Aquatic Mammals 2004, *30*(3), 419-426, DOI 10.1578/AM.30.3.2004.419

Diving and Feeding Behaviour of Sperm Whales (*Physeter macrocephalus*) in the Northwestern Mediterranean Sea

Violaine Drouot,[1,2] Alexandre Gannier,[1, 2] and John C. Goold[3]

[1]*GREC, 741 chemin des Moyennes Bréguières, BP715, 06633 Antibes Cedex, France*
[2]*Centre de Recherche sur les Cétacés, Marineland, 306 Avenue Mozart, Antibes, France*
[3]*Institute of Environmental Science, University of Wales, Bangor, Robinson Building, Deiniol Road, Bangor, Gwynedd. LL57 2UW, UK*

Abstract

Sperm whale (*Physeter macrocephalus*) is one of the common cetacean species inhabiting the western Mediterranean Sea. The aim of this study was to describe the dive cycle of sperm whales in this region and gain insight into their foraging activity. Dedicated summer field seasons were conducted from 2001-2003. Visual and acoustic measures were undertaken and their relationships analyzed. The measures included surface/dive periods, blow rate, distance traveled, timing of clicks & creak activity, and inter-pulse interval measurements of sperm whale clicks. The whales exhibited dive cycle parameters consistent with those measured in other parts of the world: approximately 45 min dive duration, 9 min surface period (i.e., inter-dive interval), with 5 blows/min, and 1.3 nmi horizontal displacement between dives. An average of 25 creaks per dive were registered. Whale body size appeared to be significantly related with both the number of creaks per dive and the dive time at which the first creak occurred, suggesting that larger whales may increase their prey intake and use deeper water layers than smaller whales. The timing of the first creak and the last click of the dive (around 6 min after fluke-up, and just before the surfacing, respectively) suggest a foraging depth of between 500 and 800 m, based on known descent and ascent rates.

Key Words: Sperm whale, dive, feed, click, Mediterranean Sea, *Physeter macrocephalus*

Introduction

Different aspects of sperm whale diving behavior have been studied in different areas of the world. The term "diving behavior" is used in this paper to describe visual and acoustic features associated with sperm whales' dive cycles. A typical sperm whale dive cycle consists of a 40-50 min dive followed by a surface period of about 8 min for breathing (Gordon, 1987; Papastavrou et al., 1989; Whitehead et al., 1992). The diving period can be divided into three phases: (1) a descent phase (preceded by the fluke-up, where the whale descends almost vertically from the surface to the foraging depth), (2) a foraging phase (where the whale undertakes horizontal movement at the foraging depth in search for food), and (3) an ascent phase (where the whale returns to the surface) (Gordon, 1987; Watkins et al., 2002; Zimmer et al., 2003). Because sperm whales feed at great depths, they have never been directly observed while feeding and, therefore, their feeding methods can only be inferred. Most authors (e.g., Goold & Jones, 1995; Gordon, 1987; Norris & Harvey, 1972; Weilgart, 1990) suggest that sperm whales use echolocation to detect prey at ranges of several hundred m. During the descent and foraging phases of the dive they produce "regular clicks" almost continuously. These are loud clicks emitted at a fairly regular rate, between 0.5 and 2 clicks per s (Drouot, 2003; Goold & Jones, 1995; Gordon, 1995; Weilgart & Whitehead, 1988). Sperm whale clicks are made up of a number of regularly spaced sound pulses resulting from multiple reflection of the initial sound within the head of the animal. The time spacing between pulses in a click, termed inter-pulse interval (IPI), has been demonstrated to be a function of the body length (Goold & Jones, 1995; Gordon, 1991). The long sequences of regular clicks are spaced with "creaks," defined as an increased click rate of up to 220 per s, persisting for between 10 and 25 s, and followed by a silence (Gordon, 1987). Creaks are thought to be produced by sperm whales investigating targets at close range and, therefore, to be indicative of feeding attempts (Goold, 1999; Gordon, 1995; Mullins et al., 1988). The increasing click rate during a creak may reflect decreasing distance to the target. Sperm whales feed upon several species of squid, and in the Mediterranean Sea, where few published data are available, the stomach content of one stranded specimen included mainly *Histioteuthis bonnellii* (Roberts, 2003).

The northwestern Mediterranean Sea has a higher abundance of sperm whales in summer than most other regions of the Mediterranean (Gannier et al., 2002), and the region also appears to be frequented mainly by males in summer (Drouot et al., 2004). The aim of this study was to describe the dive cycle of sperm whales inhabiting this area; quantify their foraging activity; gain insight into the spatial requirements of the species in terms of habitat use; and investigate the relationship between the dive cycle parameters, the length of the whales, and their feeding success.

Materials and Methods

Survey Methodology

Dedicated sperm whale surveys were performed from a 12 m motor-sailing boat in the northwestern Mediterranean Sea during the summers of 2001-2003. An active search for sperm whales was carried out, using visual and acoustic techniques. Three observers performed a continuous, naked-eye observation of the sea surface, scanning the 180° sector ahead of the boat. Acoustic sampling consisted of 1 min listening stations every 2 nmi along the survey track. When a sperm whale was detected acoustically, direction finding towards the source of clicks was attempted (by listening with the stereo headset while changing the boat's heading, and by using *Rainbow click*© software) to get closer to the whale. When the signal-to-noise ratio reached the maximum (noted as 5/5—see Gannier et al., 2002), the boat was stopped and visual searching was extended to 360° around the boat. Continuous sound recording through the hydrophone onto Digital Audio Tape was performed simultaneously to the full visual observations. When a whale stopped clicking, the acoustic operator informed the visual observers, since cessation of clicking was usually an indication of the end of the dive. Data collection was maintained as long as visual and/or acoustic observation conditions allowed the observers to be in contact with the whale and ideally spanned over several dive cycles.

When a sperm whale was sighted, the time and position of the beginning and ending of the dives were recorded, and the number of blows during the surface period was counted. The beginning of the dive was recorded when the whale fluked-up (i.e., the moment when the fluke disappeared from the surface). In most cases, the event of fluking up could be observed and recorded accurately in both time and space—the latter typically by placing the boat over a whale's dive "footprint" and obtaining a GPS reading from the boat's navigation system. The end of the dive (i.e., the start of the surfacing period) was recorded by the time the whale was first sighted at the surface, based on the assumption that the whale was sighted as soon as it broke the surface. The approximate position of a whale surfacing was typically calculated by taking an optical range and bearing measurement (since the boat and a surfacing whale would not be co-located) and computing its position relative to the GPS reading on the boat.

Analysis

A dive cycle was defined as the period between two successive fluke-ups from a given whale. The following dive cycle parameters were calculated: (1) the dive duration – time from fluke-up until the whale was re-sighted at the surface, (2) the surface duration – time from the surface re-sighting of the whale until the time it fluked-up, (3) the blow rate – number of blows divided by the surface duration, and (4) the horizontal displacement from one dive cycle to the next. Horizontal displacement was obtained by measuring the position of each whale at successive fluke-ups and entering the data into *Oedipe-Karto* software for distance computation (Massé & Cadiou, 1994). Dive cycle parameters were only included in the data set for analysis when it could be ascertained with confidence that the same individual whale was being tracked (i.e., in cases where continuous acoustical contact of the whale was kept over the dive and no other whale was acoustically detected in the area). Photo-identification was used whenever possible to confirm whale identity.

All the sound recordings performed during the survey were replayed in the laboratory and correlated with the visual observation data to calculate the following: (1) Δt_i – the time interval of silence between the start of the dive (i.e., fluke-up) and the emission of the first click, (2) Δt_f – the time interval of silence between the last click emitted and the time of the whale surfacing, (3) the number of creaks per dive in cases when the entire dive was recorded, and (4) Δt_{creak} – the time interval between the dive start and the first creak of the dive.

Good quality sections of click recordings of each individual whale were sampled onto computer hard disk at sampling frequency of 62.5 kHz, using a *Cambridge Electronic Design* (CED) 1401 laboratory interface (Goold & Jones, 1995) for 1997-2001 data, and an Extigy SB sound card and *Spectralab*© software for 2002-2003 data. From the waveform display, IPIs were measured manually wherever a clear pulsed structure was observed within a click. The average IPI was calculated for each whale and used to estimate the whale's body length according to Gordon's (1991) equation:

$$\text{Body length} = 4.833 + (1.453\ \text{IPI} - 0.001\ \text{IPI}^2)$$

Basic statistics were calculated for each variable. When successive dive measurements were performed from the same individual, the mean of each measured variable was computed for that animal so that the sample size N represents the number of individuals sampled (and not the number of dives recorded, to avoid pseudo-replication). The relationships among variables were assessed by calculating the Pearson's correlation coefficient (r) and its associated probability (p). In cases where the correlation was statistically significant ($p < 0.05$), further linear regression analysis and analysis of variance were undertaken.

Results

The dedicated surveys were carried out in July and August and represented a total coverage of 1,409 nmi performed in good weather conditions. Close approaches (< 200 m) and subsequent observation of 30 isolated sperm whales were performed. Among these sightings, 16 individual whales could be followed for more than one dive cycle, the number of cycles monitored for each whale ranging from 1 to 7.

High-quality recordings, which enabled accurate measurement of the IPIs, were available for 15 individuals. The average IPI obtained was 5.59 ms, ranging from 4.8 to 6.2 ms, corresponding to animals between 11.8 m and 13.8 m body size (Table 1).

On average, the complete dive cycle (diving and surface periods) lasted for 55 min (Table 1) and the length of dives was 44.8 min (SD = 5.3). On average, the whales spent 9.1 min (SD = 1.6) recovering at the surface, with a blow rate of 4.6/min (Table 1). The duration of the dive cycles were relatively consistent from one individual to another and fitted a normal distribution (Anderson-Darling test: A = 0.479, P = 0.208). No significant relationship was found between the surface duration, the dive duration, and the blow rate (Table 2).

On average, the whales emitted the first click 1.2 min (SD = 0.55, N = 22) after leaving the surface, although this time period was highly variable and ranged from 8 s to 3 min (Table 1). The time period between the emission of the last click of the dive and the surfacing of the whale (Δt_f) averaged 6.6 min with relatively low variation (SD = 1.0, N = 24). The mean period of silence from the last click of the dive to the first click of the next dive (including the intervening time at the surface) was 16.2 min (SD = 2.60, N = 20) or 29.5% of the dive cycle. The mean "clicking period," taken as the time between the first click of the dive to the last click of the dive, was 38.9 min (SD = 3.38, N = 14) or 71% of the dive duration.

Over a dive cycle, sperm whales traveled an average horizontal distance of 1.3 nmi (SD = 0.36, N = 16), corresponding to an average surface speed of 1.4 kts (Table 2). The magnitude of the mean whale horizontal displacement over a dive cycle was not significantly correlated to any of the variables measured (Table 2). In cases where individual sperm whales were followed over successive dive cycles, the distance traveled from one cycle to the next appeared to be very consistent. On the seven occasions where individuals were followed over three or more dives cycles, the whales never returned twice to the same area but seemed to follow an approximately steady heading, essentially along the bathymetry contours (Figure 1).

Table 1. Descriptive statistics of sperm whale dive cycles observed in the western Mediterranean Sea during 2001-2003 surveys

	Mean	SE	SD	Minimum	Maximum	N
Dive duration (min)	44.77	1.18	5.28	31.00	55.00	20
Surfacing time (min)	9.14	0.31	1.59	6.00	13.00	27
Cycle duration (min)	54.78	1.28	5.58	39.00	64.28	19
Blow rate (/min)	4.60	0.11	0.54	3.67	5.71	25
Number of creaks	24.77	0.89	3.67	19.00	32.00	17
Dt_{creak} (min)	6.39	0.16	0.77	5.00	8.00	23
Dt_i (min)	1.18	0.12	0.55	0.13	3.00	22
Dt_f (min)	6.78	0.21	1.01	4.80	8.60	24
Distance (nmi)	1.28	0.09	0.36	0.78	2.07	16
Speed (kts)	1.44	0.10	0.39	0.83	2.34	15
IPI (ms)	5.59	0.09	0.34	4.80	6.20	15
Whale size (m)	12.93	0.13	0.49	11.78	13.80	15

SE: Standard Error; SD: Standard Deviation; N: Number of whales measured, Δt_{creak}: time interval between the dive start and the first creak; Δt_i: time interval between the start of the dive and the first click; Δt_f: time interval between the last click and surfacing

Table 2. Values of Pearson's correlation coefficient and associated probability between the measured variables; * Indicates a significant correlation.

	Surface duration	Dive duration	N blows	N creaks	Δt_{creak}	Distance	IPI	Δt_i
Dive duration	0.100							
	0.685							
Blow rate	-0.275	-0.165						
	0.183	0.527						
Number of	-0.157	0.146	0.181					
creaks	0.546	0.589	0.518					
Δt_{creak}	0.222	0.239	0.110	0.620				
	0.308	0.339	0.634	0.008*				
Distance	-0.134	0.163	0.380	-0.213	-0.177			
	0.635	0.546	0.162	0.464	0.544			
IPI	0.080	0.398	0.134	0.572	0.529	-0.078		
	0.768	0.159	0.662	0.033*	0.05*	0.810		
Δt_i	-0.278	0.478	-0.026	0.124	-0.008	0.378	0.419	
	0.222	0.061	0.909	0.661	0.974	0.183	0.175	
Δt_f	-0.125	0.344	-0.045	0.139	0.033	0.213	0.342	0.391
	0.569	0.138	0.841	0.596	0.888	0.428	0.232	0.098

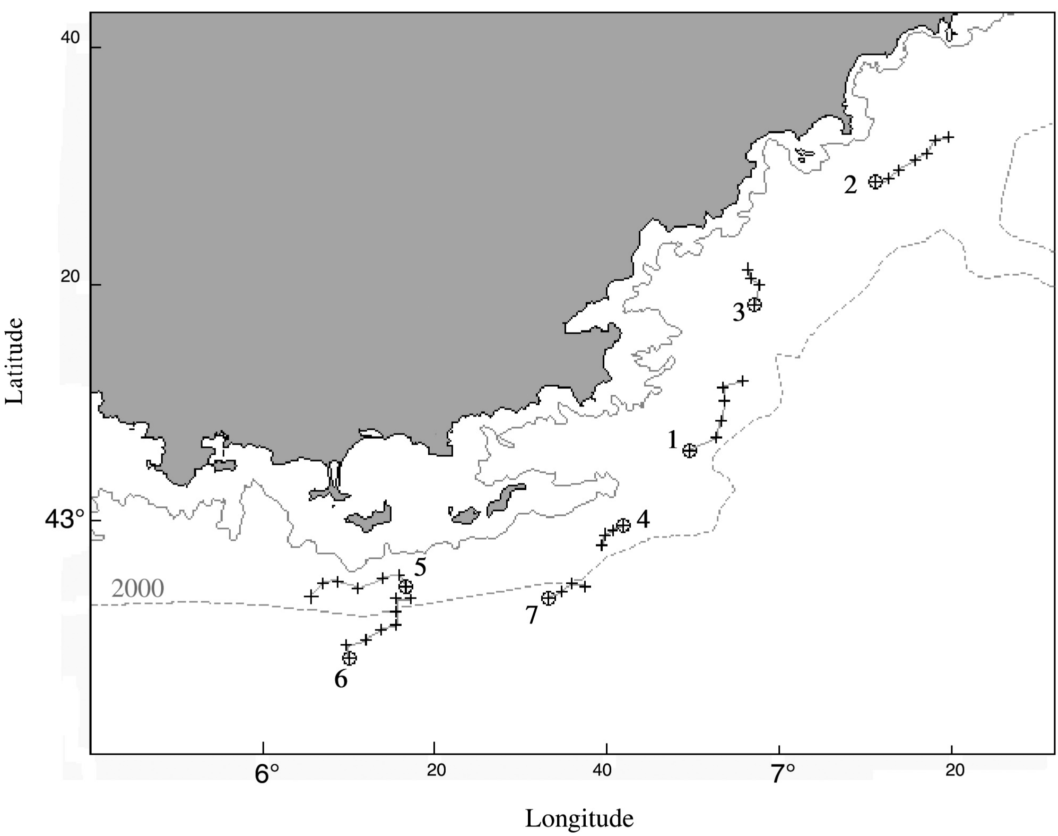

Figure 1. Map showing the position of the fluke-ups (+) during successive dives of seven sperm whales followed over three or more dive cycles off the coast of Provence (France); circled positions refer to the first fluke-up observed: 1, 19/08/01; 2, 05/07/02; 3, 08/08/02; 4, 15/08/02; 5, 05/08/02; 6, 06/08/03; and 7, 07/08/03

Table 3. Results of the regression analysis conducted between the number of creak (N creaks) and the whale size in m

Regression Equation: N creaks = - 38.4 + 4.93 whale size

Predictor	Coefficient	SD	t	p
Constant	-38.450	26.550	-1.450	0.173
Whale size	4.926	2.040	2.410	0.033

S=2.861 R^2=32.7%

Analysis of Variance

Source	DF	SS	MS	F	p
Regression	1	47.741	47.741	5.830	0.033
Residual error	12	98.254	8.188		
Total	13	145.995			

Table 4. Results of the regression analysis conducted between the time of occurrence of the first creak (Δt_{creak}) and the whale size (in m)

Regression Equation : Δt_{creak} *= -3.84 + 0.788 whale size*

Predictor	Coefficient	SD	t	p
Constant	-3.477	4.756	-0.730	0.479
Whale size	0.788	0.365	2.160	0.052

S=0.5125 R^2=27.9%

Analysis of Variance

Source	DF	SS	MS	F	p
Regression	1	1.223	1.223	4.650	0.052
Residual error	12	3.152	0.263		
Total	13	4.375			

Sperm whales produced an average of 24.8 creaks per dive (Table 1), corresponding to a rate of 0.55 creak/min (SD = 0.09, N = 15). The time of occurrence of the first creak was relatively consistent. Creaks were emitted at 6.4 min after the whale fluked-up, and this time interval showed little variation (SD = 0.77, N = 23). It is interesting to note that, statistically, the time intervals Δt_{creak} (between the fluke-up and the first creak) and Δt_f (between the last click and the surfacing) were not significantly different (paired t-test: t = 0.55, p = 0.582).

It appeared that both the average number of creaks produced and the timing of the first creak (Δt_{creak}) were significantly correlated to the whale's size (Table 2): the larger the animal, the more creaks it produced over the dive and the longer the interval between the fluke-up and the first creak. The regression analysis showed that whale size accounted for 32.7% of the variability in the number of creaks (Table 3) and 27.9% of the variability in the time of occurrence of the first creak (Table 4).

Discussion

Although aspects of the diving activity of sperm whales have been investigated in other parts of the world, very few data on diving behavior have been published for the Mediterranean Sea (Zimmer et al., 2003).

Surfacing Periods

The average dive and surface periods of 45 and 9 min, respectively, are consistent with other studies reporting on sperm whale diving behavior in other areas. The majority of dive times measured by Gordon (1987) in Sri Lanka ranged between 25 and 50 min. Off the Galapagos Island, Papastavrou et al. (1989) measured dives of about 40 min, followed by 10 min at the surface. Watkins et al. (1985) reported sperm whale dives of over 2 h duration in the southeast Caribbean.

Our results suggest there is no consistent relationship between the length of the dive and the length of the surfacing period or the number of respirations, although it might be expected that the recovery time at the surface would increase as the dive time increases. Gordon (1987) also observed no significant correlation between these variables, while Lockyer (1977) reported that surface times increased with dive time. Other variables, such as the depth of dives, which could not be measured here, could influence the time required to recover at the surface.

Range

Results from this study suggest that sperm whale foraging activity extends over a mean horizontal range of 1.3 nmi between dive cycles. This corresponds to an average speed of 2.7 km/h, which is consistent with the speeds of diving males measured in other parts of the world (Gordon et al., 1992; Jaquet et al., 2000; Watkins et al., 2002). It could be extrapolated that the whales travel horizontal distances of up to 33 nmi per day (24 h); however, this extrapolation needs to be treated with caution because information was not gathered over a full 24 h period, and we do not know the spatial foraging pattern at depth. The proportion of the day dedicated to diving/feeding activity in this region is unknown. In the Azores, it appears that whales spend 75-80% of their time in "feeding mode" (Gordon & Steiner, 1992). If a similar behavior is observed in the Mediterranean Sea, and assuming the whale is stationary when not involved in diving activity, the associated distance traveled during the 24-h period would be approximately 25 nmi.

Some of the whales observed over several dive cycles remained within the continental slope isobaths and seemed to maintain a direction relatively parallel to the coastline. This observation is consistent with other observations made off Nova Scotia, where sperm whales followed over three dive cycles appeared to travel in fairly straight lines along the contours of the Scotian shelf, at about 2 kts (Mullins et al., 1988). Further surveys are encouraged to investigate the movement of individual sperm whales and habitat use over extended periods of time as movement patterns might vary with topography and feeding success (Whitehead, 2003). Particularly, it would be interesting to know if sperm whales return to the same areas to feed—that is, effectively "looping back" to the beginning of a feeding run—and if this is the case, to determine periodicity over which such returns take place. If sperm whales are attracted to the northwestern basin of the Mediterranean Sea because of profitable foraging opportunities, it would be useful, for management purposes, to know their movement and residency patterns in this area.

Clicking Time and Periods of Silence

The periods of silence during dives were small and accounted on average for about one min at the beginning and 5.6 min at the end of the dive. Thus, the lag at the start was much shorter than at the end of the dive. Consequently, sperm whales in the Mediterranean Sea spent 70% of the time producing echolocation clicks during an entire dive cycle (i.e., including the surface period). These proportions were very similar to those obtained in other parts of the world. Hiby & Lovell (1989) showed that sperm whales around the Azores were active acoustically for 75% of the time when engaged in cycles of long feeding dives. Mature males feeding off New Zealand were shown to spend approximately 72% of their time clicking when engaged in cycles of long feeding dives (Gordon et al., 1992).

Foraging Activity

Assuming that a creak signifies a feeding event, and that each event represents the successful capture of at least one squid, the average of 25 creaks produced per dive would correspond to at least 25 squid consumed per dive cycle. Therefore, with an average dive cycle of 55 min, and considering whales are involved in diving activity 80% of the time (Gordon & Steiner, 1992), it could be extrapolated that around 750 squid are being eaten per day (24-h period). If there are multiple prey captures at each feeding event, then this figure would increase accordingly (i.e., whales would creak into shoals of squid rather than chasing individual prey). There is a conjecture that some squid may be detected visually, without the use of echolocation (Fristrup & Harbison, 2002), and some cephalopod families such as Histioteuthidae and Ommastrephidae are known to have bioluminescent organs and could be conspicuous at depth (Clarke, 1985). If there is some visually targeted feeding, based on bioluminescence, such feeding events could explain the short but periodic interruptions of the regular click sequences which often occur (i.e., short periods of silence between long sequences of clicks); however, even without visually based foraging, our figures seem credible in terms of prey capture since Clarke's (1987) calculations suggested, from studies of stomach contents, that the number of cephalopods eaten by a sperm whale ranges from around 800 to 2,000 over periods of 1 to 2.5 days. Furthermore, the analysis of one sperm whale's stomach content in the Mediterranean Sea (Roberts, 2003) showed that the squids consumed ranged from 11 to 25 cm of mantle length. Taking an average squid size of 1 kg, the feeding rate observed in this study would correspond to a daily food intake of 750 kg, which is consistent with the anticipated food requirement of the 12-13 m long whales observed in this study (weighing approximately 25 tons); Lockyer (1981) estimated that sperm whales ought to consume a daily quantity of prey equivalent to 3% of their body weight.

Foraging Depth

This study showed the first creak of the dive occurred consistently around 6 to 7 min after the whales fluked-up. This would imply, considering a descending speed of between 75 and 120 m/min (Drouot, 2003; Gordon, 1987; Lockyer, 1977; Madsen et al., 2002; Mullins et al., 1988; Papastavrou et al., 1989; Watkins et al., 2002), a foraging depth of around 490 to 780 m. This implication is consistent with recent work from time-depth recording tags showing that the first creak of the dive is emitted as the whale reaches the foraging depth where it levels off (Zimmer et al., 2003). This result would be consistent with the midwater habitat of Mediterranean squid species such as *Histioteuthis bonnellii* and *Histioteuthis reversa* (Mangold & Boletzky, 1987; Roberts, 2003), known to be part of the sperm whale diet.

Interestingly, the same time interval was observed between the fluke-up to the first creak of the dive and the last click of the dive to the surfacing(i.e., 6.6 min). Assuming the whale stops clicking as it starts its vertical ascent to the surface, and considering an ascending speed of about 117 m/min (Rice, 1989), these results suggest that sperm whales remain in the same depth layer during the dive to chase prey.

The whales observed during this study measured between 11.8 and 13.8 m long and were probably all males (Rice, 1989). The results showed that the number of creaks produced during the dive and the timing of the first creak increased significantly with whale size. This is coherent with the biological needs of the animal: the larger the whale is, the more food intake it requires. The increasing time between the whale fluke-up and the first creak of the dive might reflect an increased travel time to reach the foraging layer, suggesting that larger animals tend to reach deeper layers to search for food, perhaps to find larger prey items or a higher abundance of squid. This trend could also reflect a lesser diving capacity in smaller whales. An unusual observation was made of a sperm whale with half of the tail fluke missing (Figure 2). This whale produced apparently fewer creaks per dive than the average and produced its first creak after a longer interval than the other whales. The injury, probably resulting from a collision with a boat, is very likely to have altered the swimming behavior and foraging activity of the whale.

Figure 2. Photograph of an injured sperm whale sighted off the coast of Provence (France) in August 2003 (from A. Gannier)

No significant correlation was found between the foraging activity and the dive duration or the distance traveled, although in the Gulf of California, these variables have been shown to be related to food resources (Jaquet et al., 2000, 2003).

Conclusion

This study demonstrated that the northwestern Mediterranean is intensively used by sperm whales for foraging. This description of habitat use provides elements to strengthen the conservation status of this species in an area were commercial boat traffic, already intense, is to increase steadily in the forthcoming years

Acknowledgments

We thank Marineland, the Ministère de l'Ecologie et du Développement Durable, and the Conseil Regional de Provence-Côte d'Azur for having funded this study. We thank all the members of the GREC who benevolently participated in the surveys. We thank H. Whitehead and S. Magalhaes for their helpful comments on the manuscript.

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