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Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*)

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Summary

1. Digital tags were used to describe diving and vocal behaviour of sperm whales during 198 complete and partial foraging dives made by 37 individual sperm whales in the Atlantic Ocean, the Gulf of Mexico and the Ligurian Sea.

2. The maximum depth of dive averaged by individual differed across the three regions and was 985 m (SD = 124·3), 644 m (123·4) and 827 m (60·3), respectively. An average dive cycle consisted of a 45 min (6·3) dive with a 9 min (3·0) surface interval, with no significant differences among regions. On average, whales spent greater than 72% of their time in foraging dive cycles.

3. Whales produced regular clicks for 81% (4·1) of a dive and 64% (14·6) of the descent phase. The occurrence of buzz vocalizations (also called 'creaks') as an indicator of the foraging phase of a dive showed no difference in mean prey capture attempts per dive between regions [18 buzzes/dive (7·6)]. Sperm whales descended a mean of 392 m (144) from the start of regular clicking to the first buzz, which supports the hypothesis that regular clicks function as a long-range biosonar.

4. There were no significant differences in the duration of the foraging phase [28 min (6·0)] or percentage of the dive duration in the foraging phase [62% (7·3)] between the three regions, with an overall average proportion of time spent actively encountering prey during dive cycles of 0·53 (0·05). Whales maintained their time in the foraging phase by decreasing transit time for deeper foraging dives.

5. Similarity in foraging behaviour in the three regions and high diving efficiencies suggest that the success of sperm whales as mesopelagic predators is due in part to long-range echolocation of deep prey patches, efficient locomotion and a large aerobic capacity during diving.

Key-words: diving behaviour, echolocation, foraging behaviour, *Physeter macrocephalus*, sperm whales.

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Introduction

Aquatic reptiles, birds and mammals that feed underwater but must breathe at the surface make decisions about how best to dive to acquire prey within the constraints of a finite oxygen supply. The interaction between diving physiology and foraging strategies of pinnipeds and seabirds has been explored for decades (Kooyman & Ponganis 1998; Butler 2004), but much less is known about the foraging behaviour of deep-diving toothed whales (Kooyman & Ponganis 1998). The largest deep-diving toothed whale is the sperm whale *Physeter macrocephalus* (Linnaeus), a cosmopolitan species that forages in mesopelagic and benthic habitats, primarily targeting cephalopods (Clarke 1980; Kawakami 1980), but occasionally also fish (Clarke, Martins & Pascoe 1993). The yearly turnover of biomass by sperm whales is estimated to be comparable to the

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total catches of human fisheries, and the impact of sperm whales on deep ocean food webs and nutrient cycling in the ocean is probably significant (Clarke 1976; Kanwisher & Ridgway 1983; Whitehead 2003). However, little is known about how and at what depth this large, air-breathing predator locates and captures its prey.

The diving behaviour of sperm whales has been studied previously using visual observation (Clarke 1976; Whitehead & Weilgart 1991; Whitehead 2003), transponder tags (Watkins *et al*. 1993), radio and satellite tracking (Watkins *et al*. 1999), acoustic localization of individual vocalizations (Watkins & Shevill 1977; Wahlberg 2002) and sonar tracking (Lockyer 1977; Papastavrou, Smith & Whitehead 1989). These studies have reported that sperm whales dive to depths of 400–1200 m (Watkins 1980; Papastavrou *et al*. 1989; Watkins *et al*. 1993; Amano & Yoshioka 2003) and for durations of up to 138 min (Watkins, Moore & Tyack 1985). The majority of sperm whale dives have been reported to last from 33 to 53 min (Mullins, Whitehead & Weilgart 1988; Papastavrou *et al*. 1989; Watkins *et al*. 1993; Jaquet, Dawson & Slooten 2000; Amano & Yoshioka 2003). Due to the difficulty of observing sperm whales during their long, deep dives, little is known about their subsurface behaviour, giving rise to an array of speculations on how sperm whales find prey, including luring (Beale 1839; Gaskin 1964), touch (Tomlin, 1936, cited in Berzin 1972), passive listening (Sleptsov 1952, cited in Berzin 1972), echolocation (Backus & Schevill 1966) and vision (Fristrup & Harbison 2002).

One obstacle to studies of foraging behaviour in diving animals is determining precisely when foraging events occur during a dive (Ropert-Coudert *et al*. 2002). Sensors measuring stomach or oesophagus temperature or mouth-opening events are not feasible with sperm whales because of the required handling of the animal for device attachment and calibration, and underwater cameras have limited utility in dark conditions at depth. Here we make use of an alternate indicator of feeding events, echolocation buzzes (Miller, Johnson & Tyack 2004a). The vocalizations and movements of sperm whales during foraging dives follow the pattern observed in beaked whales and bats, where echolocation behaviour has been described more completely. The foraging behaviour of Blainville's beaked whales *Mesoplodon densirostris* (de Blaineville) and insect-eating bats (suborder Microchiroptera) involves three stages: searching for prey, selecting and approaching a particular prey item and finally capturing the prey item (Schnitzler & Kalko 2001; Madsen *et al*. 2005). Sperm whale regular clicks have properties suited for detection of cephalopod prey, such as high directionality, high source levels and frequencies around 15 kHz suitable for long-range sonar (Møhl *et al*. 2003). Modelling with the sonar equation suggests that sperm whales could detect cephalopod prey patches at a maximum range of more than 500 m (Madsen, Wahlberg & Møhl 2002; Møhl *et al*. 2003; Zimmer *et al*. 2005). In the capture phase for beaked whales and bats, the interclick interval, amplitude and signal duration decrease dramatically and suddenly to give rapid updates on the location of the prey just before capture. In bats, the repetition rate of signals during the capture (terminal) phase is so high that it has been named the terminal buzz (Griffin 1958), and the analogous signal in beaked whales has also been termed a buzz (Johnson *et al*. 2004). In sperm whales there is a similar transition from regular clicking to brief periods of rapid clicking, termed creaks (Madsen *et al*. 2002; Miller *et al*. 2004a). Miller *et al*. (2004a) found that peaks in the movement of tagged sperm whales coincided with creaks and concluded that these marked the terminal phase of echolocation-mediated foraging. We will therefore refer hereafter to creaks by their functional term (buzzes) rather than their descriptive name (creaks, *sensu* Martin & Bateson 1993).

As with any proxy, taking buzzes as indicative of prey capture does not guarantee that every buzz signifies a capture nor that prey items are not ingested without a buzz (Wilson & Culik 1995; Plötz *et al*. 2001). The proxy does rely on the assumption that sperm whales use echolocation to locate and capture prey. As for all other toothed whales (Au 1993), the data on diving sperm whales support overwhelmingly the echolocation hypothesis (Møhl *et al*. 2000; Jaquet, Dawson & Douglas 2001; Madsen *et al*. 2002; Møhl *et al*. 2003) and Miller *et al*. (2004a) calculated that the number of buzzes during dives was consistent with the estimated daily prey intake for sperm whales. We therefore conclude that this technique, which is practical for a wild, non-capturable animal, does give an adequate proxy of timing and depth of foraging activity. Recording vocalizations of diving sperm whales therefore presents a non-invasive opportunity to document feeding activity.

In this paper we analyse data collected by non-invasive, digital archival recording tags that were deployed on sperm whales in three different locations: the north-western Atlantic Ocean, the Gulf of Mexico and the Ligurian Sea. We demonstrate that sperm whales employ a stereotypical foraging behaviour involving on average 45-min dives to exploit food patches at 400–1200 m depth. The whales produced echolocation clicks and initiated many capture attempts during all deep dives analysed, showing that sperm whales are effective in finding food patches. We demonstrate that sperm whales have a high diving efficiency and conclude that the global distribution of this species may relate to the combination of efficient food location with a long-range biosonar, efficient locomotion and a large aerobic capacity for repeated, long foraging dives.

Materials and methods

Sperm whales were tracked from a research vessel in the Gulf of Mexico (R/Vs *Gordon Gunter*, *Gyre* and *Ewing*; July 2000, July 2001, August–September 2002 and June 2003), the Atlantic Ocean (R/V *Delaware*; July 2003) and the Ligurian Sea (R/V *Alliance*; September

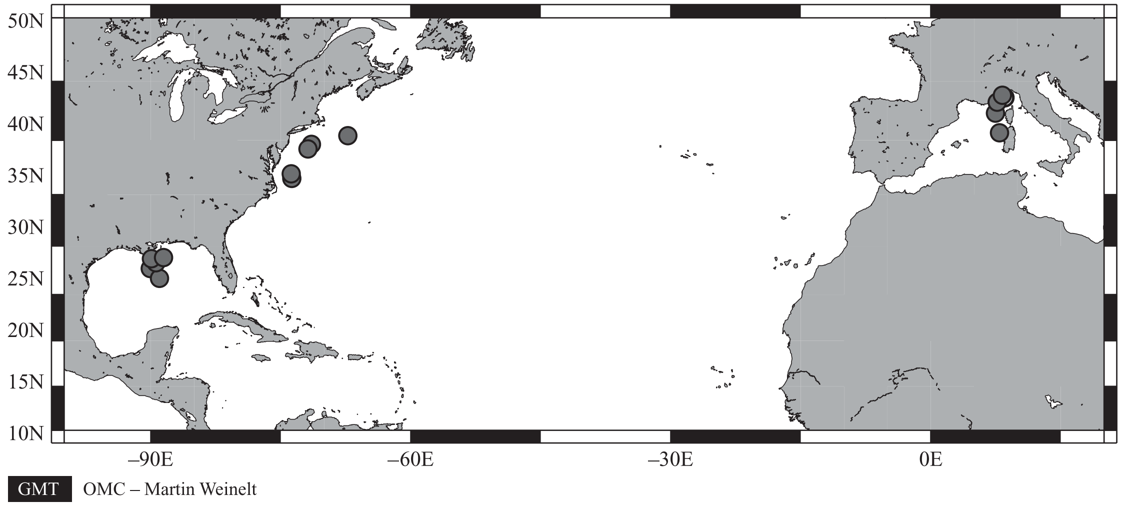

Fig. 1. Locations of tagging events.

2000, September–October 2001, July 2002, September 2003). Figure 1 shows the locations of tagging events, which were chosen for logistical reasons. Dtag acoustic recording tags (Johnson & Tyack 2003) were brought close to sperm whales using a 12–15 m pole mounted in a small boat and were attached to the dorsal surface of whales with suction cups (Johnson & Tyack 2003; for details of tag attachment, see Miller *et al.* 2004b). The dtags sampled acoustic data at 16 kHz (2000), 32 kHz (2001–June 2003) or 96 kHz (June 2003–September 2003) with either a 12-bit or 16-bit analogue-to-digital converter. The pressure data from the depth sensor were converted to metres using calibrated values. The data from the three-axis magnetometers and accelerometers were converted to heading, pitch and roll using the techniques described in Johnson & Tyack (2003) and Miller *et al.* (2004b).

Whales were tracked acoustically with a towed hydrophone array, allowing the observation vessel to remain an average of 2·1 km (0·9) (range 0·8–5·1 km) away from surfacing tagged whales. Two of the ships used as follow vessels (RVs *Gordon Gunter* and *Alliance*) used diesel–electric propulsion and so were quiet by design, and therefore probably caused little additional disturbance. Tags were carried for 2·9 h (1·6) in the Atlantic Ocean, 6·5 h (7·0) in the Gulf of Mexico and 6·3 h (4·0) in the Ligurian Sea. The majority of tags were deployed in the morning or early afternoon and were retrieved in the evening. Therefore, diurnal variation in diving and foraging behaviour will not be addressed in this study.

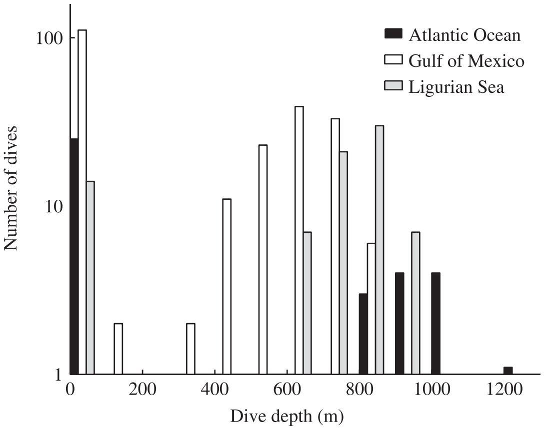

Fig. 2. Histogram of dive depths for 344 dives from 37 sperm whales in the Atlantic Ocean, Gulf of Mexico and Ligurian Sea.

DIVE CHARACTERISTICS

The dives made by sperm whales fell into two categories: dives < 150 m (shallow dives) and dives > 300 m (deep dives; Fig. 2). In total, 229 complete deep dives were recorded from 49 dtag attachments. Eight partial dives, in which the dtag released from the animal during the bottom phase of a dive, were included for analyses of descent parameters. Based upon genetic analysis of skin retained in suction cups two whales were found to have been tagged twice, and we pooled the data for each individual. Data from four tagged whales that did not dive below 300 m were included for calculation of the percentage of time spent in foraging dives. Whales carried dtags for an average of five deep dives per animal (5·2) (range 1–27), with fewer dives per individual recorded from animals in the Atlantic Ocean and more dives per individual in the Ligurian Sea. As the first dive made by sperm whales immediately after tagging is shorter than subsequent dives (Miller *et al.* 2004a), we removed the first dive in each dive record from the analysis if it began within 30 min of tagging. Six animals were excluded from analysis as only one dive immediately following tagging was recorded on the dtag. Therefore, all analyses of foraging dives are based on 190 complete and eight partial dives from 37 animals.

Dive periods were divided into four phases: surface phase, descent phase of dive, bottom period of dive and ascent phase of dive (Fig. 3). The descent phase was defined as starting when the whale fluked out and ending when the whale's pitch first became positive (the whale was no longer orientated downwards). The ascent was defined as starting when the whale was last orientated downwards (pitch < 0°) and ending when the whale reached the surface (Miller *et al*. 2004b). The bottom phase of the dive contained the time between the end of the descent and the beginning of the ascent. The surface phase lasted from when the whale reached the surface after a deep dive until the following dive to greater than 10 m, i.e. greater than approximately one body length. The percentage of time within 10 m of the surface was recorded. Swim speed was calculated as the average vertical velocity divided by the average of the sine of the pitch angle.

VOCALIZATIONS

In this study of foraging during deep dives, we focused on the behavioural context of regular clicks and buzzes. Clicks produced by the tagged animal were identified by their consistent waveforms and high amplitudes. Given the echolocation potential of each click, sperm whales were scored as searching actively for prey during the period between the first and last regular click produced during a dive. As outlined above, buzzes can be considered evidence of a close approach to a prey item and so minimally represent prey capture attempts, and most probably capture events (Miller *et al*. 2004a). We defined the period from the first to last buzz recorded during a dive to be when sperm whales were actively encountering prey items. We termed this the 'foraging' phase, and to determine the general timing of prey capture within a dive, we considered this active foraging phase a continuous state. Diving efficiency was calculated as the fraction of the dive cycle in the foraging phase, i.e. diving efficiency = foraging phase duration/(dive duration + post-dive surface phase duration) (Ydenberg & Clark 1989; Cherel *et al*. 1999; Tremblay & Cherel 2000; Charrassin, Le Maho & Bost 2002).

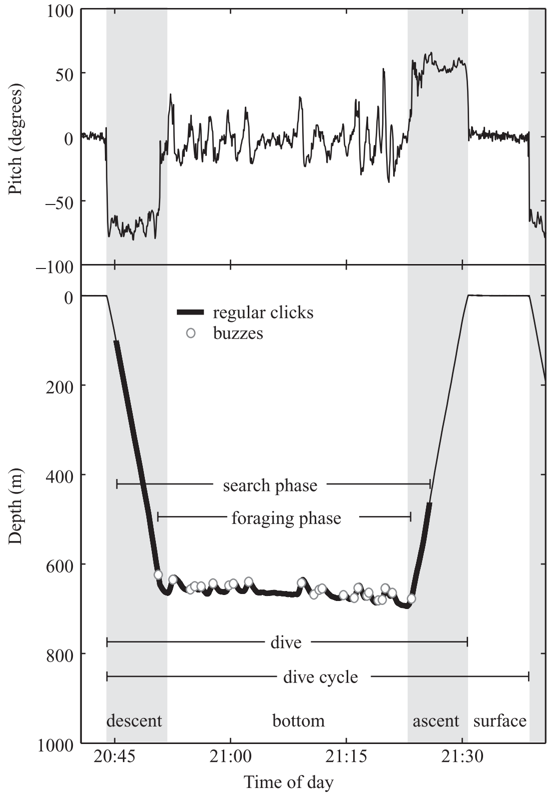

Fig. 3. Dive parameters used in characterizing sperm whale diving and foraging behaviour.

For statistical tests, all data were log-transformed to approximate normality and homogeneity of variance. We compared diving and foraging parameters among locations using nested one-way ANOVAS. For correlations, only animals with at least three deep dives were included. Each datum was subtracted from the appropriate individual mean to remove individual effects, and combined within location. The data pair with the largest *x*-deviation and the pair with the largest *y*-deviation were removed to account for extreme deviations. Correlations were run separately for whales from the Gulf of Mexico and the Ligurian Sea, to describe location effects on the parameters of interest. Correlations were not run for whales from the Atlantic Ocean, due to a small sample size (few whales and few dives per whale). *P*-values were adjusted for multiple comparisons by multiplying the *P*-value of each test by the combined number of correlations for each pair of variables in any given correlation.

Results

The analyses described here are derived from eight, 29 and 12 successful dtag deployments in the Atlantic Ocean, the Gulf of Mexico and the Ligurian Sea, respectively. Animals encountered in the first two regions were primarily females and immature whales. Dispersed single animals (some known to be males) were also encountered in the Ligurian Sea. Because females and immature whales made up the predominant composition of groups that included tagged whales, the results are most relevant for these age/sex classes.

Sperm whales in all three areas made repeated deep foraging dives with occasional extended periods at the surface of shallow diving behaviour. Figure 4 shows a representative time vs. depth dive profile for one whale from each location. Basic dive parameters were similar in all three regions, although there was variation among individuals within each location (Tables 1 and 2). The structure of the deep dive cycle was highly stereotyped and consistent across regions. Typical sperm whale dives lasted 45 min (6·4) (range 14–64 min). Whales descended for approximately 9·0 min

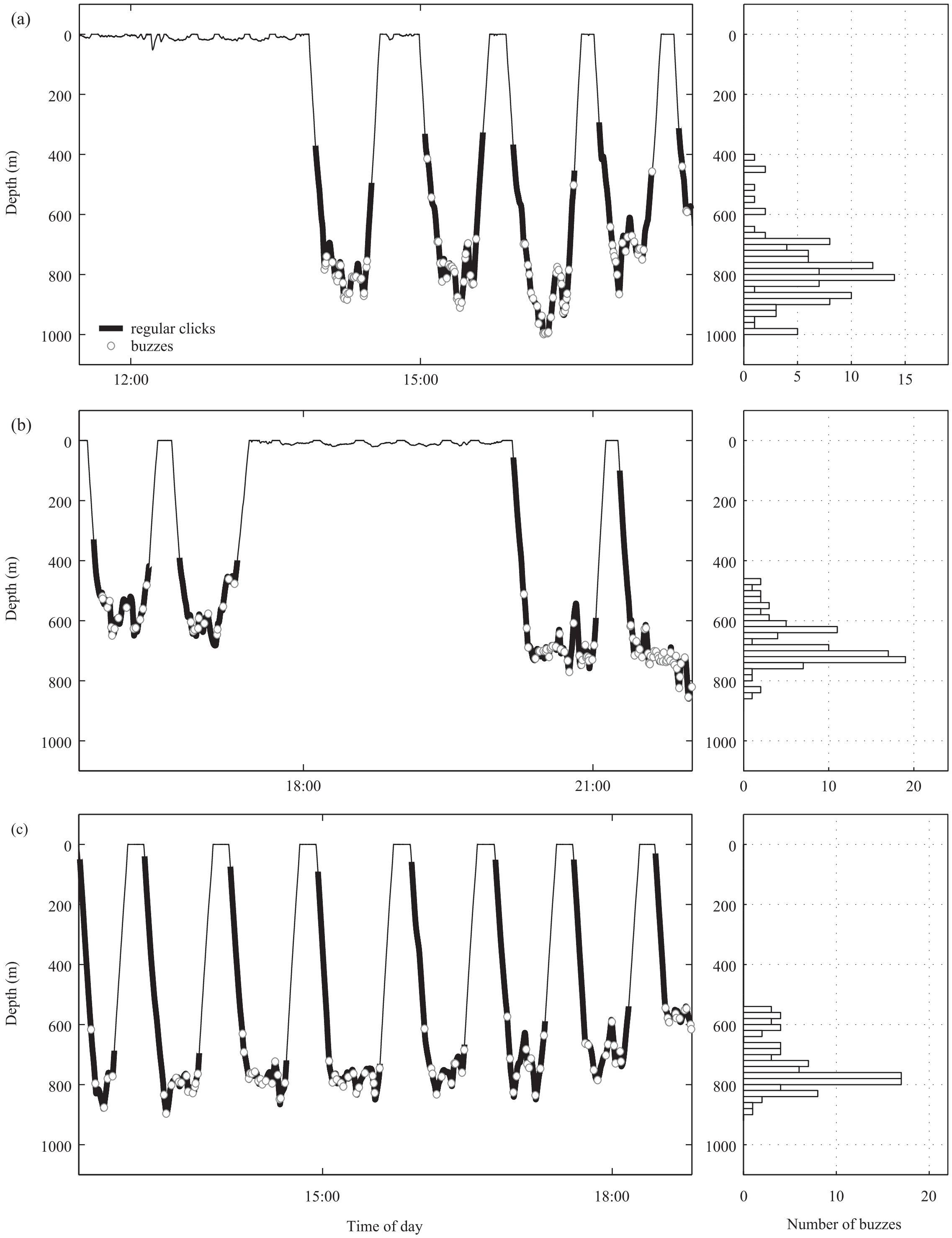

Fig. 4. Dive track and histogram of depth of buzz production for a whale from (a) the Atlantic Ocean, (b) the Gulf of Mexico and (c) the Ligurian Sea.

(2·1) at 1·2 m s^{-1} (0·2). Whales began producing regular clicks during the descent phase. Whales remained in the bottom phase of the dive for an average of 28·3 min (6·2), which coincided with the period of active foraging. Foraging phase duration (defined by the presence of buzzes) averaged 28 min (6·0) and accounted for 62% (7·4) of the dive duration. Buzzes were produced in all deep dives analysed, and there were on average 18 buzzes per dive (7·6). As whales began their ascent, they stopped producing buzzes and regular clicks and returned to the surface at a rate of 1·4 m s^{-1} (0·2). Whales remained at the surface for 8·9 min (3·0) before beginning another dive. Over the course of the dive, whales spent approximately 81% (4·1) of their time submerged producing regular clicks, interspersed at times with buzzes. This amounted to 68% (3·5) of their dive cycle. Below we discuss relationships between dive parameters.

Table 1. Mean (SD) of dive parameters for sperm whales in three different locations

	No. of dives analysed > 300 m	Dive duration	Descent duration	Descent vertical velocity	Descent pitch	Bottom duration	Bottom start depth**	Bottom end depth**	Minimum depth of bottom phase**	Maximum depth of bottom phase**	Ascent duration*	Ascent vertical velocity	Ascent pitch**	Post-dive duration surface
Atlantic Ocean	2·2 (1·6)	45·7 (5·6)	9·8 (1·8)	1·2 (0·1)	–53·7 (5·3)	27·0 (6·5)	683·7 (83·1)	729·9 (98·5)	636·2 (44·6)	985·2 (124·3)	8·9 (0·4)	1·4 (0·2)	53·7 (6·6)	9·3 (2·8)
Gulf of Mexico	5·9 (5·9)	45·5 (7·4)	8·4 (1·9)	1·1 (0·2)	–51·0 (7·5)	30·0 (6·8)	546·9 (130·0)	543·8 (133·1)	467·8 (82·3)	643·6 (123·4)	7·3 (1·5)	1·3 (0·2)	52·57 (8·8)	8·1 (2·6)
Ligurian Sea	6·0 (4·3)	44·2 (4·7)	9·6 (2·3)	1·3 (0·2)	–57·9 (7·2)	26·2 (4·2)	702·2 (82·5)	722·8 (73·9)	621·8 (59·3)	827·0 (61·8)	8·4 (1·3)	1·5 (0·2)	64·0 (7·2)	9·9 (2·1)

Durations in minutes, depth in metres, pitch in degrees, velocity in metres s^{-1}. Values based on individual means of six, 20 and 11 whales from the Atlantic Ocean, the Gulf of Mexico and the Ligurian Sea, respectively. Nested ANOVA difference between oceans: *$P < 0·05$, **$P < 0·01$. Significant differences among individuals within one location for all parameters ($P < 0·05$).

Table 2. Mean (SD) of foraging parameters for sperm whales in three different locations

	Search phase start depth**	Search phase end depth**	Search phase duration	% of dive in search phase	% of descent in initial search phase*	Foraging phase start depth*	Foraging phase end depth**	Foraging duration	% of dive in foraging phase	Vertical distance between start of search phase and first buzz	No. of buzzes per foraging phase	Diving efficiency
Atlantic Ocean	222·7 (107·5)	548·5 (86·8)	37·0 (6·3)	80·7 (3·7)	61·1 (20·0)	622·5 (41·6)	669·6 (65·3)	28·7 (6·9)	62·3 (9·7)	425·1 (113·8)	22·6 (8·7)	0·54 (0·02)
Gulf of Mexico	214·9 (69·0)	429·8 (71·5)	37·4 (7·4)	81·2 (4·7)	61·0 (13·0)	514·8 (90·5)	523·7 (122·3)	28·6 (6·9)	61·3 (8·1)	299·4 (104·8)	17·0 (8·6)	0·54 (0·06)
Ligurian Sea	96·7 (43·53)	611·5 (79·5)	36·0 (4·7)	81·4 (3·6)	70·6 (13·4)	635·6 (67·2)	679·8 (69·9)	28·2 (3·9)	63·5 (4·1)	538·5 (65·7)	18·5 (4·1)	0·53 (0·04)

Durations in minutes, depth in metres. Values based on individual means of six, 20 and 11 whales from the Atlantic Ocean, the Gulf of Mexico and the Ligurian Sea, respectively. Nested ANOVA difference between oceans: *$P < 0·05$, **$P < 0·01$. Significant differences among individuals within one location for all parameters ($P < 0·05$) except percentage of dive in search phase, percentage of dive in foraging phase and diving efficiency.

DIVE DURATION

Dive duration was significantly correlated with maximum dive depth for whales in the Gulf of Mexico ($r = 0{\cdot}43$, $t_{89} = 4{\cdot}87$, $P < 0{\cdot}002$), but not for those in the Ligurian Sea ($r = -0{\cdot}03$, $t_{47} = -0{\cdot}197$, $P > 0{\cdot}90$).

DESCENT PHASE

Descent vertical velocity and pitch angle were significantly correlated with maximum dive depth in the Gulf of Mexico (velocity: $r = 0{\cdot}30$, $t_{89} = 3{\cdot}192$, $P < 0{\cdot}002$; pitch: $r = 0{\cdot}35$, $t_{89} = 3{\cdot}75$, $P < 0{\cdot}001$), but not in the Ligurian sea. Whales began producing regular clicks (start of the search phase) at a depth of 223 m (107·5) in the Atlantic Ocean, 215 m (68·8) Gulf of Mexico and 97 m (43·5) in the Ligurian Sea. Whales in the Ligurian Sea started clicking significantly earlier than whales in the other two regions (nested ANOVA, $Fs_{2,34} = 29{\cdot}23$, $P < 0{\cdot}001$).

BOTTOM PHASE

The maximum dive depths differed significantly among the three locations (nested ANOVA, $Fs_{2,33} = 17{\cdot}78$, $P < 0{\cdot}001$). The deepest dive recorded was to a depth of 1202 m in the Atlantic Ocean. Whales started and ended the bottom phase at shallower depths in the Gulf of Mexico than in the other regions (nested ANOVA, $Fs_{2,34} = 5{\cdot}58$, $P < 0{\cdot}01$ and $Fs_{2,33} = 12{\cdot}20$, $P < 0{\cdot}002$, respectively). The water depth in the vicinity of tagged whales averaged 2015 m (range 1287–2786 m) in the Atlantic Ocean, 893 m (range 679–1631 m) in the Gulf of Mexico, 1952 m (range 602–2900 m) in the Ligurian Sea (Smith & Sandwell 1997). Judging from echoes from the sea floor recorded on the dtag, sperm whales occasionally forage all the way to the sea floor. For this paper we do not distinguish between pelagic and infrequent benthic foraging.

The first buzz (by our definition the start of the foraging phase) was generally produced close in time to the start of the bottom phase [mean: 6 s (95·7) after the start of the bottom phase, range: 8·5 min before to 6·4 min) after]. The initial search phase, defined as the interval between the start of the search phase and the start of the foraging phase, represents a period in which the whale may have been searching for, but probably not encountering, prey suitable for a capture attempt. The depth change of the whale during this period was on average 425 m (113·8) in the Atlantic Ocean, 299 m (105·7) in the Gulf of Mexico and 539 m (65·7) in the Ligurian Sea. The depth change during the initial search phase was largest in the Ligurian Sea due to a shallower start of clicking than in the other two regions and deep dive depths (nested ANOVA, $Fs_{2,33} = 16{\cdot}05$, $P < 0{\cdot}001$). The initial search phase accounted for 14% (4·3) of the dive duration and 61·0% (14·4) of the descent phase duration for whales in the Atlantic and the Gulf of Mexico and 71% (13·4) in the Ligurian Sea.

The durations of the foraging and bottom phases were strongly correlated for both the Gulf of Mexico (GOM) and the Ligurian Sea (LIG) (GOM, $r = 0{\cdot}86$, $t_{90} = 17{\cdot}58$, $P < 0{\cdot}001$; LIG, $r = 0{\cdot}87$, $t_{47} = 12{\cdot}66$, $P < 0{\cdot}001$). The majority of buzzes occurred in the bottom phase of the dive cycle. The foraging and bottom phase durations differed by 3·3 min (1·8) in the Atlantic Ocean, 2·5 min (2·0) in the Gulf of Mexico and 2·4 min (1·2) in the Ligurian Sea.

The bottom phase was on average 2 s (176·4) shorter in duration than the foraging phase (range 9·2 min shorter to 17·1 min longer than the foraging phase). The foraging phase duration was significantly correlated with dive duration for whales in both the Gulf of Mexico and Ligurian Sea (GOM, $r = 0{\cdot}75$, $t_{90} = 12{\cdot}49$, $P < 0{\cdot}001$; LIG, $r = 0{\cdot}83$, $t_{48} = 11{\cdot}88$, $P < 0{\cdot}001$). Therefore, whales remained in the foraging phase longer during longer dives. The duration of the foraging phase was significantly correlated with the number of buzzes produced per dive for whales in both the Gulf of Mexico and the Ligurian Sea (GOM, $r = 0{\cdot}72$, $t_{89} = 10{\cdot}42$, $P < 0{\cdot}001$; LIG, $r = 0{\cdot}40$, $t_{47} = 3{\cdot}36$, $P < 0{\cdot}01$).

ASCENT PHASE

The last buzz was produced on average 5 s (1·9) after the end of the bottom phase (range 16·2 min before to 5·1 min after the end of bottom phase). Overall, whales stopped regular clicking 2 min (1·7) after the last buzz and returned to the surface. Whales in the Ligurian Sea ascended at significantly steeper pitch angles than whales in the other two regions (nested ANOVA, $Fs_{2,33} = 8{\cdot}74$, $P < 0{\cdot}01$). Average vertical velocity during the ascent was significantly greater than during descent for whales in all areas (paired *t*-test, $t_{189} = -6{\cdot}6804$, $P < 0{\cdot}001$), due primarily to swimming speed being significantly faster during ascents than descents (paired *t*-test, $t_{189} = -8{\cdot}11$, $P < 0{\cdot}001$). Average ascent and descent pitch angles were not significantly different in any location (paired *t*-test, $t_{189} = -0{\cdot}21$, $P > 0{\cdot}84$). Ascent and descent pitch angles were significantly correlated for whales in the Gulf of Mexico ($r = 0{\cdot}52$, $t_{89} = 6{\cdot}10$, $P < 0{\cdot}001$) but not for whales in the Ligurian Sea ($r = -0{\cdot}09$, $t_{47} = -0{\cdot}69$, $P > 0{\cdot}90$). Ascent vertical velocity and ascent pitch were significantly correlated with dive duration for whales in the Gulf of Mexico and the Ligurian Sea (vertical velocity: GOM, $r = 0{\cdot}33$, $t_{89} = 3{\cdot}50$, $P < 0{\cdot}003$; LIG, $r = 0{\cdot}66$, $t_{47} = 6{\cdot}71$, $P < 0{\cdot}001$; pitch: GOM, $r = 0{\cdot}44$, $t_{89} = 4{\cdot}91$, $P < 0{\cdot}002$; LIG, $r = 0{\cdot}51$, $t_{47} = 4{\cdot}56$, $P < 0{\cdot}002$). Ascent vertical velocity was similarly significantly correlated with bottom phase duration (GOM, $r = 0{\cdot}50$, t_{89}, $P < 0{\cdot}001$; LIG, $r = 0{\cdot}70$, $t_{47} = 7{\cdot}49$, $P < 0{\cdot}001$). Whales in the Ligurian Sea also increased ascent swimming speed with increased dive duration ($r = 0{\cdot}52$, $t_{47} = 4{\cdot}63$, $P < 0{\cdot}002$). Whales therefore increased their ascent rate during longer dives. Ascent pitch angle was significantly correlated with maximum dive depth for whales in the

Gulf of Mexico ($r = 0{\cdot}38$, $t_{89} = 4{\cdot}19$, $P < 0{\cdot}002$) but not in the Ligurian Sea.

SURFACE PHASE

Whales spent on average 9 min (3·0) at the surface following a deep dive. There were no differences in surface duration among locations (nested ANOVA, $Fs_{27} = 1{\cdot}67$, $P > 0{\cdot}21$). Intervals between deep dives ranged from 5·1 to 24·2 min. Tagged whales spent 28% (18·1) of their time less than 10 m from the surface. There were no differences among locations in percentage of time at the surface (one-way ANOVA $Fs_{42} = 1{\cdot}33$, $P > 0{\cdot}20$). However, on average, whales in the Ligurian Sea were at the surface less [Atlantic Ocean (ATL), 37% (26·7); GOM, 28% (17·6); LIG, 20% (4·4)], which was probably related to the lower levels of social behaviour observed in tagged whales there.

Dive duration was weakly correlated with the following surface phase duration in the Ligurian Sea, but not in the Gulf of Mexico (GOM, $r = 0{\cdot}16$, $t_{76} = 1{\cdot}57$, $P > 0{\cdot}9$; LIG, $r = 0{\cdot}41$, $t_{37} = 3{\cdot}06$, $P = 0{\cdot}045$). Conversely, dive duration was weakly correlated with the preceding surface phase duration in the Gulf of Mexico, but not in the Ligurian Sea (GOM, $r = 0{\cdot}30$, $t_{73} = 2{\cdot}94$, $P = 0{\cdot}048$; LIG, $r = -0{\cdot}08$, $t_{36} = -0{\cdot}55$, $P > 0{\cdot}09$). The weak correlations and contrasting results in the two locations suggest flexibility in the relationship between dive phase duration and surface phase duration in different sites.

Tagged whales spent 72% (32·7) of their time in foraging dive cycles in the Atlantic Ocean and Gulf of Mexico and 97% (5·7) in the Ligurian Sea. There was large individual variation, with the range being 0–100% in both the Gulf of Mexico and the Atlantic Ocean. Over the average entire dive cycle whales had a diving efficiency (foraging phase duration/dive cycle duration) of 0·53 (0·05). Thus, whales foraged for over half of their time during the dive cycle.

Discussion

The data presented here provide a detailed view of the behavioural ecology of individual sperm whales sampled throughout the dive cycle using high resolution tags. Combined data from all three study areas suggest an average sperm whale dive duration of 40–50 min and dive depths of 400–1200 m, which is comparable to previous work (Watkins *et al.* 1985; Papastavrou *et al.* 1989; Gordon & Steiner 1992; Amano *et al.* 2003; Drouot, Gannier & Goold 2004).

The context of regular click production is consistent with the use of echolocation for detecting prey. Regular clicks were produced while whales descended to the depth of prey and within the foraging layer, and ended early in the ascent phase. Sperm whales spent 64% of their descent phase producing regular clicks; we conclude from this that a significant portion of the descent is devoted to searching for prey. Whales began clicking at an average range of 295–539 m from the depth of the first recorded buzz, which is well within the theoretical range over which sperm whales should be able to detect squid based on the properties of their regular clicks (Møhl *et al.* 2003). Scanning large parts of the water column during the descent may enable sperm whales to find profitable prey patches from a distance and reduce search time at the bottom of the dive (Madsen *et al.* 2002). Such a long-range sonar would facilitate the high average number of prey capture attempts in the dives in all three locations. While we cannot exclude other techniques for finding prey, the consistent clicking during all foraging dives, in concert with the source properties of the clicks, strongly support the use of echolocation as the primary sensory modality for location of prey.

Optimal foraging models suggest that diving animals should maximize their time foraging during dives by minimizing transit costs and time required for post-dive recovery (Thompson, Hiby & Fedak 1993). Sperm whales have a streamlined body form with a low drag coefficient at typical travel speeds (Miller *et al.* 2004b). In addition to body shape/anatomical adaptations, sperm whales make extensive use of gliding during transit using buoyancy forces to power more efficient dives (Williams *et al.* 2000; Miller *et al.* 2004b). Deep divers from diverse taxa increase descent and/or ascent rates during dives to greater depths to maximize time spent at foraging depths [penguins (Charrassin *et al.* 2002; Cherel *et al.* 1999), seals (Beck, Bowen & Iverson 2000), narwhals *monodon monoceros* (Linnaeus) (Laidre *et al.* 2003), belugas *Delphinapterus leucus* (Pallas) (Martin & Smith 1999) and bottlenose whales *Hyperoodon ampullatus* (Forster) (Hooker & Baird 1999)]. This study presents additional evidence that sperm whales also make use of efficient locomotion behaviour during transit to and from foraging depth. Sperm whales in both the Ligurian Sea and the Gulf of Mexico increased their vertical velocities by increasing their ascent pitch angle during longer duration dives. Increasing pitch angle increases the amount of time that oxygen stores can be devoted to foraging, as less time is needed for travelling to the prey patch. Swimming speed also increased during ascents from longer dives in the Ligurian Sea. In the Gulf of Mexico, dive duration and foraging phase duration were correlated with dive depth. Increased foraging phase durations correlate with increased buzz rates in these whales (Miller *et al.* 2004a), as has been seen elsewhere in foraging dives of male sperm whales (Jaquet *et al.* 2001). Whales therefore appear to stay in productive patches longer, and make up for the increased time spent at depth with faster, more efficient ascents (Mori *et al.* 2002; Sato *et al.* 2004).

On average, sperm whales had a diving efficiency of 0·53 (range 0·28–0·68, median 0·54); whales spent over half their dive cycle detecting and capturing prey actively. The total number of buzzes produced during a dive increased with longer foraging phase duration,

Table 3. Diving efficiencies of various marine predators

Species	Diving efficiency	Source
Sperm whale	0·53	Present study
Harbour seal	0·52	Lesage *et al.* (1999)[c]
Australian sea lion	0·38–0·43	Costa & Gales (2003)[b]
Sperm whale	0·38	Amano & Yoshioka (2003)[b]
Antarctic fur seal	0·38	Boyd *et al.* (1995)[b]
Grey seal	0·37	Beck *et al.* (2000)[b]
Beluga whale	0·36	Martin & Smith (1999)[b]
Rockhopper penguin	0·34–0·49	Tremblay & Cherel (2000)[a], Tremblay & Cherel (2003)[a], Cherel *et al.* (1999)[a]
New Zealand fur seal	0·29	Harcourt *et al.* (2002)[c]
King penguin	0·15–0·29	Charrassin *et al.* (2002)[a]

[a]Dive efficiency reported by the authors; [b]dive efficiency calculated for individual animals based on individual parameter means presented by the authors; [c]dive efficiency calculated for multiple animals based on group parameter means presented by the authors.

demonstrating that feeding occurred throughout the foraging phase (Fig. 4). The average diving efficiency of sperm whales is higher than those reported from, or calculated for, other air-breathing marine predators (Table 3). Benthic foraging rockhopper penguins *Eudyptes chrysocome* (Forster) (0·49) and harbour seals *Phoca vitulina* (Linnaeus) (0·52) had diving efficiencies similar to sperm whales, but the sperm whale targets deeper prey than do these two species. Similarities in dive parameters among the three locations suggest a general pattern for foraging by sperm whales in subtropical and temperate latitudes after sperm whales. It remains to be seen if mature male sperm whales employ the same foraging behaviour at high latitudes after foraging behaviour.

Previous studies have indicated differences in foraging success between regions with different oceanographic features (Rendell, Whitehead & Escribano 2004; Rendell, Whitehead & Escribano 2004). Jaquet & Whitehead (1999) and Rendell *et al.* (2004) have used differences in the number of observed defecations as a proxy for foraging success and related these differences to oceanographic parameters. In all three regions examined here, whales produced at least five buzzes in 95% of dives to deeper than 300 m and on average produced 18 buzzes per deep dive. The mean number of buzzes per dive did not differ among the three locations, suggesting that whales were similarly successful in encountering potential prey in the three regions. While the prey quality and size will probably differ between dives and regions, which can lead to differences in the production of faecal matter, our results in the three regions investigated do not match the large differences in foraging success inferred from the defecation rate studies. Sperm whales appear to be generalist feeders (Berzin 1972; Kawakami 1980; Pauly *et al.* 1998), specializing in a broader array of prey species than many other deep ocean predators (Whitehead, MacLeod & Rodhouse 2003). The ability to locate and utilize a variety of prey species in different regions may enable their high diving efficiency and cosmopolitan distribution.

The lower limit of sperm whale dive durations is probably determined by transit time and prey patch quality, and the upper limit by physiological constraints, with the primary limiting constraint being the increasing cost of anaerobic metabolism once the aerobic dive limit (ADL; Kooyman, Castellini & Davis, 1981) is exceeded. The Weddell seal *Leptonychotes weddellii* (Lesson) is the only large marine mammal for which the diving metabolic rate and ADL have been measured *in situ* (Kooyman *et al.* 1981; Castellini, Fadely & Rea 1998). The measured ADL is around 21 min for an adult Weddell seal, and dives in excess of that will lead to lactic acid accumulation and thereby an oxygen debt that has to be repaid (Kooyman 1989). More than 90% of all Weddell seal dives are shorter than the measured ADL; this behaviour maximizes time available for foraging at depth by minimizing recovery time at the surface (Kooyman *et al.* 1981). Sperm whales and Weddell seals carry roughly comparable amounts of oxygen per kilogram of body weight (some 80–90 mL O; Kooyman *et al.* 1998; Davis & Kanatous 1999), so differences in ADL probably relate to the diving metabolic rate. The lean mass (M) specific basal metabolic rate of mammals scales as $\mathrm{M}^{-0\cdot 25}$ (Kleiber 1975), while oxygen stores scale in a linear fashion. Consequently, larger animals can dive longer aerobically than smaller animals (Castellini, Kooyman & Ponganis 1992). If the diving metabolic rate scales with lean body mass the way the basal metabolic rate does (Kleiber 1975), the ADL of sperm whales can be estimated from the 21 min ADL of a 450 kg Weddell seal (Kooyman 1989) having a lean body mass of about 70% of total mass comparable to that of sperm whales (Lockyer 1991). With this approach $[\mathrm{ADL}_{\text{sperm whale}} = \mathrm{ADL}_{\text{weddell}} \times (\mathrm{M}_{\text{weddell}}/\mathrm{M}_{\text{sperm whale}})^{-0\cdot 25}]$, we estimate that sperm whale ADLs should range from 43 to 54 min for the size of animals tagged in this study (estimated body mass between 8 and 20 tons for whales with body lengths between 9 and 12 metres (Lockyer 1991). As 93% of dives reported here had durations of less than 54 min, and with an overall mean dive duration of 45 min, it seems that most dives are within or do not greatly exceed the aerobic dive limit. The greater the proportion of a dive spent in aerobic metabolism the higher the diving efficiency, as less recovery time is needed at the surface.

From the fossil record, it is evident that sperm whales have exploited the world's oceans as top predators with very few evolutionary changes in the last 10 million years (Mchedlidze 2002). With a distribution in all the blue waters of the globe, the sperm whale is thus a successful species from both an evolutionary and ecological perspective (Whitehead 2003). This study demonstrates that female and immature sperm whales find food by active search at ocean depths between 400 and 1200 metres, with little variation in their foraging behaviour among the three study sites. Stereotyped patterns of repeated, long foraging dives and the effective location of food patches result in a diving efficiency that is among the highest reported for a diving animal. We conclude that the successful global distribution of this species probably relates to effective prey location in a patchy deep ocean facilitated by long-range echolocation, efficient locomotion and a large size that provides long, aerobic foraging periods during dives to a mesopelagic habitat.

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