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Distribution and relative abundance of sperm whales in the Mediterranean Sea

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ABSTRACT: The distribution of sperm whales in the Mediterranean Sea was investigated over 4 consecutive years. Field surveys took place in 1997, 1998, 1999 and 2000 between June and August from a 12 m survey boat equipped with towed hydrophones. The boat cruised at a mean speed of 6 knots on zig-zag lines. The total transect length was 12 709 km, and 3903 acoustic stations were assigned along the transects to monitor the underwater acoustic environment for sperm whale clicks. The Mediterranean Sea was divided into 6 regions for data analysis: the Ligurian Sea, the Gulf of Lions, the southwestern basin, the Alboran Sea, the Tyrrhenian Sea and the Ionian Sea. Relative frequencies and relative abundances of sperm whales were calculated from both visual and acoustic data. Acoustically, the Gulf of Lions yielded the highest relative abundance, with an average of 2.15×10^{-2} whales heard km^{-1} effort. High abundance was also seen in the southwestern basin and the Ionian Sea (1.90×10^{-2} and 1.21×10^{-2} whales heard km^{-1} respectively). Visual results indicated high relative abundance in the southwestern basin, with 4.88×10^{-2} sperm whales sighted km^{-1} effort. Intermediate values were obtained in the Ligurian Sea, and there were few sightings in the Alboran and Tyrrhenian Seas. Most of the sightings south of the 41° parallel consisted of sperm whale groups, of 5 to 7 individuals. Analysis of sperm whale distribution with respect to bathymetry did not establish a significant preference for either continental-slope waters or the open sea. High biological productivity in the northwestern basin might explain high sperm whale relative abundance, noticeably in the Gulf of Lions.

KEY WORDS: Sperm whale · Distribution · Mediterranean · Survey · Acoustics · Sightings

INTRODUCTION

Sperm whales inhabit all the world's oceans, from the equator to the edges of the polar pack ice. Sperm whale social structure is dominated by 2 types of groups: breeding schools and bachelor schools, which are known to perform seasonal migrations between temperate and polar waters (Rice 1989). Males are often found solitary or in loose groups, with larger individuals reaching higher latitudes.

Sperm whales are known to inhabit offshore and continental-slope waters (Rice 1989) and some correlation can be found between sperm whale abundance and areas of high primary production (Jaquet & Whitehead 1996). In feeding areas they perform prolonged and deep dives, usually of 30 to 60 min duration (Rice 1989), and emit clicks constantly (Watkins 1980), the characteristics of which are consistent with echolocation (Goold & Jones 1995). In most areas they appear to feed on mesopelagic squid (Kawakami 1981).

Although little dedicated research has been carried out to adequately map their distribution, the species is 1 of 8 common cetacean species in the western Mediterranean Sea (Duguy 1991), and is known to inhabit the eastern basin (Frantzis et al. 1999). Recent sightings of sperm whales in the Mediterranean Sea

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have most frequently been of isolated individuals and couples (Mangano 1983, Pavan & Borsani 1997, Gannier 1998b, Mussi et al. 1998). Social groups have occasionally been reported in recent times (Duguy et al. 1983), although schools of more than 15 individuals were observed in the 1950s (Bolognari 1951). Unlike other regions of the world, information on sperm whale populations is not available from whaling activities within the Mediterranean Sea. Stranding and by-catch data released for Italy by Centro Studi Cetacei (1988 to 1998, 1997 excluded) show a decrease of yearly mortality between the 1987 to 1989 period (19 to 13 individuals reported) and the 1990s (an average of 6 individuals reported), especially for individuals >14 m. By-catches linked to driftnet fisheries have also been reported in recent times (Di Natale & Notarbartolo di Sciara 1994), although no clear trend could be assessed as no indication is given regarding the fishing effort. The species population status in the Mediterranean Sea is presently unknown.

Sperm whale vocalisations can be detected using near surface hydrophones. Passive acoustic techniques have already proved to be efficient in finding and locating sperm whales, and estimating abundance (Leaper et al. 1992, Gillespie 1997), and have been used to relate sperm whale distribution to local topography (Gordon et al. 1998). Passive acoustic techniques can also be used to estimate individual body lengths of sperm whales (Gordon 1990, 1991, Goold 1996) and for increasing ecological and ethological knowledge on the species (Whitehead 1989, Weilgart & Whitehead 1992).

Our research attemps to assess the distribution and relative abundance of sperm whales in the Mediterranean Sea.

MATERIALS AND METHODS

Study area. We investigated a large tract of the Mediterranean Sea from the Strait of Gibraltar (5° W) to the island of Rhodes, Greece (28° E). From an oceanographic point of view, the Mediterranean Sea is formed by 2 main basins (Nielsen 1912): (1) the western basin (from Gibraltar to Sicily, including the Tyrrhenian Sea), and (2) the eastern basin (regions east of Sicily). The Tyrrhenian Sea is commonly considered as a distinct entity, because it is semi-enclosed between islands (Corsica and Sardinia) and mainland (Italy), and separated from the rest of the western basin by a channel of moderate depth, ca. 1500 m (Fig. 1). From an ecological point of view, it is justified to separate the western basin into a southwestern and a northwestern area: hydrobiological studies have shown different seasonal and primary production patterns to exist in the western basin, as apparent in satellite imagery analysis (Morel & André 1991). The boundary between the northwestern and southwestern areas is taken here as the 41° parallel because the north Balearic front is frequently located close to this latitude (Le Vourch et al. 1992).

All regions include large areas of deep water (>2000 m), and continental shelves are generally narrow. Continental slopes (200 to 2000 m) are generally steep, extreme cases being found off Provence, Minorca, southeastern Spain, northwestern Sardinia and Corsica, eastern Sicily and southwestern Peloponnese (Fig. 1). Areas of intermediate depth (1000 to 2000 m) include the Alboran Sea, the western Balearic Sea, the northern Tyrrhenian Sea, the eastern Ligurian Sea, and the Sicilian and Sardinian channels.

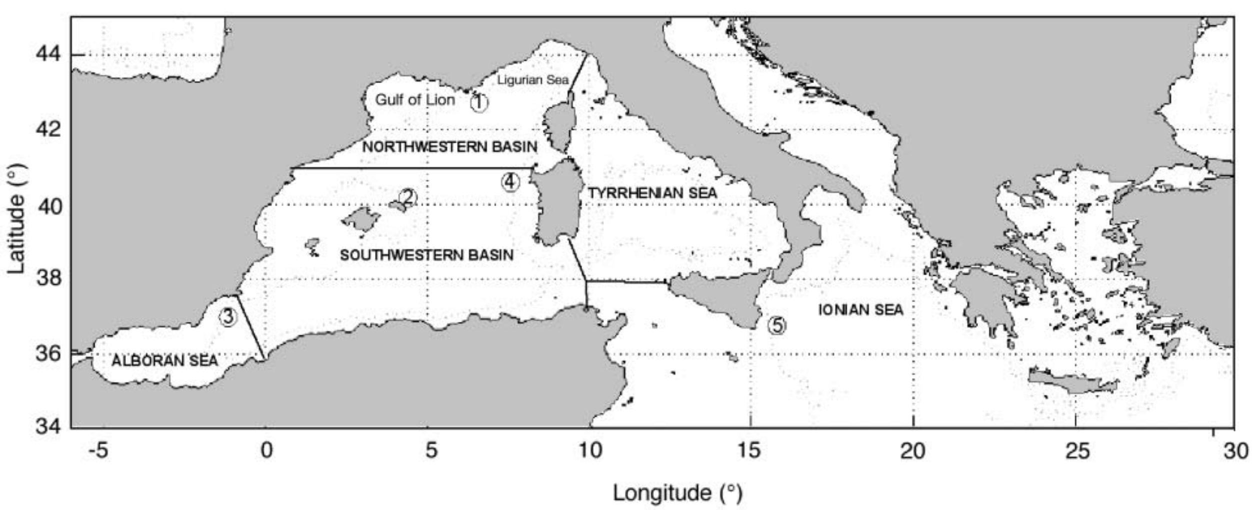

Fig. 1. The Mediterranean Sea showing the different regions sampled. Numbers indicate areas of steep continental slope: (1) Provence, (2) Minorca (Balearics), (3) southeastern Spain, (4) northwestern Sardinia and Corsica, (5) eastern Sicily and (6) southwestern Peloponese

Sampling strategy. It was not possible to survey all regions of the Mediterranean in a single year, due to its geographic extent, so different regions were surveyed during 4 consecutive summers. Survey data were collected from 7 July to 8 August 1997, 18 June to 13 August 1998, 23 June to 13 August 1999 and 19 June to 4 August 2000. The surveys covered 5 distinct regions of the Mediterranean (Fig. 1): the northwestern basin (44–41° N, 3–9° E), the southwestern basin (41–35° N, 0–9° E), the Alboran Sea (0–5° W), the Tyrrhenian Sea (43–38° N, 9–16° E) and the Ionian Sea (38° 30′–36° N, 15–21° E). In the results, we sub-divided the northwestern basin into a Gulf of Lions sector and a Ligurian Sea sector (Fig. 1). The 1997 and 1999 surveys covered part of the northwestern and southwestern basins, while 1998 and 2000 were mainly devoted to the Tyrrhenian and Ionian Seas, but also covered the northwestern basin (Fig. 2). The different data sets were pooled to gain an overall picture of sperm whale distribution in the Mediterranean, on the assumption that no large-scale summer distribution shifts occurred from year to year.

The sampling strategy was constrained by the endurance of the survey vessel, a 12 m motor-sailer with an 80 hp diesel engine allowing a mean speed of 11 km h^{-1}. The maximum continuous endurance at sea was 5 d with the nominal crew of 5 to 7 people. Another constraint was an overall survey window of about 6 wk per summer, largely dictated by vessel and crew availability, as well as good weather periods. Therefore, each of the 4 surveys was organised as a round trip from Antibes (France) to a remote area that had to be reached about 3 wk from departure (south Sardinia in 1997, Peloponnese in 1998, Gibraltar in 1999 and Rhodes in 2000). Corridors of variable width were conceptually placed around the direct paths between 2 ports of call, and within these, a zig-zag vessel course was predetermined in a manner that utilised all the available vessel time within that area. Zig-zag tracks were aligned approximately at 20 to 30° to the longitudinal axis of the corridor to limit the 'range penalty' induced by the zig-zag procedure, as opposed to a pure straight-line route. Coverage within these corridors was reasonably even, and included slope and open sea areas, depending on the local topography. Corridor widths ranged from 15 to 76 km, and lengths from 76 to 480 km. An average vessel speed of 11 km h^{-1} was maintained, giving a 9.5 to 10.3 km h^{-1} vector along the longitudinal axis of the survey boxes, sufficient to avoid double counting of sperm whales. Sperm whales had been observed during previous surveys to move at <7.5 km h^{-1} (A. Gannier unpubl. data). Whitehead (1989) also reports sperm whale swimming speeds of foraging whales of 3 to 6 km h^{-1}, and Watkins et al. (2002) measured an average 3.3 km h^{-1} on diving sperm whales.

Visual survey methods. Field observation protocol followed a method described by Gannier (1998a,b), and combined visual searching with systematic, discrete acoustic sampling. The visual survey consisted of continuous, naked eye observation by rotating shifts of 3 observers. One observer stood in front of the mast searching the ±45° sector ahead, 2 other observers, sitting on the roof, scanned the 30 to 90° sectors on either side of the centre line. Visual searching took place from 30 min after sunrise to 30 min before sunset, when wind speed was lower than Beaufort 4. Individual observers were rotated on a 2 hourly basis. An index of sighting conditions was recorded every 20 min: the index varied from 0 (null) to 6 (excellent) and was derived from wind speed, sea-state, residual swell and light conditions (Gannier 1997, 1998a). This index was used as a criterium to discard transect portions with poor observation conditions from the analy-

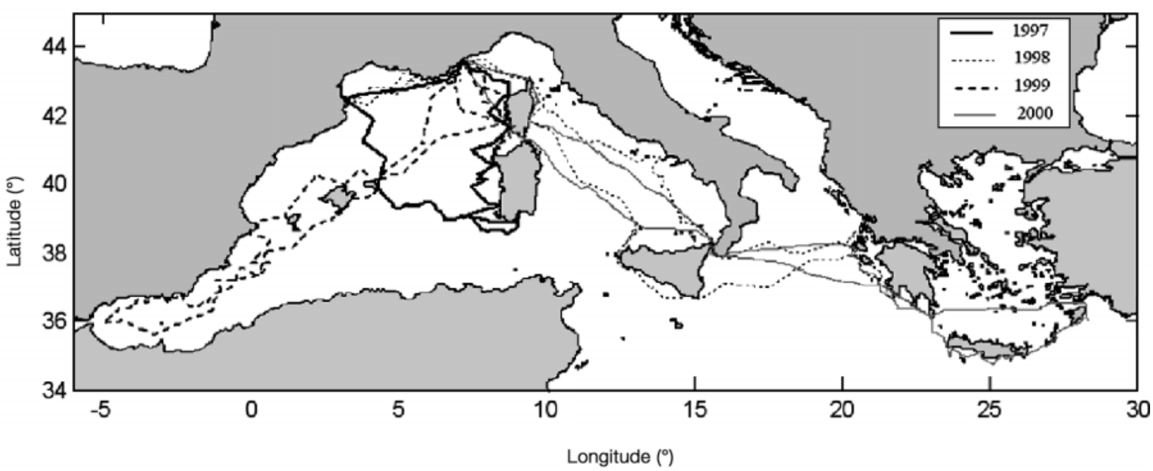

Fig. 2. The Mediterranean Sea, showing the 1997, 1998, 1999 and 2000 transects

sis, instead of considering a combination of several environmental variables. When cetaceans were sighted, various sighting parameters were recorded, e.g. distance and bearing to the boat, school size, and behaviour. When sperm whales were sighted, a close approach was usually attempted and the whale body size was estimated visually. Further data were collected when the conditions were favourable (e.g. photo identification images, sloughed skin for genetic analysis). Underwater observation and photography was attempted, weather permitting, to determine sex. Such close encounters ended when whale(s) fluked and dived, at which point the pre-defined sampling track was resumed. This period of approach for additional data collection was considered off-effort and was not included in the relative abundance analysis. Visual data obtained when the boat was static and searching for an acoustically detected sperm whale was considered on-effort. Thirty percent of the sightings occurred in such conditions.

Acoustic survey methods. During 1997 and 1999 surveys, a dual channel hydrophone (IFAW-type rebuilt by Magrec) (e.g. Leaper et al. 1992) was towed on a 100 m cable. Each unit included one Benthos AQ-4 transducer element and a miniaturised pre-amplifier, with integrated 200 Hz high-pass filter. During the 1998 survey, a mono hydrophone (Magrec, HP 30MT) of similar specifications was used, towed on a 60 m cable. The transducer elements (Benthos AQ-4) and the integral pre-amplifiers were the same in both hydrophones. Therefore, the signals received would have been virtually identical whichever of the hydrophones was used. An external high-pass filter unit, set to 1 kHz, was used on the hydrophone output to improve the quality of listening and recording, i.e. by reducing low frequency rumble and noise. The filtered signal output was connected to either a TCD-7 DAT recorder or a Sony WMD-6 analogue tape recorder, and to the operator headphones.

The acoustic survey sampling method consisted of a 1 min operator listening session every 3.7 km (2 n miles) along the cruise tracks. The vessel's propeller was de-clutched and listening was performed after the vessel had slowed to less than 6 km h^{-1}. At this speed, the hydrophone array depth was estimated from underwater observation to be 8 to 10 m for the stereo model and 6 to 7 m for the shorter mono-model. The perceived levels of both bioacoustic signal (i.e. whale clicks) and overall noise were recorded subjectively at each acoustic station using a 5 level scale based on a sample tape provided by IFAW and used previously to standardise acoustic assessment (Gordon et al. 1998, 2000). Only experienced operators performed the acoustic scoring and recording. The higher the signal, the greater the score, so that 0 relates to no detection and 5 to loud signal, the same rules applying for the background noise (however, noise scoring started from 1, as background noise is always present). When identified, the source of the noise was described (sea state, boat traffic). When the noise reached level 5, no cetacean vocalisation could be perceived, and at level 4, we generally could not be confident about segregating cetacean clicks from the background. Such noise levels of 4 and 5 were reached in 3.2% of the acoustic samples. Acoustic sampling was carried out during both daylight and night-time periods, since sperm whales are known to forage, and click, throughout the day-night cycle (Smith & Whitehead 1993, Watkins et al. 2002). Acoustic surveying was only undertaken when the bottom depth was greater than 100 m, the wind speed was less than Beaufort 5, and in sectors where fishing activity or shipping traffic was not intense; all precautions to avoid any physical damage to the hydrophone equipment. When sperm whale clicks were identified, recordings were made and the sampling interval was decreased to 1 session per 1.85 km (1 n mile). When the signal reached a level of 4 or 5 (i.e. loud clicks), the boat was completely stopped and continuous recording was carried out for 1 diving-surfacing cycle. Visual searching effort was also extended to scan the full 360° to visually locate the blows, or the flukes of a diving whale. Normal survey procedure was resumed whenever the whale could not be visually detected after 1 full dive cycle.

In order to estimate the sperm whale detection range with our hydrophones, simple acoustic experiments were carried out with both hydrophone types. The boat would steam in a straight line at 12 km h^{-1} away from a whale (12 to 14 m in length) that had just fluked nearby. One listening and recording period was performed every 1.85 km until clicks could no longer be heard. This test was performed on 5 occasions with the dual hydrophone and once with the mono hydrophone. The results supported our hypothesis that hydrophones presented similar signal detection (Fig. 3) and indicated an approximate detection range of 7 to 8 km (Table 1). The detection range assumes the whales to remain approximately stationary in the horizontal plane during the experiment, an assumption that is not totally realistic but is acceptable if the whale movement is small relative to the boat movement.

Data analysis. Data were loaded into a database and then exported to the geographic software Oedipe (Massé & Cadiou 1994), which was used for mapping of the survey track, determining the surface area of each region, as well as visual and acoustic detections. Following a method used by Jacquet & Whitehead (1996) in the Pacific Ocean, the survey track was divided into segments for data analyses. A 37 km segment length (20 n mile) was chosen, instead of 148 km segment lengths used in the Pacific surveys of Jacquet & Whitehead (1996) because of the smaller scale topography in the Mediterranean. For each of these segments, visual and acoustic observations were quantified.

Only visual data obtained with sighting-conditions index ≥4 were analysed. The variables calculated for each 37 km line segment were: a sighting frequency (SF), defined as the number of sperm whale sighting events km^{-1}, and a visual relative abundance (VRA), defined as the actual number of animals seen km^{-1} effort.

Similarly, only those acoustic contacts featuring a low to medium level of background noise (level 1 to 3) were included in the analysis. Acoustic-data processing necessitated an additionnal stage as 1 given animal, or group of animals, could be detected over several acoustic stations. Each series of consecutive positive contacts was grouped into 1 'Acoustic Sequence', with each acoustic sequence classified as an independent event (Gordon et al. 1998). Detections of sperm whale clicks were assumed to be from a new animal or group of animals when no sperm whales had been detected for at least 1 h (Gordon et al. 2000). Two variables were calculated from the acoustic data, for each 37 km line segment: an acoustic frequency (AF), defined as the number of acoustic sequences km^{-1} transect, and an acoustic relative abundance (ARA), defined as the minimum number of animals heard km^{-1}. The number of whales was determined by listening to the recordings performed over all the positive stations forming the acoustic sequence. However, the number of animals could only be reliably determined when they numbered 3 or less. If more than 3 whales were clicking simultaneously, a school size of 3 animals was allocated by default.

For regional comparison to be meaningful, visual and acoustic variables were post-stratified. For each region, mean frequencies and relative abundance estimates were first computed for the slope and open-sea stratum and then pooled to obtain an area-weighted mean, using the following equation (Buckland et al. 1993):

$$\text{Weighted mean } V = [V_{\text{slope}} \times A_{\text{slope}} + V_{\text{open-sea}} \times A_{\text{open-sea}}] / A_{\text{Total}}$$

and the corresponding variance:

$$\text{Var}(V) = [A^2_{\text{slope}} \times \text{var}(V_{\text{slope}}) + A^2_{\text{open}} \times \text{var}(V_{\text{open}})] / A^2_{\text{Total}}$$

where V is the variable (SF, VRA, AF or ARA), V_{slope} and $V_{\text{open-sea}}$ are mean estimates obtained over the slope and the open-sea stratum; A_{slope}, and $A_{\text{open-sea}}$ are the surface area of each stratum and A_{Total} the total surface area of the region.

Sperm whale sightings were also related to 3 different topography-related variables: water depth, distance to the nearest coast, and distance to the 200 m contour. Sperm whale sightings were plotted on nautical charts (Service Hydrographique et Océanographique de la Marine) from which topographic variables were measured. Mean SF, VRA, AF and ARA were also globally estimated for the continental slope (200 to 2000 m depth) and the open sea (≥2000 m). When a survey-line segment overlapped the 2000 m isobath, it was assigned either to the slope stratum or to the open-sea stratum, depending upon the proportion of the track on either side. The stratum determination was ambiguous when the proportion of open-sea or slope track was between 40 and 60 %, which happened for 2.4 % of the segments.

Table 1. Results of the 6 tests performed to estimate the detection range of the hydrophone: mean distance sailed away from the position where the whales fluked up for each signal intensity index value

Signal intensity	Mean distance (n miles)	km	SD
5	0.4	0.8	0.56
4	1.8	3.3	0.82
3	2.1	3.8	0.71
2	3.6	6.7	1.03
1	4.2	7.7	0.97
0	6.6	12.2	1.11

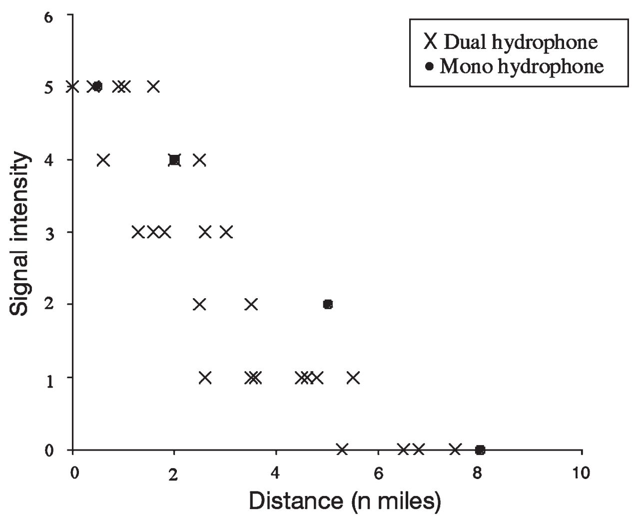

Fig. 3. Variation of the signal intensity index with distance sailed away from the position where the whales fluked up

Table 2. Distribution of acoustic and visual sampling effort (in km) and proportion of effort spent over the continental slope (bottom depth < 2000 m) and the open-sea (>2000 m). Parentheses: effort with good visual and acoustic condition: visibility index (VI) ≥4 and background noise index (NI) ≤3

Region	Area (km^2)	Oceanic area (%)	Effective effort (VI ≥ 4)	% Effort slope	% Effort open sea	n acoustic samples (NI ≤ 3)
Northwestern basin	155600	55.9	3463 (2474)	55.6	44.3	1076 (871)
Southwestern basin	268600	57.7	2216 (1166)	57.9	42.1	653 (559)
Alboran Sea	81200	20.7	1059 (750)	95	4.9	329 (245)
Tyrrhenian Sea	209400	39.2	2843 (1953)	66.9	33.1	715 (593)
Ionian Sea	195000	63.0	3128 (2068)	55.1	45.0	790 (657)
Total		–	12709 (8411)	62.1	38.0	3903 (3058)

RESULTS

Survey effort

The sampling coverage in the 5 regions was expressed in terms of visual 'effective effort' (i.e. length of transect where observation procedure was applied), and acoustic 'effective effort' (i.e. the number of listening stations), Table 2. The visual effective effort totalled 12 709 km of transect, including 8411 km with good to excellent sighting conditions (visibility index ≥ 4). The acoustic effective effort totalled 3903 sampling stations, of which 3058 featured low to medium underwater noise (noise level < 4).

The visual effective effort varied between regions (Table 2); the northwestern basin received coverage of 3463 km, the Alboran Sea 1059 km, the southwestern basin 2216 km, the Tyrrhenian Sea 2843 km and the Ionian Sea 3128 km. Although the survey attempted to balance the effort between the continental slope and open sea, the distance of effective effort globally favoured the continental shelf (62 %).

Sightings

Sperm whales were sighted on 26 occasions in good observation condition (index >3): 12 in the northwestern basin 11 in the southwestern basin, one in the southern Tyrrhenian Sea and 2 in the Ionian Sea (Fig. 4). The sightings in the Tyrrhenian and the Ionian Seas were of sperm whale groups, numbering 5 to 7 animals. Solitary animals were predominant in the northwestern basin, all 12 sightings were solitary. Eighty percent of on-effort sightings were obtained after animals had been first detected acoustically, highlighting the utility of passive acoustics for detection of this species.

Sightings of schools >2 individuals occurred on 7 occasions during the survey, and always occurred south of the 41° parallel. All 7 of these groups included calves. Schools numbering 5 or more had 2 calves. Underwater observation enabled the sex of at least 1 of the large individuals of the mixed group to be determined on 4 separate occasions, and this was confirmed by underwater photography for 3 sightings. In each

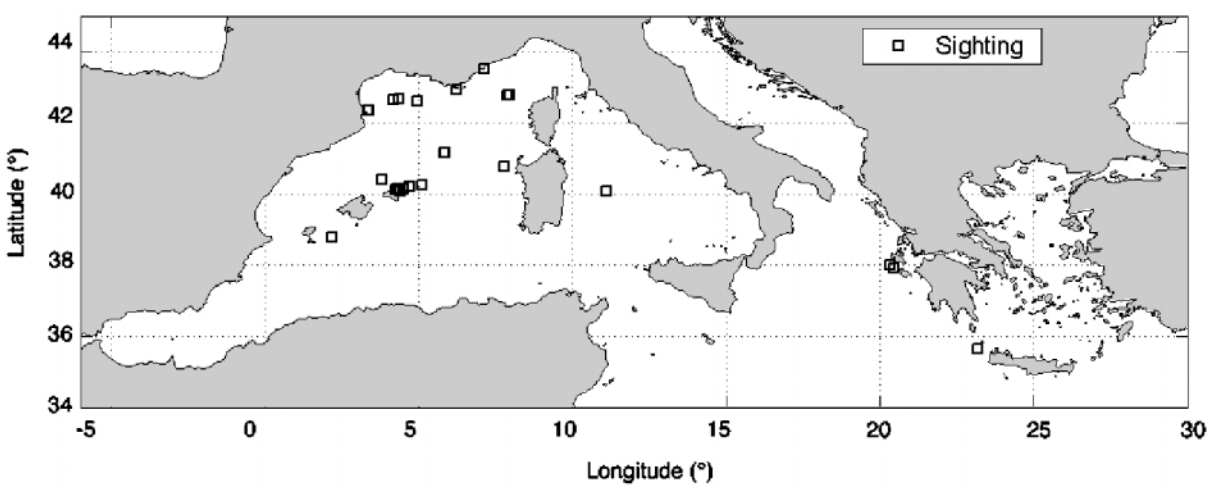

Fig. 4. Distribution of sperm whale sightings during 1997, 1998, 1999 and 2000 summer surveys

case the sex proved to be female. These groups were assumed to be breeding schools, based on observations of sperm whale social structure in other parts of the world (Rice 1989).

Table 3. Area-weighted mean sighting frequency (SF) and mean visual relative abundance (VRA) of sperm whales in 6 regions investigated

Region	No. of segments	SF (sighting km^{-1}) ± SE	VRA (whales km^{-1}) ± SE
Ligurian Sea	60	3.81×10^{-3} (1.75×10^{-3})	4.05×10^{-3} (1.77×10^{-3})
Gulf of Lion	25	3.02×10^{-3} (1.75×10^{-3})	3.02×10^{-3} (3.75×10^{-3})
Southwestern basin	43	1.78×10^{-2} (1.41×10^{-3})	4.88×10^{-2} (1.41×10^{-2})
Alboran Sea	29	0	0
Tyrrhenian Sea	65	8.21×10^{-4} (5.73×10^{-3})	4.11×10^{-3} (1.73×10^{-3})
Ionian Sea	77	1.02×10^{-3} (5.96×10^{-3})	6.00×10^{-3} (1.83×10^{-3})

Regional variations in visual relative abundance

Both 1997 and 1998 surveys covered similar areas of the northwestern basin and the results showed little inter-annual variability. Statistical tests indicated no significant inter-annual difference in the visual and acoustic abundance indices for segments (Kruskal-Wallis test performed on SF: $H = 0.06$ with $p = 0.805$; on VRA: $H = 0.03$, $p = 0.853$; on AF: $H = 0.53$, $p = 0.468$; on ARA: $H = 0.07$, $p = 0.791$). Therefore it was deemed acceptable to pool these 2 data sets to increase sample size for inter-regional analysis.

No sperm whale sighting was made in the Alboran region. In the other regions SF varied from lower values of 8.2×10^{-4} sightings km^{-1} in the Tyrrhenian Sea and 1.02×10^{-3} sightings km^{-1} in the Ionian Sea to higher values of 1.8×10^{-2} in the southwestern basin (Table 3). Statistically, sighting frequencies were significantly higher in the southwestern basin than in the other regions. The Gulf of Lions and the Ligurian Sea produced similar values to each other, 3.0 and 3.8×10^{-3} sightings km^{-1} (*t*-test: $t = 0.23$, $p = 0.82$). The low frequencies observed in the Tyrrhenian, Ionian and Alboran Seas showed no significant differences (*t*-test, $p > 0.90$). In the southwestern region, sightings appeared to be very concentrated in a few particular areas such as around the Balearic Islands, whereas sightings in the northwestern basin were more spread out (Fig. 4).

The VRA results showed a slightly different picture (Table 3). As with sighting frequency, the highest VRA was found in the southwestern basin (4.9×10^{-2} whales km^{-1}) and the lowest in the Alboran Sea (0). VRA in the other regions ranged from 3.0×10^{-3} whales km^{-1} in the Gulf of Lions to 6.0×10^{-3} in the Ionian Sea. The high relative abundance in the southwestern basin resulted from frequent sightings of large groups. In other regions, moderate values resulted either from frequent sightings of single individuals, such as in the northwestern basin, or to rare sightings of large groups, such as in the Tyrrhenian and Ionian Seas. Statistically, the southwestern basin had a higher VRA than the other regions (*t*-test; $p < 0.01$).

Regional variations in acoustic results

Out of all the effective-effort acoustic stations, 358 yielded sperm whale vocalisations. These 358 positive acoustic stations clustered into 55 acoustic sequences (Fig. 5); on average a sperm whale group was heard across 5.67 stations (or ~21 km). AF showed a

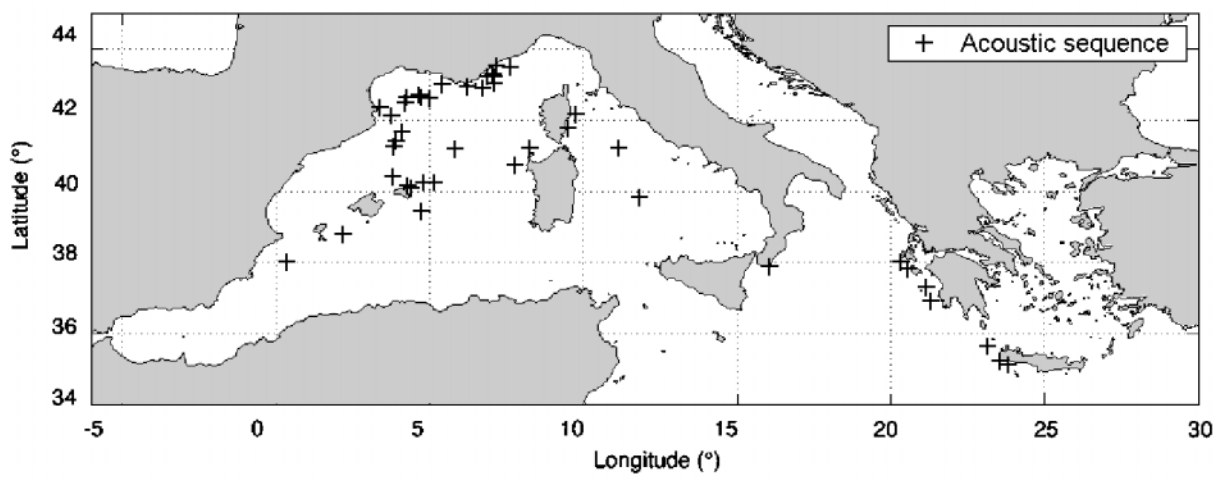

Fig. 5. Distribution of the centre of sperm whale acoustic sequences during 1997, 1998, 1999 and 2000 summer surveys

Table 4. Area-weighted mean acoustic sequence frequency (AF) and acoustic sequence relative abundance index (ARA) in the 6 regions

Region	No. of segments	AF (acoustic sequence km^{-1}) ±SE	ARA (whales km^{-1}) ±SE
Ligurian Sea	70	5.93×10^{-3} (1.19×10^{-3})	7.77×10^{-3} (1.69×10^{-3})
Gulf of Lion	27	9.94×10^{-3} (3.87×10^{-3})	2.15×10^{-2} (8.05×10^{-3})
Southwestern basin	62	7.06×10^{-3} (3.65×10^{-3})	1.90×10^{-2} (7.64×10^{-3})
Alboran Sea	32	2.91×10^{-3} (4.82×10^{-4})	2.91×10^{-4} (8.63×10^{-4})
Tyrrhenian Sea	67	2.59×10^{-3} (1.77×10^{-3})	7.43×10^{-3} (5.32×10^{-3})
Ionian Sea	80	6.03×10^{-3} (1.93×10^{-3})	1.21×10^{-2} (5.69×10^{-3})

quite regular pattern among regions (Table 4). Sperm whale acoustic sequences were frequent in 4 areas: the Gulf of Lions (9.94×10^{-3} seq. km^{-1}), the southwestern basin (7.06×10^{-3} seq. km^{-1}), the Ionian Sea (6.03×10^{-3} seq. km^{-1}) and the Ligurian Sea (5.93×10^{-3} seq. km^{-1}). Sperm whale acoustic sequences were much less frequent in the Alboran and Tyrrhenian Seas.

Three regional groups could be qualitatively distinguished from ARA results (Table 4): regions with high ARA, namely the Gulf of Lions (2.1×10^{-2} whales heard km^{-1}) and the southwestern regions (1.9×10^{-2} whales km^{-1}); regions with moderate ARA, namely the Ligurian, Tyrrhenian and Ionian Seas (range 7.8×10^{-3} to 1.2×10^{-2} whales km^{-1}); and regions of low ARA, namely the Alboran Sea (8.6×10^{-3} whales km^{-1}). The regions could not be shown to be statisticially significantly different due to high variance in the data.

Topographic related distribution

Descriptive results

Sixty-five percent of sperm whale sightings occurred inshore of the 2000 m contour, with 51 % of these occurring in areas less than 1000 m deep. The mean depth of sightings was 1374 m with a low variability (SE = 160, range 100 to 2800 m). However, this apparent preference for the continental-slope waters did not prove to be statistically significant (chi-squared goodness of fit, $\chi^2 = 1.255$, df = 1, $p > 0.05$).

The mean distance of sperm whale sighting locations to the coastline was 49.7 km (SE = 9.57, range 5 to 185 km), with 20.7 % of the sightings located less than 10 km from the nearest coastline. The coastline and the 200 m isobath are often less than 10 km apart, with the exception of the Gulf of Lions, where the continental shelf extends far offshore. Sperm whale sightings were located at a mean distance of 36.1 km from the 200 m contour (SE = 9.63, range 1 to 179 km). Of these sightings 51.7 % occurred less than 10 km from the 200 m contour, suggesting that sperm whales have an affinity for continental-slope waters, although continental-slope waters totalled 62.5 % of the effective effort.

Effort-corrected results

A sighting frequency of 0.538×10^{-2} sightings km^{-1} was obtained on the continental slope (SE = 0.21) compared to 0.213×10^{-2} sightings km^{-1} in the open sea (SE = 0.11). Acoustic sequence frequencies were respectively 0.688 and 0.555×10^{-2} sequences km^{-1}. Both VRA and ARA indices showed higher values over the continental slope than in the open-sea segments: a VRA of 1.29×10^{-2} whales km^{-1} (SE = 0.616×10^{-2}) was found in continental-slope waters, against 5.67×10^{-3} whales km^{-1} (SE = 0.328×10^{-2}) in the open sea. Likewise, an ARA of 1.486×10^{-2} whales km^{-1} (SE = 0.377×10^{-2}) was obtained in continental-slope waters against 0.952×10^{-2} whales km^{-1} (SE = 0.244×10^{-2}) in the open sea. Again these results suggest some preference for continental slopes, but again a statistical significance could not be demonstrated for either visual or acoustic results.

DISCUSSION

Comparisons of visual and acoustic results

This survey allowed us to compare visual and acoustic techniques. A greater number of acoustic sequences (55 out of 3058 samples) were found compared to the number of surface sightings across all regions (26 from 12 709 km of effective effort), with the majority of these visual sightings first detected acoustically. This fact highlights the efficiency of passive acoustic detection. Sperm whales could probably be heard up to 8 km from the boat in good noise conditions, whereas the maximum visual detection distance was 4 km (with a mean visual-detection range of 1.2 km). Higher relative abundances were obtained from acoustic data compared to visual data, with a consistent magnitude between the 2 techniques through most of the regions (Tables 2 & 3). A noticeable exception is the southwestern basin, where the acoustic indices (AF = 7.06×10^{-3} acoustic sequences km^{-1}, ARA = 1.90×10^{-2} whales km^{-1}) were substantially inferior to the visual indices (SF = 1.78×10^{-2} sightings km^{-1}, VRA = 4.88×10^{-2} whales km^{-1}). In this case, 4 sightings were groups of 3 to 6 individuals with calves and, in most instances, several members of the school remaining at the surface or just below the surface without producing loud regular clicks. On at least 1 occasion, a sperm whale school was observed resting for more than 1 h, and it was verified that clicks (as well as other vocalisations) were weak and infrequent. Thus, while the survey results underline the usefulness of acoustic methodology, the problem of the detection of social groups, where not all the animals are involved in diving (clicking), should always be borne in mind. Gillespie (1997) also faced the non-detection of apparently silent sperm whales and concluded that long duration monitoring should be carried out to gather necessary data on click-emission cycles. Previous research has shown that vocalisation rates were dependent on sperm whale social structure and activity. Leaper et al. (1992) assumed sperm whales were emitting regular clicks 50 % of the time, in agreement with the proportion of 48 % found by Whitehead & Weilgart (1990) in the Galapagos. However, these average clicking rates were obtained for breeding groups; mature males engaged in feeding dives may spend 72 % of their time clicking (Gordon 1987). Such variation in vocalisation behaviour with activity is likely to have influenced our results, since in some areas (Gulf of Lions, Ligurian Sea) we observed feeding animals, and in others (around Balearic Islands, off Peloponnese) we mostly observed social groups. Furthermore, in areas where social groups were frequent, ARA is probably underestimated since a threshold of 3 animals was taken for the index calculation (due to the methodological limitation), while up to 7 animals had been observed at the surface. In the southwestern basin particularly, a minimum number of 3 animals was assigned to 80 % of the acoustic sequences. This factor may account for the difference between the VRA and ARA estimates in the southwestern basin.

Furthermore, the visual protocol might have benefitted from the ARA survey as acoustic detection caused increased visual awareness from the visual observers. In addition, when a high signal level was received, the boat was stopped and full 360° searching was carried out, further enhancing the probability of visually detecting whales. This intensified searching seemed to be particularly successful for social group sightings, as 7 groups were detected in such conditions in the southern regions as opposed to 1 individual in the Gulf of Lions. This might be explained by the increased time spent by the social group at the surface (including alternance of individuals at the surface) compared to the 10 min typical surfacing period of a feeding animal involved in deep diving activity.

Breeding schools

Six groups contained 3 to 7 animals and included 1 or more calves. These groups were assumed to be breeding schools, based upon observations of sperm whale social structure in other regions of the world (Rice 1989) and on opportunistic underwater observation. These are considered to be large groups compared to sightings made during other Mediterranean surveys (Mangano 1983, Notarbartolo di Sciara et al. 1993, Pavan et al. 1997, Gannier 1999). However, groups of similar size (and even larger) were mentioned in the past from incidental reports in the central Mediterranean (Bolognari 1951, Mangano 1983). Breeding schools were observed south of the 41° parallel in different basins of the Mediterranean (the Tyrrhenian Sea, Ionian Sea and southwestern basin). The presence of breeding schools was previously reported in the Tyrrhenian Sea (Di Natale & Mangano 1983), and recently in the Ionian Sea (Frantzis 1999). A long-term survey of these areas would be required to determine whether sperm whale breeding schools consistently inhabit the Ionian, Tyrrhenian and Balearic Seas.

No breeding groups were observed in the northwestern basin, where sperm whale relative abundance was high. However, due to the relatively small size of the western Mediterranean Sea, breeding schools close to the Balearic Islands are separated by less than 300 km from other whales in the Gulf of Lions. It is tempting to think of the overall picture as a microcosm of the situation found in oceans, particularly the nearby Atlantic, where males and bachelor groups tend to feed in higher latitudes during summer, and breeding schools are more constrained to temperate/sub-tropical latitudes (Rice 1989). In spite of smaller distances and temperate latitudes, sperm whales in the Mediterranean do appear to show spatial segregation, at least in summer, although the observations are not sufficient to draw up a comparative model with the nearby Atlantic Ocean, and seasonal aspects have yet to receive attention.

Regional variation in sperm whale relative abundance

The Gulf of Lions appears to be highly frequented by sperm whales as indicated by the highest acoustic relative abundance results (2.15×10^{-2} whales km^{-1}), compared to the other regions. Remarkably, this observation was not mirrored in the visual results, for which the Gulf of Lions ranked in 5th position (3.0×10^{-3} whales km^{-1}). However, this result was much influenced by a segment during which 0.52 whales km^{-1} were heard and no whale was seen because of Beaufort 4 to 5 wind conditions. In this region, where occurrence of solitary individuals is the norm, a higher number of detections were made acoustically than visually, with in general 2 or 3 whales detected simultaneously within the range of the hydrophone. Thus, sperm whales tended to form clusters in certain zones of the Gulf of Lions to feed, without forming cohesive groups at the surface. The southwestern basin presented the highest sperm whale visual relative abundance due to high group sizes, and 1 of the 2 highest ARA. If we notice that most whales in the southwestern basin were seen and heard around the Balearic Islands, an area adjacent to the Gulf of Lions, it becomes clear that sperm whales favour the area stretching from these islands to the French continental shelf in summer. The Ligurian, Ionian and Tyrrhenian Sea both featured moderate estimates of ARA or VRA (not significantly different one from each other), depending on the school type encountered (i.e. social group or feeding cluster). The Alboran Sea was the least frequented region. A suitable inter-regional comparative image could only be reached by considering results from the combined acoustic and visual survey.

Overall, these results are consistent with previous observations made on the species in the Mediterranean. In the northwestern basin, Gannier (1999) already noted that sperm whales occur frequently in the Gulf of Lions, while they are less common in the Ligurian Sea during summer. In the southwestern basin, sperm whales appeared to concentrate in the surroundings of the Balearic Islands and, to a lesser extent, in the western continental slope off Sardinia (Figs. 4 & 5). Viale & Frontier (1994) also reported on the sperm whale presence in the southwestern basin, which they assumed to be related with deep scattering layers found in the same area. In the eastern Ionian Sea, the location of acoustic and visual detections off Peloponnese and Crete can be compared with recent results obtained by Frantzis (1999). Both studies suggest the continental slope off southwestern Greece could be a favourable area for sperm whales. The Tyrrhenian Sea featured low sighting and acoustic frequencies, but moderately high abundance indices due to the large school sizes encountered. Notarbartolo di Sciara et al. (1993) previously reported a low sperm whale sighting frequency in the Tyrrhenian Sea (0.48 per 100 h of survey) from a purely visual survey. Pavan & Borsani (1997) reported acoustic detection of sperm whales, particularly in the southeastern part of the Tyrrhenian Sea. They also detected sperm whales off the steep continental slope, immediately east of Sicily, in the western Ionian Sea. No sperm whales were sighted in the Alboran Sea during our survey, but 1 acoustic sequence was recorded. A recent study has shown the presence of sperm whales, mostly solitary animals, close to the Almeria-Oran frontal system (Prieur et al. 1993) in the eastern Alboran Sea (Canadas et al. 2000). These authors hypothesized that the transit of adults and subadults occurs through the Strait of Gibraltar. Recently, De Stephanis et al. (2002) showed the presence of sperm whales in this area from September to June. Should individuals transit from the Gibraltar Strait to Almeria-Oran front (and further into the Balearic area), inter-breeding between Mediterranean and Atlantic whales might occur. This is an important point to research in future studies as it would influence the status of sperm whale in the Mediterranean Sea.

Several authors have previously noticed a link between sperm whale density and primary production (Jaquet et al. 1995, Jaquet & Whitehead 1996). During summer, moderate levels of primary production are found in the northwestern Mediterranean, while the rest of the western basin is oligotrophic, with the exception of Alboran Sea. The Gulf of Lions, in particular, is one of the few areas remaining mesotrophic throughout the summer (Millot 1979, Morel & André 1991). The trophic web of this region might benefit from the general current flowing west along the continental slope of Provence, Gulf of Lions and into the Balearic Sea (Millot 1987, Béthoux et al. 1988), which might contribute to the dispersal of the food chain westward from the Ligurian Sea frontal system, known as a permanent source of primary production (Prieur 1981). The westward drift of the maturing food chain may favour higher trophic level organisms, suitable to sperm whale feeding, in the Gulf of Lions. Furthermore, northwesterly wind gales are common in the Gulf of Lions, even during summer, which generate coastal upwelling in this area (Hua & Thomasset 1983, Johns et al. 1992), as well as vertical mixing linked to the complex canyon topography. Hence, several factors might contribute to high sperm whale abundance in this part of the western basin.

Topography-related distribution

Both visual and acoustic results suggest that sperm whales have some affinity for the continental slope, although statistical significance could not be demonstrated. Acoustic results may be influenced by the detection range of the hydrophones (<8 km), i.e. clicks generated over the slope region could possibly be detected at oceanic sampling stations and vice-versa, especially where the slope is steep. Single individuals as well as larger schools have been detected both in the open sea and over the continental slope (Fig. 4). An affinity for the continental slope was apparent, to some extent, in some previous studies (Notarbartolo di Sciara et al. 1993, Pavan et al. 1997).

However, these studies were not effort-corrected and did not feature an even coverage of both strata. From effort-corrected analysis, Gannier (1999) suggested a higher affinity for open-sea waters in the Ligurian Sea. In the same area, Gordon et al. (2000) showed a widespread distribution, with some preference for waters >1000 m. The widespread distribution of sperm whales in the Mediterranean Sea is likely to be linked to food resources. At present, knowledge on the diet of Mediterranean sperm whale and information on cephalopod distribution are lacking. Nevertheless, it is known that species like *Todarotes sagittatus* and *Histioteuthis bonnellii* are part of the sperm whale diet in the Azores (Clarke 1956), Galapagos (Smith & Whitehead 1993) and off South Africa (Clarke 1966) and both species are abundant in the Mediterranean, as shown from stomach contents of other odontocete species (Orsi Relini & Garibaldi 1992, Würz et al. 1992, Würz & Marrale 1993). Ommastrephid squids are found over both the continental slope and the open sea in the Mediterranean (Mangold-Wirz 1963), in particular, they are known to feed over the Balearic continental shelf and slope (Quetglas et al. 1999) whereas histioteuthid squids are suspected to be purely pelagic species (Mangoldt & Boletski 1987). Hence, the mixed diet of sperm whales in the Mediterranean would explain their wide distribution over both habitat types. Unfortunately, an informed discussion is difficult due to the lack of sperm whale stomach-content data for the Mediterranean.

CONCLUSION

Sperm whales are widely distributed across both the eastern and western Mediterranean. Higher relative abundances are found in the western basin, particularly in the Gulf of Lions area, where sperm whales feed, and close to the Balearic Islands, where sperm whales may be foraging and/or breeding. In the eastern Mediterranean, the Greek islands appear to be frequented by mixed groups as well. Longer-term local studies are required to assess the consistency of different areas as sperm whale feeding and breeding habitats. Potentially important areas still need to be surveyed in the Mediterranean Sea in order to complete the sperm whale distribution picture glimpsed through this work (the continental slope off Algeria and Tunisia, for example). Large-scale, co-operative research might be needed to gain sufficient knowledge to assess the sperm whale population status in the Mediterranean Sea. Advances in acoustic survey techniques should be implemented to help achieve such goal.

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