = 0{\cdot}02$, d.f. = 39; median buzzes/dive 1·5 in dives with sprints and 0 in dives without) suggesting a connection between these events. In contrast, no connection was seen between sprints and buzzes in night-time deep dives (same test, $P = 0{\cdot}76$, d.f. = 18).

THE DEEP DAYTIME FORAGING TACTIC OF RENERIFE PILOT WHALES

DD dives were performed by 14 of the 20 pilot whales tagged for more than one daylight hour, with an average rate of 0·7 DD dives per hour (40 DD dives in the 57 h recorded before sunset, individual data in Table 2). DD dives had a median duration of 15 min (11–21), maximum depths between 538 m and 1019 m (median: 762) and contained a median of 1 buzz per dive (0–4). Most buzzes were recorded near the deepest point of the dives, with a median depth difference of 18 m between the start of the buzz and the maximum depth of the dive (Fig. 6). The median depth of the buzzes was 744 m (3–1016).

The 39 sprints recorded in DD dives lasted a mean of 23 s (10–50) and 80% of them were directed steeply downwards, judging from the pitch recording, giving a mean increase in depth of 70 m (–121–203). The mean of the maximum vertical speeds recorded for each sprint (1 Hz bandwidth) was 6 m s^{-1},

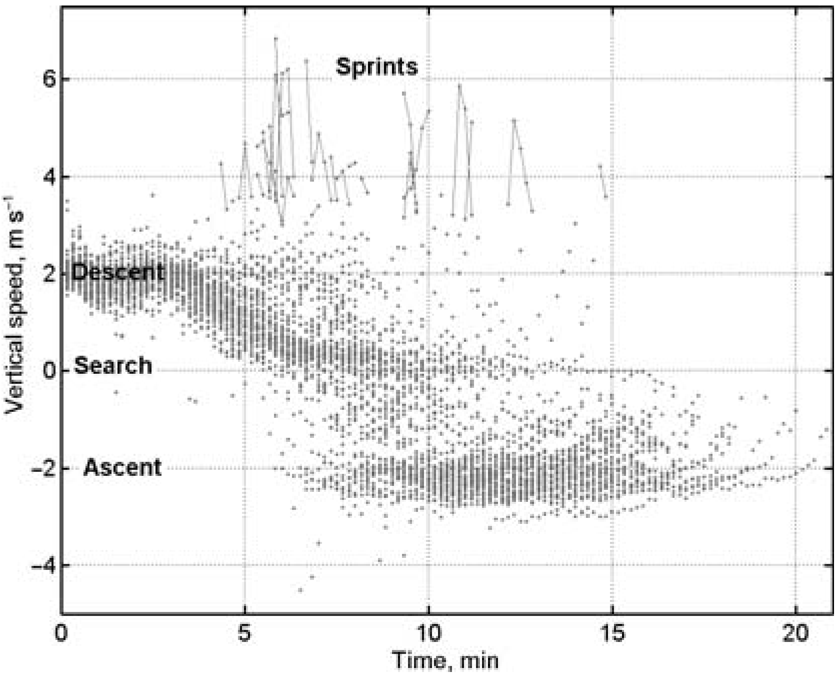

Fig. 4. Vertical speed vs. time averaged over 10 s bins during the 59 deep dives in the data set. Time 0 marks the beginning of each dive. Although there is some variation, most dives contain distinct descent and ascent phases and a slower search phase. The mean vertical speed during the first 4 min of descent in these dives (before most of the sprints) is 2 m s^{-1}. During the ascent the vertical speed averages 2·2 m s^{-1}. Sprints are apparent as high speed traces (drawn as lines for clarity) mostly occurring in the central, i.e. deepest, part of dives.

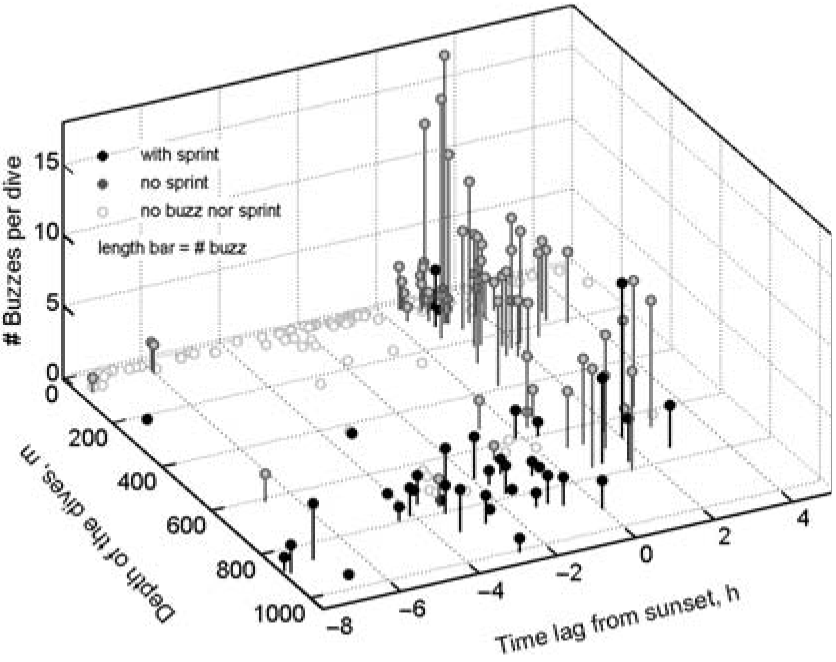

Fig. 5. Details of the 192 dives > 20 m recorded from the 23 tagged pilot whales. Dives are plotted by their maximum depth and start time with respect to sunset. The buzz count in each dive is indicated by the height of its bar (no bar means no buzz) and dives with no sprints and no buzzes are shown as empty circles in light grey. Dives with and without sprints are shown with circles filled in black and grey, respectively. It is evident that dives recorded before sunset have a lower number of buzzes than nocturnal dives while sprints tended to occur in the deep daytime dives, which are the deepest in the data set.

with an overall maximum of 9 m s^{-1}. The final depth of sprints was most often closely related to the maximum depth of the DD dives that contained them (Fig. 6) and dives with sprints tended to be deeper (median 800 m, SD 92, $n = 29$) than those without sprints (median 658 m, SD 70, $n = 12$) (Student's *t*, $P = 0$, d.f. = 38). However, the vertical speed during the ascent was positively correlated with the maximum depth of deep dives (Pearson, $r = 0·9$, $P = 0$), with the result that sprinting dives were not significantly longer than dives with no sprints (Student's *t*-test, $P = 0·35$, d.f. = 38).

RELATION BETWEEN SPRINTS AND BUZZES

As shown in Table 1 and Fig. 6, buzzes and sprints in DD dives tended to occur within a few tens of seconds of one another. To explore the relation between sprints and buzzes we analysed their temporal and depth co-occurrence in the 20 DD dives containing both events (in sum 27 sprints and 38 buzzes). The time lag from the end of each sprint to the start of the nearest buzz was measured together with the depth range covered by the whale over this sprint-buzz interval. The median time lag was 6 s (interquartile range, IQR: 11,

Table 1. Occurrence of sprints and buzzes in the 59 deep dives of the data set. The results show that the fraction of deep dives with buzzes that also contain sprints is much higher during the day (84%) than at night-time (28%)

Deep dives, *n* = 59		With sprint	Without sprint
Day, *n* = 40	With buzz	21	4
	Without buzz	7	8
	Mean number of buzzes per dive	1·5	0·6
Night, *n* = 19	With buzz	5	13
	Without buzz	0	1
	Mean number of buzzes per dive	4·8	5

Table 2. Details of the Dtag recordings obtained from 23 pilot whales in 2003 off Tenerife

		Tag hours					
Tag	Gen	Total	Day	No. DD (no. DD h^{-1})	Depth DD, m Mean (SD)	Length DD, min Mean (SD)	No. sprints per DD Mean (SD)
074a	♂	1·84	1·84	1 (0·5)	624 (0)	16·6 (0)	0
076a	I	2·63	2·63	0	–	–	–
076b	I	5·22	5·22	2 (0·4)	750 (77)	15·3 (1)	1·5 (1–2)
077a	I	0·87	0·87	0	–	–	–
077b	I	6·41	2·60	0	–	–	–
078a	♂	2·46	2·46	3 (1·2)	912 (42)	16 (1·2)	1·7 (1–2)
078b	♂	5·04	2·69	0	–	–	–
082c	I	0·69	0·69	1 (1·4)	892 (0)	15·5 (0)	1
082d	♂*	1·96	1·96	0	–	–	–
082e	I	2·06	2·06	2 (0·9)	815 (114)	15·6 (0·8)	0·5 (0–1)
Total spring	29·56	23.40	9 (0·4)	820 (112)	15·8 (0·9)		
306a	I	1·85	1·85	3 (1·6)	781 (20)	19 (2·6)	0·7 (0–1)
306b	I	9·27	4·29	6 (1·4)	735 (96)	14·8 (0·5)	0·7 (0–2)
306d	I	7·26	2·34	2 (0·9)	734 (186)	13·9 (2)	1 (1)
307a	I	5·58	1·55	1 (0·6)	869 (0)	16·2 (0)	1
307b	♂	4·74	1·31	0	–	–	–
307c	I	2·88	1·27	0	–	–	–
308a	I*	2·90	2·90	2 (0·7)	892 (179)	16.7 (2)	2 (1–3)
308b	♂	3·96	3·96	5 (1·3)	738 (122)	16 (1·1)	0·6 (0–1)
308c	♂	7·34	3·92	6 (1·5)	761 (96)	15·6 (2·7)	1·2 (0–4)
308d	I	1·31	0	0	–	–	–
309a	I*	2·12	2·12	0	–	–	–
309b	♂*	7·59	4·47	2 (0·4)	767 (26)	12 (0·7)	1·5 (1–2)
309c	♂	4·06	4·06	4 (1)	691 (109)	12.8 (0·7)	1 (0–2)
Total autumn	61·23	34·35	31 (0·9)	756 (105)	15.3 (2·4)		
Total	90·79	57·75	40 (0·7)	770 (109)	15.4 (2·1)		

Tag: code of the whale formed by the Julian day and a letter showing the serial order of tagging of the day. Gen: gender of the whale determined on the basis of characteristics of their body shape and size (Yonekura, Matsui & Kasuya 1980; Kasuya & Matsui 1984) as ♂ (adult male) or I (indeterminate, including adult females and subadult males or females). Tag hours: length in hours of the recording (both total and amount prior to sunset); DD, deep daytime dive.

*Whales for which genetic analysis of sloughed skin was performed to confirm the visual classification.

quartiles: 2 and 14), and only three of the 28 intervals exceeded 60 s. The median vertical separation between the end of the sprint to the start of the nearest buzz was 5 m (IQR: 10, quartiles: –6 and 4), with only four pairs separated in depth by more than 26 m. Thus, some 24 of the 28 sprints in DD dives were closely followed by a buzz in time and space, supporting the hypothesis that, if buzzes are associated with attempts to capture prey, then the combination of sprint-buzz is also. The remaining four sprints that were not followed closely by buzzes had their nearest buzz some 100–400 m shallower, during the ascent. These sprints may, along with the sprints in another 7 DD dives without any buzzes, represent failed capture attempts, given that they start at similar depths as do buzz-related sprints.

DIVE PROFILE

The presence of a sprint just prior to the deepest point in many DD dives (Fig. 6) contributes to the distinctive dive profile for these dives shown in Figs 1 and 7. Although there are numerous variations, the typical pattern involved three phases.

1. *Initial descent*: the steep descent from the surface is performed at a vertical speed of about 2 m s^{-1} but with very little

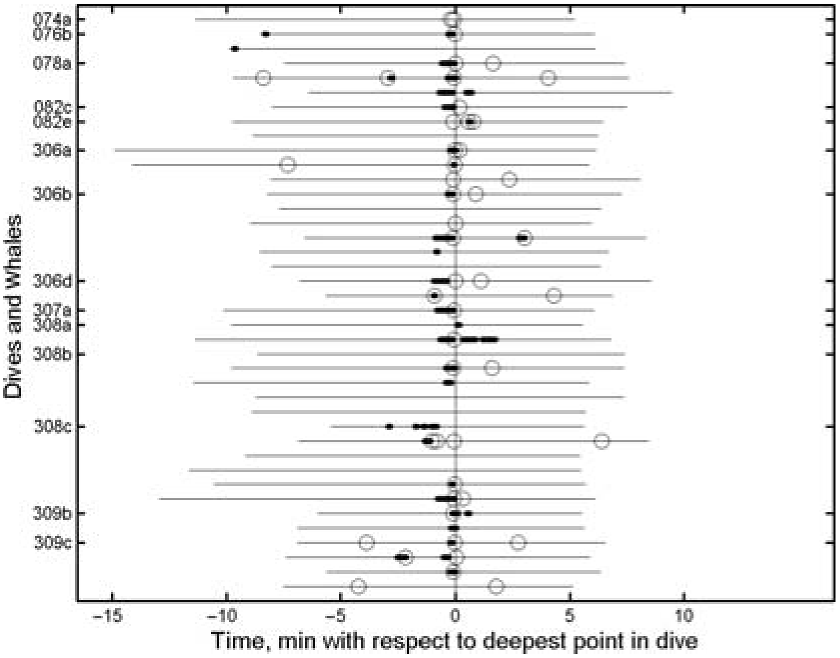

Fig. 6. Occurrence of buzzes (48 circles) and sprints (thickened black lines) with reference to the maximum depth (vertical central line) of each of 40 deep daytime dives made by 14 of the 23 tagged whales. Each horizontal line represents a dive, with the time at which it reaches the maximum depth aligned at the 0 in the abscissa. The codes of the whales making each dive or set of dives are represented in the ordinates. Each whale made one to six deep daytime dives.

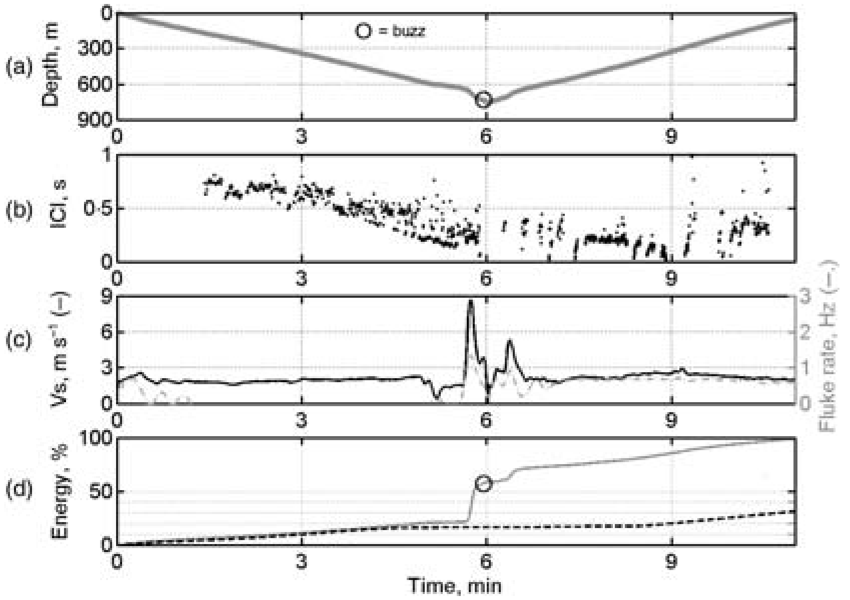

Fig. 7. Detailed view of a daytime deep dive with a sprint. (a) Dive profile with the buzz shown by a circle. (b) Inter-click interval (ICI) throughout the dive (the few clicks with ICI > 1 s are not shown). (c) Vertical speed, black dashed line, showing the maximum recorded speed of 9 m s^{-1}, and fluking rate of the whale extracted from the acceleration, grey line. (d) Relative cumulative energy spent in drag-related locomotion cost as a function of time for the same dive (continuous grey line) and for another deep dive of similar duration that did not contain sprints (dashed black line). The cumulative cost is approximated by integrating the cube of the vertical speed. In both dives the cumulative energy is normalized to the maximum of the sprinting dive. The circle marks the time of the only buzz recorded in the two dives. Note in (c) the short period of fast fluking during the sprint and the difference in fluking effort required during descent (almost zero after an initial period of fluking near the surface) and ascent (a 4-min interval of 0·7 Hz fluking).

fluking effort. A short interval of continuous fluking is required to travel the first some 100 m from the surface but isolated fluke strokes suffice thereafter to maintain downward motion (Fig. 7c). Few clicks are produced, indicating that little effort is invested in echolocation. This phase extends to a typical depth of 300–400 m.

2. *Search and attempt to capture*: regular clicking begins at some 300–400 m depth during the descent, with a pattern of long series of clicks separated by short pauses. The ICI is initially long at about 0·6 s and decreases to some 0·2 s as the whale descends, suggesting that the whale is adjusting the timing of its sonar clicks to search for prey in a given depth layer (see similar observations in sperm whales: Zimmer *et al.* 2003; Thode 2004). In this phase the pitch angle of the whale gradually reduces accompanied by a decrease in vertical speed, flattening out the dive profile at about 500–600 m. Most of the deeper dives included sprints, which were usually followed by one or more buzzes. All but eight sprints occurred in a downwards, nearly vertical orientation. In dives with neither sprints nor buzzes (18%), the slow descent phase transitions directly into the ascent with no acceleration at the bottom of the dive (e.g. dive 3 in Fig. 1).

3. *Ascent*: the ascent is defined as starting after the deepest point of the dive. The ascent is made at fairly constant vertical speed averaging 2·2 m s^{-1} (SD 0·2) maintained with nearly continuous fluking. As in the initial descent, clicking is sporadic with interspersed tonal sounds.

Discussion

Numerous species of birds, reptiles and mammals dive to forage (Kooyman 1989) and several penguins, pinnipeds and cetaceans exploit deep water prey (e.g. Kooyman *et al.* 1980; Le Boeuf *et al.* 1988; Castellini, Kooyman & Ponganis 1992; Kooyman & Kooyman 1995; Burns *et al.* 2004; Tyack *et al.* 2006; Watwood *et al.* 2006) below the photic zone. Search and foraging behaviours of animals are governed by their sensory systems and locomotor capabilities (Bell 1991). The scarcity of light in the mesopelagic habitat may have led deep diving toothed whales, with an acute hearing sense, to rely on echolocation as their primary means to locate and catch prey at depth, although vision may be used to detect bioluminescent prey. Studies on biosonar foraging by free-ranging sperm and beaked whales (Johnson *et al.* 2004; Miller *et al.* 2004b; Madsen *et al.* 2005) have shown that these species use long series of clicks to echolocate prey during deep dives, while capture attempts are marked by short series of clicks emitted at high repetition rate (so-called creaks or buzzes). Here we have shown that short-finned pilot whales off Tenerife dive deep to forage during day and night producing click and buzz sounds consistent with biosonar-based foraging. As all of the tagged pilot whales produced clicks throughout the deepest part of deep dives, we surmise that echolocation is a dominant mode of prey location in deep foraging.

Predator–prey interactions shape the searching and hunting techniques of top predators (Bell 1991; Scheel 1993; Begon, Harper & Townsend 1999) and their hunting behaviours when foraging in similar habitats reflect their adaptation to different niches. Short-finned pilot whales foraging in the same depth range as sperm and beaked whales (Aguilar de Soto 2006) perform the most energetic hunting tactic that has been recorded until now in breath-hold deep divers. This stereotyped behaviour involves an energetic burst of high speed swimming, up to 9 m s^{-1}, near the deepest part of the dive and is usually followed closely by one or two buzzes, which we take as indicating attempts to capture prey. This foraging pattern is remarkable for two reasons: (i) it is quite different from the stereotyped long dives described for other deep-diving echolocating cetacea (Johnson *et al.* 2004; Tyack *et al.* 2006; Watwood *et al.* 2006), and (ii) the energetic sprints are surprising given the expectation that deep-diving breath-holding animals would conserve oxygen by slower steady swimming (Kooyman 1989; Fedak & Thompson 1993; Williams *et al.* 1999; Wilson & Liebsch 2003; Reina *et al.* 2005; Wallace *et al.* 2005). Hereon we explore the hypothesis that sprinting forms a key component of day time deep foraging in pilot whales off Tenerife and examine some of the ecological and energetic implications of such a highly specialized foraging tactic for a deep diving mammal.

THE DEEP DAYTIME FORAGING TACTIC

The deep night-time dives of pilot whales are broadly similar to, although shorter in duration than, those described from sperm and beaked whales (Watwood *et al.* 2006; Tyack *et al.* 2006), involving steady swimming and multiple prey capture attempts on most dives. In contrast, the daytime sprinting tactic of Tenerife pilot whales stands out in comparison with the behaviour of other deep diving, echolocating whales. Sperm whales and beaked whales have been reported to make long (40 min to > 1 h) deep foraging dives containing some 20–50 prey capture attempts per dive (Tyack *et al.* 2006; Watwood *et al.* 2006) but with no indications of high speed swimming. Despite diving capabilities being broadly related to body mass (Kooyman 1989; Mori 2002), beaked whales routinely perform dives similar in depth and duration to those of the much heavier sperm whale. Blainville's beaked whales, deep divers of similar size to pilot whales, were tagged off El Hierro in the Canary Islands and found to forage at similar depth ranges as short-finned pilot whales off Tenerife (Aguilar de Soto 2006). However, Blainville's beaked whales try to capture some 30 prey items in deep foraging dives lasting on average 40 min, while pilot whales perform deep dives that are less than one-half the duration and contain on average only 2·4 buzzes (1·2 during the day). This comparison made in a broadly similar area, the Canary Islands, supports the idea that pilot whales employ a highly specialized tactic, particularly during DD dives, in which only a few items are selected from a probable much wider range of possible prey.

The DD diving foraging tactic involves a consistent suite of echolocation and movement behaviours. Whales start clicking early in the descent, progressively increasing the production rate of clicks as they descend, presumably in sympathy with the reducing distance to the depth layer at which prey are located as has been reported for some other odontocete species (Zimmer *et al.* 2003; Thode 2004; Akamatsu *et al.* 2005). The speed of descent is constant until about 500–600 m depth at which point the pitch angle and vertical speed gradually reduce. In dives with sprints, the sprint frequently follows this interval of slower descent and is most often directed vertically downwards. This behaviour resembles the hawking tactic employed by some species of echolocating bats (Holderied *et al.* 2005) or by birds of prey hunting by vision (Hedenstrom *et al.* 1999) in which a slow or stationary search for prey is followed by a fast capture attempt functionally comparable with the sprints of the pilot whales.

If this is the correct interpretation, the preferred search position for pilot whales appears to be above the expected depth of prey allowing the whale to search a greater area than it could from within the prey layer while saving transport cost in the event that a suitable prey is not found. Some 40% of deep dives performed during the day contain regular echolocation clicks but neither buzzes nor sprints, probably representing a failure to locate a suitable prey item. These dives tend to be shallower, but not shorter, than those with prey capture attempts, presumably reflecting a longer search phase in the case of unfruitful dives. Optimal dive duration models (Mori 1998; Thompson & Fedak 2001) predict that deep divers, having invested a long time travelling from the surface to the foraging depth, should maximize the duration of the bottom search in spite of low prey densities.

There are exceptions to the apparent tactic of low-pitch-angle search followed by downward-directed sprint. A few sprints are performed while ascending. In other cases the whale does not slow its descent before sprinting and/or buzzing (e.g. dive 1 of Fig. 1), suggesting that the whale may detect prey occasionally during the initial descent and proceed directly towards them. None the less, the pattern of low-pitch search followed by sprinting occurs in some 55% of DD dives and is performed by 12 of the 14 tagged whales that dive deep during the day (52% of all tagged whales) leading us to propose that this is a common foraging behaviour of Tenerife pilot whales.

Locomotion cost of sprints: how to pay the bill?

If sprints are an important component of DD foraging by short-finned pilot whales off Tenerife, then the energy outlay and potential reward of this behaviour should be considered. Although lack of data on the drag coefficient and metabolic rate of pilot whales prevents absolute calculation of the cost of sprinting, we propose a simple conservative model to estimate the minimum cost of locomotion during sprints in relation to the total locomotion cost of a dive. This model quantifies only the energetic cost associated with the increase in drag force at sprinting speeds during the dive. Under the conservative assumption that the drag coefficient of a pilot whale (Δ) is constant over a range of swimming speeds up to and including sprints, the drag force increases with the square of the swimming speed, V (Vogel 1994). Neglecting gravitational forces, the power required to swim scales with the cube of the speed, and the cost of locomotion (CL) can be approximated by $CL \approx \Delta \int V^3 dt$ (Hind & Gurney 1997; Fish 2002). For a whale that makes a sprint of duration t_s seconds in a dive of total duration t_d s, the cost of locomotion of the sprint, CL_s, relative to that during the full dive (CL_d) can be estimated as:

$$\frac{CL_s}{CL_d} \approx \gamma / \left(\int_{t_s} |V|^3 dt \right) \left(\int_{t_d} |V|^3 dt \right)^{-1}$$

For the 28 DD dives with sprints, this ratio averaged 22% (SD 9, range 10–36%) although the time invested in sprinting per dive was on average only 3% (26 s, SD 17, range 19–79 s) of the mean deep-dive duration (15 min). The mean vertical speed of 4 m s^{-1} (averaging over 10 s intervals) during the sprints involves some eightfold increase in power as compared with the mean sustained vertical speed during nonsprinting portions of deep dives (2 m s^{-1}). The use of vertical speed as a proxy for swim speed introduces some error when comparing the cost of sprinting and nonsprinting portions of a dive. However, as steep pitch angles are adopted during much of the descent and ascent of deep dives as well as during sprints, it is only the transport cost associated with the low-pitch-angle search phase in DD dives t-hat will be greatly underestimated. As apparent in Figs 1 and 7, the portion of DD dives spent at a low pitch angle is small and so the accumulated error is unlikely to be large. Certainly, the dramatic increase in power required to overcome drag during sprints means that, despite their short durations, sprints represent a significant energetic investment in a foraging dive.

Bursts of high speed in terrestrial animals, such as cheetahs *Acinonyx jubatus* (Schreber), typically require the use of anaerobic pathways (Williams *et al.* 1997). Such exercise has been found to increase the postexercise oxygen consumption, e.g. by up to 90% in rodents (Baker & Gleeson 1999), suggesting that the total energetic cost of sprinting in pilot whales might be larger than our simple model estimates. Moreover, adaptation for fast sustained speeds incurs the cost of an increased overall metabolic rate (Dickson 1995; Katz 2002; Chappell *et al.* 2004). If pilot whales have a higher metabolic rate than other deep-diving mammals to enable sprinting, this would be an additional factor influencing the relatively short duration of pilot whale dives (15 min) when compared with marine mammals of similar or smaller size (e.g. Weddell seal, Kooyman 1989). This apparent lower diving capability, also observed in long-finned pilot whales (Heide-Jørgensen *et al.* 2002), may stem from the physiology of a high performance athlete with an emphasis on speed at the expense of dive duration.

CAUSES AND ECOLOGICAL IMPLICATIONS OF SPRINTS

While it cannot be excluded that predator avoidance or other exogenous stimuli may explain some of the sprints performed by pilot whales, they generally seem to be closely linked with foraging. The combined acoustic–orientation data show a highly stereotyped behaviour with buzzes, similar to those associated with prey capture attempts in other echolocating species (Griffin 1958; Miller *et al.* 2004b; Madsen *et al.* 2005), happening on average very close in depth to, and only a few seconds after, the sprints. Some terrestrial carnivores, such as cheetahs (e.g. Hunter, Durant & Caro 2007) target large and energetic prey that are skilled at detecting and evading predators. These felines may pay a high energy cost for each chase and may fail often but are compensated by the high nutritional value of the prey (Caro 1994; Bothma & Coertze 2004) in a typical carnivore strategy (Carbone, Teacher & Rowcliffe 2007). Some 40% of the DD dives of the tagged pilot whales did not contain buzzes, although nearly half of these dives contained sprints at depth, suggesting that the whales did not find a suitable prey or that the prey was successful in avoiding the capture.

If pilot whales are balancing energy investment and calorific uptake by selecting a few highly calorific prey items that require considerable energetic investment to catch, and that seem to be capable of avoiding the whales in some cases, then this suggests that the prey chased during sprints have muscle power and agility. Prey must also have sufficient calorific content to render the sprints profitable. Some of the prey species found in the stomach contents of pilot whales in the Canary Islands (Hernandez-García & Martín 1994) such as the ommastrephid *Todarodes saggitatus* (Lamarck) or the lepidotheuthid *Lepidoteuthis grimaldii* (Joubin), fit these requirements. These species can reach lengths of 75 and 97 cm, respectively (Nesis 1982; Roper, Sweeney & Nauen 1984) and are active swimmers with muscular mantles. Muscular squid have relatively high calorific contents of about 4·5 kJ g^{-1} wet mass (Clarke *et al.* 1985) comparable with that of fish (Doyle *et al.* 2007), have higher relative contents of protein (Lee 1994), can move rapidly, and make good targets for echolocation (Madsen *et al.* 2007). Although there are scarce data on the maximum burst speed of deep-diving cephalopod species, some muscular ommastrephids have been recorded to reach 7–10 m s^{-1} (Nixon & Young 2003) at the surface. Hence the high absolute energy content of large squid can compensate the cost of sprints, while the ability for fast swimming of the prey makes them necessary.

A tantalizing indication of another possible large prey target during DD dives is the common finding of freshly severed pieces of giant squid *Architeuthis dux* (Steenstrup) floating in the main area of distribution of the pilot whales. Although beaks of very large squid such as *Architeuthis* have not been found in the two stomach contents analysed from the Canary Islands, pilot whales have been observed regurgitating beaks of cephalopods off Tenerife and in other places (Hernandez-García & Martín 1994) and they may also not eat the entire prey. In any case, there is evidence that a part of the diet of short-finned pilot whales is composed of large and calorific prey capable of moving fast, matching the energetic foraging strategy reported here. We suggest that the sprints, which appear to challenge the common view on optimal foraging in breath-holding, deep-diving predators, reflect a high-cost foraging strategy that is necessary to capture high-value, evasive prey. This athletic hunting tactic is comparable with that used by some terrestrial mammals (Scheel 1993; Caro 1994) and probably requires similar physiological adaptations as observed in other speed specialists such as cheetahs (Williams *et al.* 1997), allowing pilot whales to broaden the niches available for marine mammals in deep-water ecosystems.

Acknowledgements

Thanks to P. Aspas, J. Gonzalez, C. Aparicio, M. Guerra, A. Hernández and V. González Otaola for help in data collection, to T. Hurst and K. A. Shorter for tag engineering, and to A. Guerra for helpful comments on cephalopod swimming abilities and calorific content. We are very grateful for the thoughtful comments of B. Wurzig, G. Hays, and an anonymous reviewer. Work was supported by SERDP (program CS-1188) and NOPP in the USA, and by the Canary Islands Government-Spanish Ministry of Defence. Research was conducted under a permit to La Laguna University from the Government of the Canary Islands. Research was approved by the Woods Hole Oceanographic Institutional Animal Care and Use Committee.

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Received 23 December 2007; accepted 30 January 2008
Handling Editor: Graeme Hays