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Sperm whale occurrence, site fidelity and population structure along the Hellenic Trench (Greece, Mediterranean Sea)

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ABSTRACT

1. Twelve summer surveys conducted each year between 1998 and 2009 along the Hellenic Trench have been analysed to provide information about a previously unknown sperm whale population unit. Sperm whales were detected acoustically 238 times; 178 of these led to a visual encounter with social units (96), male aggregations (45), solitary males (32) or unclassified groups (5). The overall detection rate was 10.9 detections per 1000 km of acoustic effort.

2. A pronounced peak in sperm whale density was observed along the 1000 m depth contour: 74% of visual encounters (corrected for effort) were within 3 km of this contour. Density decreased both in shallower waters and deeper waters further offshore.

3. One hundred and eighty-one whales were photo-identified. Fifty-seven percent of 136 social unit members and 36% of 25 males segregated from social units were encountered in multiple years. Social units were resighted in up to six different years spanning 9 years (15 if opportunistic photo-identifications are included). Several males were resighted in three different years usually spanning up to 4 years. This indicates a high level of site fidelity.

4. The mean group size was 2.47 (range = 1–5) for males and 8.21 (range = 4–13) for social units. Maximum group size reached 15 whales when casual visitors were included. The 16 identified social units were generally stable although some individuals moved between social units, and some social units split or mixed. Female to male sex ratio was 1.55:1 within social units and 1.06:1 overall.

5. Calves (≤2 years old) were present in 79% of social unit encounters, accounting for 16.6% of social unit members. Observations of 15 newborns indicate a mid-summer calving season.

6. This study indicates that the Hellenic Trench is core habitat for the eastern Mediterranean sperm whale sub-population. This population, which is very small, is believed not to exceed a few hundred individuals. Given the endangered status of the entire Mediterranean population, managing threats in this area and creating a marine protected area for sperm whales along the Hellenic Trench is a conservation priority.

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KEY WORDS: cetacean; *Physeter macrocephalus*; Mediterranean Sea; photo-identification; social unit; male; calf; newborn

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INTRODUCTION

Despite the absence of significant historical or modern exploitation (but see Sanpera and Aguilar, 1992; Aguilar and Borrell, 2007 for whaling activities in the area of the Straits of Gibraltar), the Mediterranean population of sperm whales (*Physeter macrocephalus*, L., 1758*)* has been recently listed as 'Endangered' (IUCN Red List). Entanglements in illegal driftnet fisheries and ship strikes seriously threaten the survival of this small and apparently isolated population, but there is still no or little knowledge on its abundance, social structure, critical areas and movements (Notarbartolo di Sciara *et al*., 2006). Because of lack of dedicated surveys and sighting data, all that was known about sperm whales in the eastern Mediterranean in 1986 were four strandings on Greek islands, two in Egypt and one in Tel Aviv (Marchessaux, 1980; Kinzelbach, 1986). It is surprising that the sperm whale was considered rare or infrequent in the eastern Mediterranean basin until the late 1990s, and its regular presence in the Greek Seas (Frantzis *et al*., 2003) had passed unnoticed (Marchessaux, 1980; Notarbartolo di Sciara and Demma, 1994; Frantzis, 1997).

In 1998 a long-term research programme to examine the occurrence of sperm whales and subsequently monitor their population unit in the Greek Seas was established (Frantzis *et al*., 2000). Although surveys included the Aegean plateau (Frantzis *et al*., 2003), most of the effort focused on the waters of the Hellenic Trench, which present topographic characteristics compatible with the occurrence of sperm whales. Data from 12 yearly surveys have been analysed to investigate the occurrence and distribution of sperm whales in the area, their abundance, their social structure and their residency patterns. This knowledge will be crucial for planning an action plan for the conservation of the Endangered Mediterranean sperm whale population and the potential creation and management of a Mediterranean marine protected area for sperm whales along the Hellenic Trench, as has been proposed by ACCOBAMS (Anonymous, 2007; Resolution 3.22).

MATERIALS AND METHODS

Study area and data collection

The Hellenic Trench is a 1100 km long bathymetric feature that runs parallel to the western, southern and south-eastern coasts and islands of Greece (Figure 1). It consists of a series of linear trenches and small troughs, in which the depth increases steeply. The 1000 m contour is typically within 3–10 km of the closest island or mainland coast. The extent of the study area expanded over the course of this project. Between 1998 and 2001 it comprised a

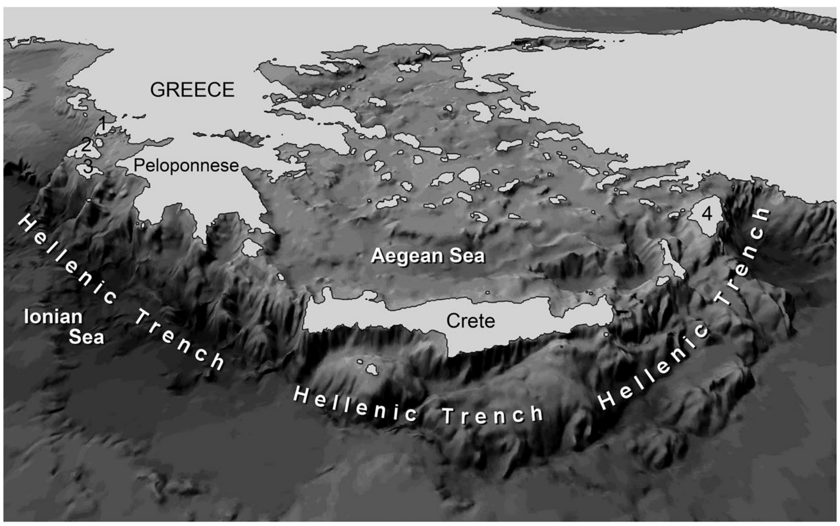

Figure 1. Topography of the Hellenic Trench using data from NASA World Wind 1.4 (http://worldwind.arc.nasa.gov/) 1: Lefkada, 2: Kefallonia, 3: Zakynthos 4: Rodos.

limited part of the Hellenic Trench, off south-west Crete, while from 2002 and until 2009 it was extended to cover a 900 km long section of the Hellenic Trench, from north of Lefkada Island to the south-eastern part of Crete (Figures 1, 2). From 2002 onwards yearly surveys started in the north Ionian Sea and moved south and eastwards towards south-east Crete, returning in the opposite direction to maximize the chances of re-encountering the same whales and collecting additional data (e.g. changes in the composition of whale groups or appearance of newborns). Transects were not systematically designed, but tracks were shaped to cover all of the shelf-break in the study area each year (Figures 1, 2). The width of the survey area varied between 4 and 32 km depending on topography. The sea surface delimited by the research vessel tracks was approximately 12 600 km^2 (Figure 2). However, the area surveyed acoustically was much larger (approximately 27 900 km^2), since the effective acoustic range (as estimated from the relevant acoustic detection function; Gkikopoulou *et al.*, in prep.) was approximately 12 km around the hydrophone and the research vessel (Figure 2). The depth along the vessel tracks while on acoustic effort ranged between 100 and 3200 m, with 88% of listening stations lying above depths of 500 to 2500 m. ArcView 3.2 GIS analysis software was used to calculate surfaces, distances and depths.

Data were collected from either a 13 m sailing vessel or a 16 m motor vessel, typically moving at 8–10 knots when on search effort, and during the daytime from late June to mid-October 1998–2009. The vast majority of the effort (91% of survey days) was in July and August. The data logging software 'Logger 2000' (developed by IFAW; http://www.ifaw.org) was run continuously on a PC linked to a GPS. Sea conditions, acoustic and visual search effort, visual and acoustic detections of cetaceans, as well as notes on their behaviour were entered manually into Logger whenever conditions changed. The numbers of whales heard clicking regularly and whales visually present were entered in Logger every time they changed during all encounters with sperm whales. During the latter 5 years of the survey (2005–2009) the depth was recorded continuously using a Simrad ES60

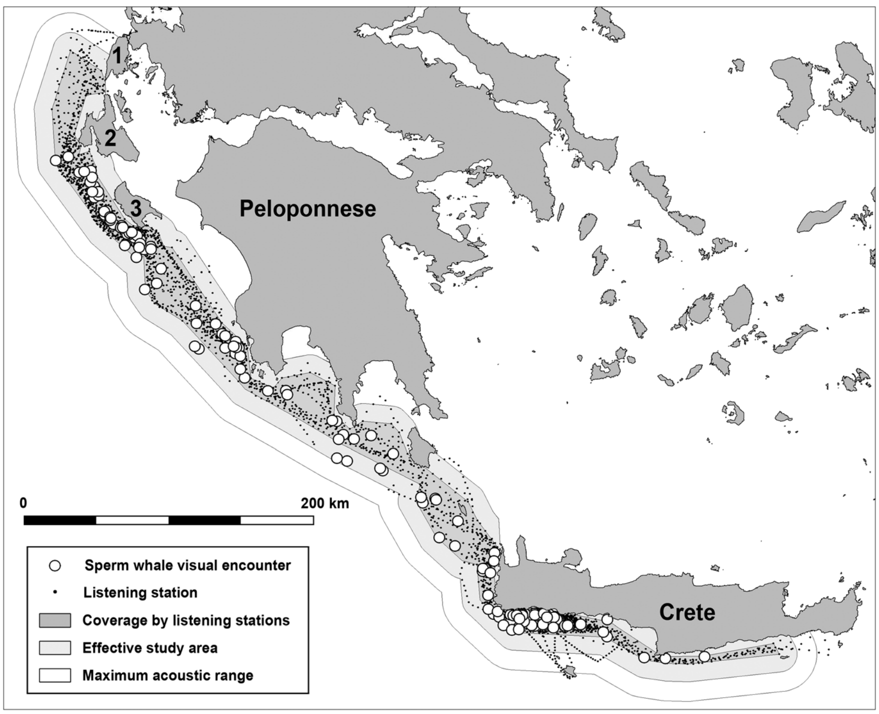

Figure 2. Study area, showing listening stations and sperm whale visual encounters along the Hellenic Trench, during the yearly surveys in the period 1998–2009. 1: Lefkada 2: Kefallonia 3: Zakynthos.

Echosounder. Depth data were used to create a more detailed bathymetric surface profile of the entire study area.

Sperm whale detection and approach

Sperm whales were detected by listening for their characteristic clicks through a streamlined hydrophone array, which contained two elements (Benthos AQ-4, linked to a Magrec HP02 preamp with a low cut filter providing an effective acoustic bandwidth of 100 Hz–22 kHz) spaced 3 m apart and towed on 100 m of strengthened cable. While on acoustic effort, 1 min listening stations were completed every 15 min. During these the vessel's engine was put in neutral (or idle when the sea conditions did not allow for a complete stop) to minimize noise. When sperm whale clicks were detected the whales were tracked acoustically and approached until they were eventually sighted. Since the maximum acoustic detection range was in the order of 25 km, the whales were often tracked for one or more hours before the vessel reached their position.

After surfacing, the focal whale(s) were gradually approached to allow individual photo-identification images to be taken. Animals were typically approached at very low speed from behind to minimize the risk of disturbance to the whales (IFAW (International Fund for Animal Welfare), 1996; Frantzis and Alexiadou, 2008). The position of the first individual observed was recorded as the position of the visual encounter.

Acoustic effort and detection/encounter rate

Detection rate was estimated as the number of acoustic detections per 1000 km of acoustic effort or per 100 listening stations. A detection was considered as the first click heard from a sperm whale or group of sperm whales, independent of the number of whales present in the group. In the exceptional case that neighbouring groups were subsequently found to be two distinct social units in temporary proximity, they were considered as two different detections.

For survey purposes, the vessel was considered to be 'on acoustic effort' for the estimation of detection rates when on a predetermined trackline until the first acoustic detection was made. It was considered to be 'off effort' while tracking detected whales and during visual encounters. At the end of an encounter with a whale or a group of whales (which could extend over many hours) the vessel steamed away for at least 5 km before acoustic monitoring effort resumed. Furthermore, while leaving a whale or whale group and until reaching 20 km of distance, any detection that had a bearing coming from behind the hydrophone was not considered. In addition, no sea area was searched acoustically more than once during the same day, so no acoustic effort was considered when a second passage occurred (e.g. when returning to the port of departure on the same day using the same route in the opposite direction).

Results of photo-identification were used to estimate the 'individual encounter rate' (IER), i.e. the number of different individual whales encountered per acoustic effort. To estimate the IER only one encounter of each individual (or social unit) was kept per season (i.e. year). In order to compensate for the acoustic detections that never resulted in visual encounters (and provided no photo-identification results), and to extrapolate an overall IER (OIER), the IER was multiplied by the ratio: number of detections (nD)/number of visual encounters (nVE). Hence $\mathrm{OIER} = \mathrm{IER} \times (\mathrm{nD}/\mathrm{nVE})$. OIER was calculated separately for all sperm whales, males, social unit members and social units (considered as entities).

Visual encounters, encounter types and group size

Once sperm whales were observed, all single animals or small clusters in the area were assumed to be part of the same single visual encounter (i.e. sighting); unless the whales' specific distribution and post hoc photo-identification revealed a different situation (e.g. two different social units were temporarily in the same area). Visual encounters with sperm whales were considered to be different, unique encounters if: (a) they were made on different days (including consecutive days), or (b) in the case of two neighbouring distinct groups encountered the same day, their members always stayed much closer to members of their own group than to those of the second group and their group identity (determined post hoc through photo-identification) was shown to be different, or (c) the closest whales of two whale groups/individual(s) were separated by more than 25 km (i.e. the practical maximum detection range with the hydrophone array).

All encounters were classified as being with one of the following four encounter types: solitary male, male aggregation, social unit, and unclassified, as defined in Table 1. Some social unit encounters were characterized as 'mixed groups' when composed of one core social unit plus (a) one group of whales being another social unit or part of it, or (b) one small male group (possibly 'bachelor group' *sensu* Whitehead, 2003), or (c) a combination of both (a) and (b). All whale groups of at least four individuals that included calves or juveniles in at least one encounter and were not 'mixed groups' were considered to be social units *sensu* Whitehead (2003). Re-sightings of many photo-identified whale groups over a period of 12 years showed that this assumption was correct.

The number of whales present in each visual encounter was determined by a combination of visual observation, photo-identification, and acoustic monitoring. The main effort focused on finding and photo-identifying all whales present in the area (see below). Usually, social units were followed until all their members gathered at the surface in order to socialize. During such occurrences repeated direct counts and photo-identification were used to assess the group size, if no regular clicking of other whales could be detected through the hydrophone. In cases of whale groups that never gathered all together at the surface (typical in male aggregations), the group size was estimated by summing the direct count of all visible whales, the number of regularly clicking whales that could be detected simultaneously and the number of potentially non-visible and non-clicking calves previously observed. This procedure was repeated several times during the encounter until there was confidence about the group size. Repeated encounters with the same social unit on consecutive or close days confirmed the group size estimation, when no direct total count was possible.

Group size was estimated in this way with certainty for 84% of the encounters. In 11% of encounters the estimated group size included uncertainty of one or two individuals (e.g. seven to nine whales) and either the mean or the group size observed for the same group in the previous or next encounters was used. Two different estimations of the mean group size of encounters with males and social units were made. The first consisted of averaging group sizes of all visual encounters, and is presented for the results to be comparable with other studies. In a second more accurate method the group size was determined while combining relevant photo-identification data to discard some encounters or individuals after the following rules: (a) consecutive encounters of the same solitary male or aggregation of the same males were counted only once in the average estimation; (b) the group size of each social unit

Table 1. Sperm whale encounter types observed during the present study

Encounter type	Definition
Solitary male	A single male with no other sperm whales detectable visually or acoustically for at least 2 h before and 2 h after the visual encounter
Male aggregation	A loose aggregation of sub-adult or adult males spread in a radius of usually up to 10, but possibly up to 20 km (two out of 45 such cases encountered). Whales usually follow independent dive cycles without approaching each other to less than *c*. 2 km. Rarely, especially when young sub-adult males are present, whales may approach one another and synchronize their dive cycles and flukings, come into visual or even physical contact while socializing and/or producing social codas (*sensu* Frantzis and Alexiadou, 2008)
Social unit	Stable group of 4 to 13 or more whales that either include calves among them, or have been encountered together more than once in different years; they may be encountered either as a close formation socializing at surface or travelling together, or dispersed at a radius of up to 20 km while foraging. Social units may be encountered with occasional male or female visitors among them
Unclassified	An encounter that cannot be classified with certainty in any of the above encounter types because it ended before all the necessary data could be collected, or represents small groups or individuals in a phase of transition between the above encounter types

was counted only once per year, unless it changed (in number or composition) during the season. In this case, if the group size changed owing to the appearance of a newborn during the season, only the maximum group size (i.e. with the newborn) was kept. Furthermore, the ‘core’ social unit size was estimated by excluding transient male or female casual visitors (equivalent to ‘casual acquaintances’; Whitehead *et al*., 1991) from the count. Casual visitors to a social unit were defined as individual whales observed among its members on one or more consecutive encounters in the same year, that were absent in earlier and later encounters during the same or different years.

Age classes, size and gender determination

Calves bearing foetal folds were considered to be newborns. When a whale had been observed as a newborn, it was considered as a calf for the two next seasons. When the year of birth was not known calves were taken to be individuals with a total estimated length of less than 6.0 m, that did not fluke or produce regular clicks and creaks during feeding dives (therefore, calves could not be detected or counted acoustically). When a whale had been first observed as a young first-year calf, it was considered a second-year calf and then a juvenile in the two next seasons, respectively. Whales between 2 and 4 years that had attained a length of 6.0 to 7.0 m were classified as juveniles. Juveniles did fluke and produce regular clicks.

In several encounters with social units, when the whales gathered at the surface to socialize, they were approached, photographed and videotaped underwater by snorkelling to allow for gender determination of several photo-identified individuals through a combination of photos and frames showing characteristic marks photographed above and below the sea surface. Assuming that the sample of whales that could be sexed underwater was random since all whales were closely socializing together, these sex determinations were used to estimate the sex ratio within social units. A previous study (Frantzis and Alexiadou, 2008) has shown that of 15 sperm whales segregated from social units, including animals less than 12 m, all were males. On this basis, all whales that were observed segregated from social units in this study were also considered to be males.

The size of 28 photo-identified sperm whales was estimated acoustically by measuring the inter-pulse intervals in their coda clicks (Gordon, 1991). The maximum range for length estimations of the same whale from different coda clicks was always less than ±10 cm and in two-thirds of cases it was ±5 cm. Further details on the methods used for gender determination and size estimation of individual sperm whales are given in Frantzis and Alexiadou (2008). Two more photo-identified whales were measured after they stranded.

Photo-identification methods

Once visually detected, whales were followed until it was believed that good photos had been obtained of all animals present or weather conditions and daylight made further observation impossible. Body areas most useful for photo-identification included right and left dorsal fin area, trailing edge and both surfaces of the flukes, and presence, number, shape and pattern of peduncle humps (these were especially useful in the case of poorly marked calves that did not fluke). Long-lasting white pigmentation patches (that did not change in any of the 78 individuals examined for a period of up to 15 years and included newborns and calves; Figure 6) and nicks, notches, scars or other irregularities of the trailing edge of the flukes were used to identify individuals (Whitehead and Gordon, 1986). The best photos ($Q > 3$; Arnbom, 1987) allowing positive identification of all individuals photographed each year of survey together with photos showing additional characteristics of the same individuals (2084 in total) were stored in a digital database (the GREek PHYSeter Catalogue), that facilitated visual comparisons and matchings among individual whales.

In addition to the photos collected during the surveys, other images taken opportunistically mainly along the Hellenic Trench or in the Aegean Sea were included in the database (see acknowledgements for contributors). Some of these had been taken before the period of the fieldwork of this study. Whenever they were used in the analysis, this is specified in the text.

Table 2. Detection rate for sperm whales (i.e. number of detections per effort) along the Hellenic Trench estimated for two different units of acoustic effort: distance and number of listening stations. Separate estimations are provided for the total study period 1998–2009 (n = 12 for yearly values) and the last 8 years 2002–2009 (n = 8 for yearly values). Min-max ranges are given in parentheses

per 1000 km of acoustic effort				per 100 listening stations			
1998–2009 (limited coverage of the study area the first 4 years)		2002–2009 (yearly coverage of the entire study area)		1998–2009 (limited coverage of the study area the first 4 years)		2002–2009 (yearly coverage of the entire study area)	
Overall	Average of yearly values	Overall	Average of yearly values	Overall	Average of yearly values	Overall	Average of yearly values
14.9	18.5 sd = 11.1 (4.8-38.3)	10.9	12.3 sd = 5.5 (4.8-23.3)	5.4	5.5 sd = 2.0 (2.9-9.5)	4.7	5.0 sd = 1.9 (2.9-8.2)

RESULTS

Effort and detection/encounter rate

In the course of 361 survey days and 36 299 km of routes, 15 973 km of on-effort trackline and 4399 listening stations were completed. While on effort sperm whales were detected on 238 stations and 178 of these detections (i.e. 75%) eventually resulted in visual encounters (whales were not found visually on the other 60 occasions because tracking effort stopped because of unfavourable conditions or the end of daylight). Visual encounters extended over 501 h in total (median duration: 2 h 14 min; range: 1 min to 9 h) and the vessel travelled more than 2800 km while following whales.

The overall detection rate and the average and range of yearly detection rates are presented in Table 2. Effort was not spread evenly over the 12-year study period. Considering only the last 8 years (2002–2009), when the entire study area was covered (Table 2), 111 of 146 detections resulted in visual encounters (76%). The average overall individual encounter rate (OIER) and separate OIERs for males, members of social units and social units are presented in Table 3. OIERs for social units and for males were not significantly different (two Wilcoxon paired-sample tests, all $T+$ and $T- > T$ 0.05(2), 8), meaning that a similar amount of effort was needed to encounter two different male sperm whales or two different social units of sperm whales. Consequently, OIERs for social unit members were almost 10 times higher than for males (significantly different, two Wilcoxon paired-sample tests, all $T+ < T$ 0.05(2), 8), meaning that 10 times more effort was needed to encounter two different male sperm whales than two different social unit members.

Distribution and environmental parameters

Sperm whales were observed throughout most of the study area along the Hellenic Trench (Figure 2). However, no sperm whales were detected in the northern part of the study area (north of S Kefallonia Island) despite effort in all years of the period 2002–2009. Water depth for visual encounters ranged between 571 and 2459 m and their distance from the closest coast ranged between 2.7 and 29.4 km. A very pronounced peak in sperm whale distribution was observed all along the 1000 m contour of the Hellenic Trench, with 74% of visual encounters occurring at a distance ±3 km from it, after correction for acoustic effort in each distance category (i.e. number of contributing acoustic stations weighted for distance according to the detection function).

Table 3. Average overall individual encounter rate (OIER) for all whales, males, social unit members and social units (as entities) for the years 2002–2009 (n = 8). OIERs are expressed as number of individuals (males or social unit members) or number of social units encountered per 1000 km of acoustic effort and per 100 listening stations. Differences between OIERs are not significant for males and social units, but are significant between males and social unit members (Wilcoxon paired-sample tests). SD and min-max are given in parentheses

	All whales	Males	Social unit members	Social units
per 1000 km of acoustic effort	33.1 (12.2, 6.3–52.1)	3.1 (2.8, 0–9.4)	29.9 (11.1, 4.6–49.5)	3.5 (1.5, 1.2–7.1)
per 100 listening stations	13.3 (3.3, 7.2–18.6)	1.3 (0.9, 0–3.0)	12.0 (3.1, 6.2–17.3)	1.4 (0.4, 0.7–2.1)

The number of visual encounters decreased rapidly in shallower waters and deeper waters further offshore (Figure 3). This was particularly obvious in some areas such as west of Zakynthos Island (Figure 4), off south-west Peloponnese and off west and south-west Crete (Figure 4).

Photographic re-captures and site fidelity

Over the study period 744 independent identifications took place, of which 583 were resightings (78%). These identifications involved 161 individual sperm whales. The maximum number of different individuals identified in a single season was 77, while the average for the years 2002–2009 was 39.4 individuals (sd = 19.5, range = 20–77, n = 8). Twenty of the sperm whales that were photo-identified in July and August (both males and social unit members) during this study were resighted along the Hellenic Trench in opportunistic sightings in February (five individuals), March (one), May (four) and mid-October (12). Photo-identification results when only one photo-identification per year was considered for each individual are shown in Table 4.

Out of 63 sperm whales identified during surveys independent of our own, or of other research teams, or during opportunistic sightings in the entire Hellenic Trench (Table 4), 43 (68%) were also photo-identified during the surveys of this study and 20 were new raising the total to 181 identified

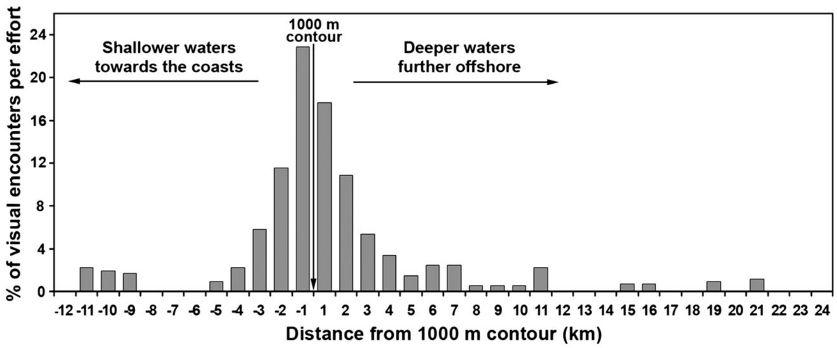

Figure 3. Distribution of relative encounter rate with distances from the 1000 m bathymetric contour for all 178 visual encounters made during the surveys 1998–2009. Encounter rates were corrected for acoustic effort (4399 listening stations) and are expressed as percentage of the total within each 1 km bin. Each listening station contributed to the effort within the 1 km bins after being weighted for distance according to the detention function.

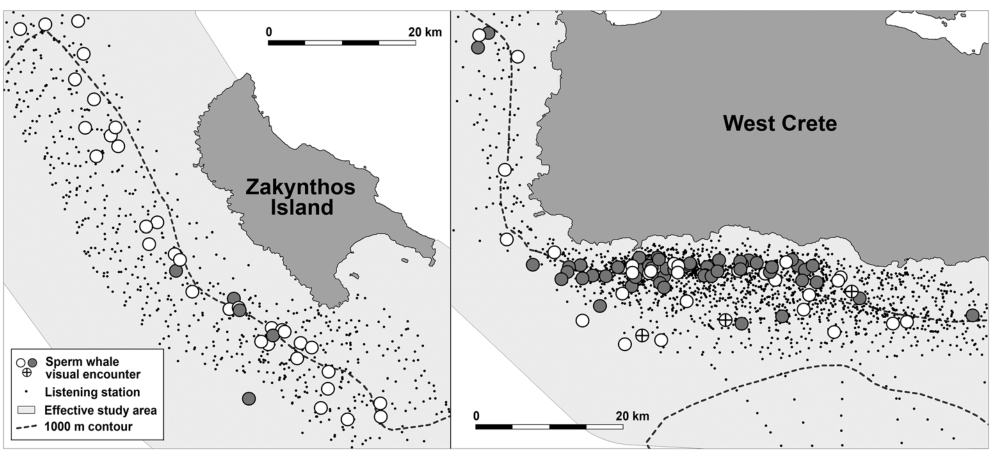

Figure 4. Detailed maps of distribution of sperm whale visual encounters off Zakynthos Island (left) and W-SW Crete (right) showing the very pronounced preference for a narrow zone along the 1000 m bathymetric contour. Four out of five male encounters off Zakynthos Island (plus one slightly south of the limits of the figure) were with the same individual and spanned 8 days in the same season. White dots: social units, grey dots males, crossed dots unclassified encounters.

Table 4. Number of photo-identifications and resightings (only one photo-identification per year is considered for each individual) and numbers of photo-identified and resighted individuals. SU: social unit. As resightings in the row of independent sightings we consider the photo-identifications of individuals already photo-identified during the surveys of this study

	Whale type	Photo-identifications	Resightings	Identified individuals	Individuals sighted at least in 2 years
Surveys of this study	Males	38	13 (34%)	25	9 (36%)
	SU members	310	174 (56%)	136	77 (57%)
	Total	348	187 (54%)	161	86 (53%)
Independent sightings*	Total	92	72 (78%)**	63***	-

*Observations made during independent surveys of our own, or of other research teams, or during opportunistic sightings.
**Photo-identifications of individuals identified during surveys of this study were considered as resightings.
***Of these 63 individuals, 43 were identified during the surveys of this study and therefore are included in the 161 individuals in this table.

individuals. Of five sperm whales identified in the Aegean Sea opportunistically, one was resighted along the Hellenic Trench (south Crete) during this study

Sixteen social units were identified during the study period. Of these, 10 (62%) were observed in at least two different years, three (19%) mixed with other social units or were the result of mixing of two social units, but had most of their members observed at least in two different years, and three (19%) were observed only in one year. Four social units were captured in five or six years. The discovery curve of social units (Figure 5) appears to be reaching a plateau indicating that most of the social units of the local population unit have been captured. Resightings of social unit members extended over 9 years, or 15 years when earlier opportunistic photo-identifications were considered. One female sperm whale opportunistically photo-identified as a newborn calf in the Ionian Sea in 1994 was resighted during this study in both 2006 and 2007 as an immature female, and in 2009, at the age of 15, as a mother with her first calf and with calluses on her dorsal fin (Figure 6). This is the first instance of which we are aware where the age of first calving in a sperm whale has been directly determined.

Males were resighted mainly in consecutive years. Only six out of 25 males were sighted in three different years (compared with 55 out of 136 social unit members sighted in at least three different years), typically over a period of up to 4 years with one instance of a 7 year interval. Within a season, however, males (especially large individuals estimated to be >12.5 m) were often repeatedly resighted within a limited area of about 40 km across, along the Hellenic Trench over periods of up to 24 days. Three males originally sighted as immature individuals among social units were later resighted independently, as a pod segregated from social units. The age of one of these was subsequently determined after it stranded, and, based on this, it was estimated to

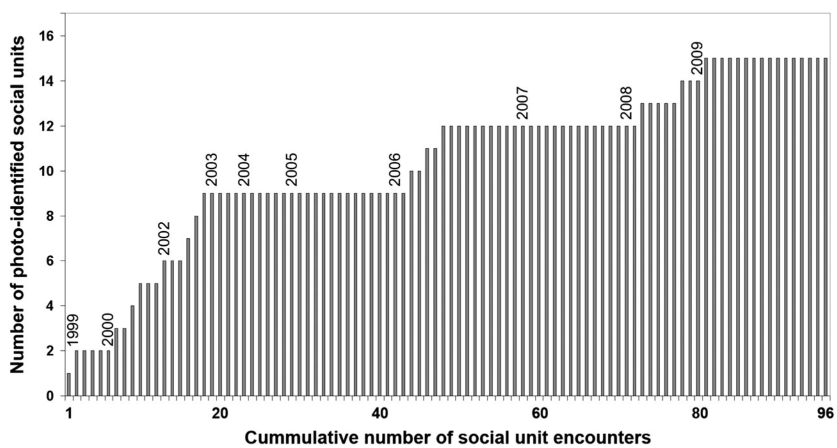

Figure 5. Discovery curve of photo-identified social units (cumulative number) during the study period (1998–2009). The total number of social units is 15 rather than 16 mentioned in the text, since one social unit encountered in 2009 resulted from the merging of parts of two previously known social units all the members of which had already been photo-identified.

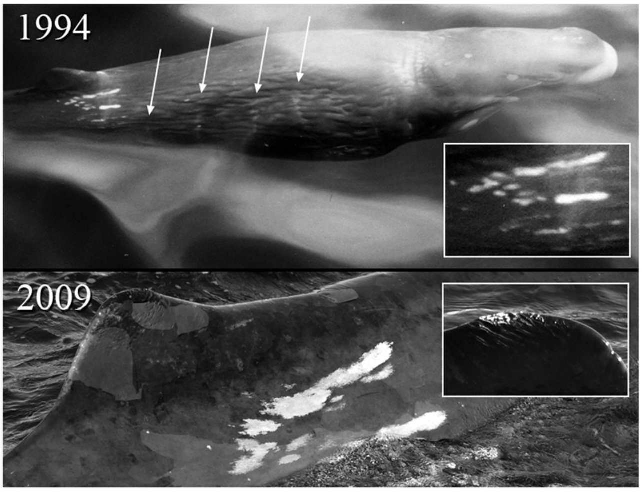

Figure 6. The sperm whale named 'KERON' was first photographed as newborn with foetal folds (indicated by white arrows) on 1 August 1994. White pigmentation patches photographed on the right side of the dorsal fin area are shown in detail (upper small framed photo). The same whale was resighted several times; as an immature female in 2006 and 2007 and finally as mother with her first calf in 2009 (15 years after her birth). In 2009 calluses were evident on the top of her dorsal fin (lower small framed photo).

have left its social unit when 11–15 years old (Frantzis *et al.*, 2011).

If on an encounter with a social unit that had previously contained a calf, it was judged that all the animals had been photo-identified and the calf's supposed mother was present but the calf was absent, the calf was considered to have died. Out of 55 calves and juveniles photo-identified during the period 2000–2008, at least 15 were thought to have died. Eleven of them never reached more than three years of age. Fifteen different newborns were encountered in total, of which 14 were in the years 2004–2009. Of 10 newborns observed between 2004 and 2007, at least four were considered dead before the third year of their life, indicating a calf survival rate of less than 60% in this 4-year period.

Group size

Group size data are presented in Table 5 and Figure 7. On two occasions social unit members were observed in small groups of two and three individuals with no other whales within detection range. These encounters were characterized as 'unclassified' and they were believed to represent individuals venturing away from their social unit, with which they had been observed in earlier or later encounters.

Aggregations formed by more than one social unit were very rare. On one occasion two social units of six individuals each, which were observed as discrete units on earlier and later occasions, were observed together mixing and socializing in one cluster. Four independent 'gatherings' of 17, 18, 19 and 20 sperm whales within a radius of up to 10 km were observed during this study. However, photo-identification data revealed that these involved two discrete social units (with visitors in some cases) in three cases, and one social unit and a male aggregation in a fourth case. The discrete social units/male aggregation remained separated during the entire time of the observations. The closest distance between their members ranged from 3.5 to 17 km.

Population structure and size distribution

The ratio of social unit members and males segregated from social units was 5.4:1 (136/25) when data from all 12 years were considered, but increased to 7.9:1 (126/16) when only the last 8

Table 5. Group size for male and social unit encounters estimated by two different methods, while ignoring and considering the photo-identification data respectively (see 'Materials and methods' for details). 'Core' social unit size was estimated by excluding from size count the transient casual visitors (i.e. individual whales observed among the members of a social unit one or more consecutive times in the same year, while they were absent in earlier and later encounters during the same or different years)

				Percentage per group size category				
	Encounter type	Mean group size	Range	Solitary	2	3	4	5
Photo-id data ignored	Male(s)	1.8 (n = 77, sd = 0.90)	1–5	41.6	39.0	14.3	3.9	1.3
	Social units	8.4 (n = 90, sd = 2.93)	4–15	-	-	-	-	-
Photo-id data considered	Male(s)	2.5 (n = 59, sd = 0.81)	1–5	35.6	40.7	16.9	5.1	1.7
	Social units	10.3 (n = 48, sd = 3.31)	4–15	-	-	-	-	-
	'Core' social units	8.2 (n = 42, sd = 2.53)	4–13	-	-	-	-	-

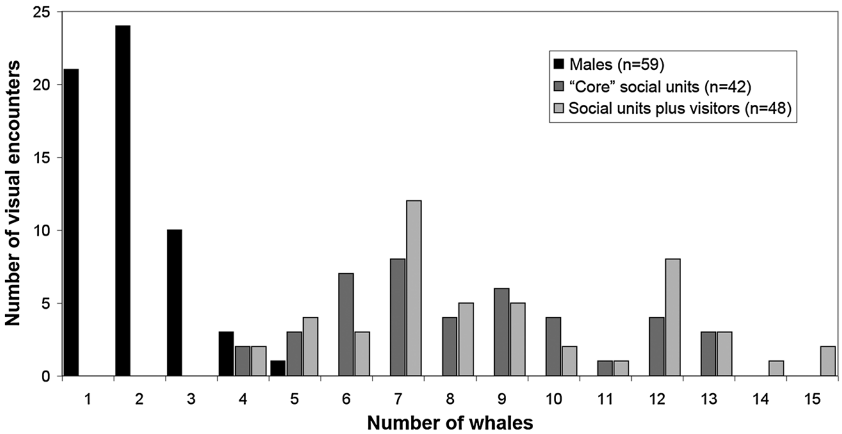

Figure 7. Histograms of group sizes for male encounters, encounters of 'core' social units and social units including 'visitors' (i.e. temporary members).

years were considered (2002–2009; period over which the whole study area was covered).The gender of 28 members from five different social units were determined through underwater photos. The sex ratio of females to males (calves, juveniles and apparently immature males) within social units was 1.55:1 (17/11). By extrapolating this ratio to the 136 members of social units and considering also the 25 segregated males, an overall sex ratio of 1.06:1 can be estimated. When applied to the data of the last 8 years only, the same extrapolation resulted in a sex ratio of 1.17:1.

Visual encounters comprised social units (96), male aggregations (45), solitary males (32) and unclassified encounters (5). Social units were encountered either as (a) 'core' social unit (i.e. all members except their new offspring had been observed together in previous years), (b) social unit with 'visitors' (i.e. 'core' social units together with usually one or two whales or a group of whales that had not previously been observed among them), or (c) as 'satellite' social unit that stayed in relative proximity (3.5–5.5 km) from another social unit for several days, without approaching further or mixing with it. Only one satellite social unit of four whales (including one juvenile whale) was observed, while following for at least 8 days a large social unit of 13 whales.

'Visitor' sperm whales were found to be: (a) adult or sub-adult males that usually spent hours or a very few days with the social unit as short-term visitors (possibly representing reproductive activity); (b) young males that spent at least several weeks with the social unit; (c) individual(s) or small groups of whales that could be either another social unit, or part of it, or a male group (possibly 'bachelor group'), or a combination of both, forming a temporary mixed group with the core social unit.

Mixed groups (see methods for the definition of this term) were observed on four occasions, and twice they reached the maximum group size observed during the study (15 whales). The other two cases involved two mixed social units (6 + 6 whales) and one social unit plus four more individuals (9 + 4 whales). Short-term visits of males lasting 1 or 2 days were observed in five cases involving three different male whales. These three males were the largest (14.6 m) and two of the smaller males (9.7 and 9.8 m), which were all also observed as segregated from social units during this study. One small (9.8 m), short-term male visitor was observed underwater while trying to mate with social unit members or to 'sexually harass' young whales of the social unit. Sperm was ejected during this activity. Three days later, the same male was observed among another social unit. Long-term visits of males lasting at least for several weeks were observed in two cases (eight visual encounters with the males repeatedly observed among the members of a social unit) and concerned three males; two associated with each other and a single one. One of the associated males was observed to alternate four times between two social units from 2002 to 2006, always observed with only one of the two social units every season. Later in 2006, he was eventually observed three times in a male trio (possibly a 'bachelor group'), segregated from social units. The second associated male also passed from the same two social units in 2005 and 2006, before joining the trio. All but one other large male observations (individuals estimated to be from 12.5 to 13.6 m) involved only feeding behaviour occurring on different days and far away from social unit encounters. Descriptive statistics for the estimated sizes of 28 sperm whales are presented in Table 6.

Despite the stability observed in several associations between mature members of social units (Table 7), some other individuals were observed to change social unit within the same year or from one year to the next. Furthermore, some social units have been observed to split, and parts of ex-social units were observed to mix with other social units in a non-random way, in order to form new social units (unpublished data).

Males segregated from social units accounted for 16% (25/161) of all photo-identified individuals. Both the number of segregated male encounters per acoustic effort and the ratio of segregated males/social unit members dramatically declined over the course of the study. However, the turning point in decline coincides with expansion of the study area in 2002. Males that were segregated from social units shared the same geographical area with social units. There were more encounters with male aggregations (45) than solitary males (32). Of 25 individually identified males, one was encountered only as a solitary individual (in one encounter), 18 only in male aggregations (in 25 encounters), four in both these contexts (in 32 and 24 encounters, respectively) and two only as visitors in social units (in four encounters). The five whales encountered as solitary males were among the six largest males in this study (the sixth was encountered only as a short-term visitor of a social unit). Repeated encounters of the same male association (pairs or trios) occurred on six occasions (four for pairs and two for trios). The maximum intervals between encounters of the same male associations ranged between 2 and 15 days.

Table 6. Total length estimations (m) for sperm whales encountered during this study. The total length of two male whales was measured after they were found stranded and all others were estimated acoustically through IPIs of their coda clicks (see 'Material and methods')

Sex	Mean total length	Range
Segregated males	11.37 (n = 19, sd = 1.66)	8.9–14.6
Largest females	9.05 (n = 9, sd = 0.26)	8.6–9.5

The birth of a sperm whale was observed once in late July, and newborns with their umbilicus cord still present were observed twice in late July and August. Observations of 15 newborns indicate a mid-summer calving season spanning from June to August with births peaking in July (unpublished data in preparation). Calves or newborns were present in 67 out of 85 (79%) social unit encounters for which all whales were visually observed and in 29 out of 33 (88%) social units when only yearly summary data for each unit were considered. Fifteen out of 16 social units were observed with calves at some point during the study. The average of the 10 yearly mean percentages of newborns, calves and juveniles in social units, estimated by two different methods are presented in Table 8. The first method considered data from all available encounters with social units (n = 85). The second method used photo-identification data in order to consider each social unit only once per year (n = 33), and discarded any short-term male or female visitors. There was no significant difference between any of

Table 7. Photo-identification data for 16 core members of four different social units that were always observed associated together (per social unit) for several years. These individuals were never observed apart, and their social unit was not observed at all in the intervening years that do not appear in the column 'Years of observation'

Name of social unit	No of associated individuals	Years of observation	Max.span in years
Chromo	3	1999, 2004, 2006, 2007, 2008	9
Ippolyti	5	2000, 2006, 2008	8
Palaio	5	2000, 2006, 2007	7
Pylos	3	2002, 2004, 2006, 2007, 2008, 2009	7

Table 8. Proportion of different types of young whales in social units. Means, sd and minimum and maximum of yearly percentages are presented. Data were available for 10 years, no social units were observed in 1998 and 2001, years of short survey periods. Two different estimated percentages are presented and no significant differences were found for any of the five categories presented (Wilcoxon paired-sample test). Those in the first row are based on all visual encounters of social units while, in the second row each social unit was considered only once per year and any temporary male or female visitors were discarded (through photo-identification). For age class definitions refer to the methods

Method	No of encounters	Newborns	Calves	Juveniles	Newborns + calves	All young classes
Data from all available encounters used	85	3.5% sd = 3.3 0–9.3%	12.9% sd = 6.8 4.4–25%	12.4% sd = 5.6 5.6–23.4%	16.4% sd = 7.3 8.5–30.7%	28.8% sd = 8.4 16.7–41.7%
Photo-id data used to discard ‘duplicates’ and ‘visitors’	33	3.6% sd = 3.0 0–7.3%	13.0% sd = 6.4 5.5–25%	13.5% sd = 4.6 5.6–22.0%	16.6% sd = 6.0 11.1–27.3%	30.1% sd = 7.2 16.7–41.7%

the averages obtained with the two different methods (five Wilcoxon paired-sample tests, all $T+$ and $T- > T$ 0.05(2), 10).

DISCUSSION

General

This study shows that a small and quite discrete sperm whale population unit is found in the Hellenic Trench. As suggested by previous studies (Gannier *et al*., 2002; Frantzis *et al*., 2003; Lewis *et al*., 2007), the Hellenic Trench is a key area for sperm whales in the eastern Mediterranean Sea and possibly constitutes the most important habitat in this basin. Although the surveys were conducted mainly during summer months, the opportunistic resighting of 12% (20 out of 161) of the photo-identified individual whales along the Hellenic Trench in winter, spring or autumn indicates a year-round presence.

Distribution

Sperm whales were found in the Hellenic Trench from south-west Kefallonia Island to central south Crete. Sightings from other surveys (Dede *et al*., 2009; Frantzis, 2009; Boisseau *et al*., 2010) and opportunistic sightings (Frantzis, 2009; Öztürk *et al*., 2010) indicate that the presence of sperm whales extends further east along the Turkish coast as far as the western part of Antalya Bay (Öztürk *et al*., 2010). The importance of the Hellenic Trench at a larger scale is shown by surveys of the eastern Mediterranean basin (Lewis *et al*., 2007, in prep.). Of 22 sperm whale detections made in the entire eastern Mediterranean basin during two dedicated surveys, 14 (64%) occurred over a 120 km wide zone along the Hellenic Trench.

The eastern Mediterranean basin and especially the waters of the southern Hellenic Trench are some of the most nutrient-depleted waters in the world (Walle *et al*., 1993), with extremely low levels of chlorophyll *a* concentration (Notarbartolo di Sciara *et al*., 2008; Figure 1). The regular presence and strong preference of sperm whales for the habitat of the Hellenic Trench (Lewis *et al*., 2007, in prep.; Boisseau *et al*., 2010; this study) might seem to present an ecological paradox: the largest predator in the animal kingdom thriving in the most oligotrophic sea area of the world. Clearly, in this area, the prey of sperm whales locally, which is thought to consist exclusively of meso- and bathypelagic squid (Roberts, 2003; Frantzis, 2009) is not linked spatially to the primary production in surface waters. This is in contrast with observations in other parts of the world ocean, where a link between sperm whale distribution and sea surface chlorophyll could be established (Jaquet, 1996; Jaquet *et al*., 1996; O’Hern and Biggs, 2009). As noted by Jaquet *et al*. (1996), even if chlorophyll concentration is an important factor influencing sperm whale distribution over large spatial and temporal scales, other factors have to be considered in certain areas, and the Hellenic Trench seems to be such an area. In this sense, the Hellenic Trench is more similar to the relatively oligotrophic and less productive environment of the Azores than the areas where sperm whales have been studied in the Pacific Ocean (Antunes, 2009).

One of the most interesting and useful findings of this study is the strong peak of sperm whale density along the 1000 m depth contour (Figures 3, 4). This depth is close to the maximum depth for routine feeding dives by sperm whales (Watwood *et al.*, 2006) and in most areas of the Hellenic Trench this depth is in the middle of the continental slope. In some areas of the western Mediterranean Sea (Gannier, 1999; Cañadas *et al.*, 2002) and in a survey in both Mediterranean basins (Gannier *et al.*, 2002), no significant preference for slope and offshore waters was observed in sperm whales and in some cases the offshore waters (depths > 1000 and beyond 2500 m) were preferred (Gordon *et al.*, 2000). A possible explanation that may help to reconcile contradictory results regarding slope as a predictor of sperm whale presence in the Mediterranean was proposed by Pirotta *et al.* (2011), who suggested that a steep slope alone might be insufficient to support sperm whale presence but that it might be important that it was oriented correctly in relation to the directionality of the main water currents.

Detection rates and abundance

The overall detection rate observed for the entire study area (10.9 detections per 1000 km of acoustic effort) was much higher than those recorded by two other sperm whale surveys in the region of the Hellenic Trench. The survey by Gannier *et al.* (2002) covered the entire Hellenic Trench and had a detection rate of 6.03 detections per 1000 km of acoustic effort, while the survey by Lewis *et al.* (2007) covered only the northern and western part of the Hellenic Trench and reported 3.6 detections per 1000 km of acoustic effort (data reported by these authors have been adjusted to make them compatible with the definition of 'encounter' used in this study). These lower detection rates can be explained by the corresponding study areas, which included regions much further away from the 1000 m contour than in the present study, where sperm whale density is likely to be much lower as suggested by this study.

The detection rate recorded during this study was higher than that in any of the Mediterranean areas considered by Gannier *et al.* (2002), although not significantly different (falls within 95% CI) from detection rates in the Gulf of Lions and the south-western basin (9.9 and 7.1 detections per 1000 km of acoustic effort, respectively). However, such comparisons are only indicative, since the sperm whale distribution in the Mediterranean Sea appears to be concentrated in hotspots (Lewis *et al.*, in prep.), such as the Hellenic Trench, or the east and south Balearic coasts (Drouot *et al.*, 2004a; Pirotta *et al.*, 2011). In addition, most of the detections along the Hellenic Trench concern social units with numerous individuals (accounting for only one detection in the same way a solitary male does), which rarely occur in the north-western Mediterranean Sea (Drouot *et al.*, 2004a; Moulins and Würtz, 2005).

This study found 181 photo-identified individuals, of which 17 died during the study. Although the remaining 164 whales are not the total population and some social units remain to be discovered, the very high resighting rate of social units and their discovery curve (Figure 5) indicate that most of them are already known (a formal mark–recapture analysis using the data from this study is in progress). Males segregated from social units appear to disperse further away from the Hellenic Trench, and therefore much wider effort would be needed to achieve adequate photo-identification sampling. Nevertheless, their contribution to the number of sperm whales inhabiting the Hellenic Trench appears to be approximately 8 times lower than that of social units. Furthermore, 78% of photo-identifications and 68% of the photo-identified individuals that occurred independently of the surveys of this study along the Hellenic Trench or in sea areas neighbouring the study area, concerned individuals also captured by our surveys, also suggesting that a large majority of the population unit has already been photo-identified. These results are inconsistent with a total number of sperm whales inhabiting the Hellenic Trench around double the individuals already discovered. Therefore until a reliable abundance estimate becomes available for the Hellenic Trench, an advisable working hypothesis for the size of the local population unit would be between 200 and 250 individuals.

The results of the acoustic surveys conducted over the entire eastern Mediterranean basin indicate that the majority of the sperm whales concentrate along the Hellenic Trench (Lewis *et al.*, 2007, in prep.; Boisseau *et al.*, 2010). The first abundance estimate that resulted from these surveys suggests a total of 107 whales for the eastern basin (Lewis *et al.*, in prep.). The authors acknowledge that this is an underestimation of the total abundance, because as suggested also by the present study: (a) it does not include young non-clicking whales, which may account for approximately 20% of the social units; (b) social units that stay silent for periods of well over 1 h (as already observed during these surveys) may have been missed by the survey; and c) the Hellenic Trench was not surveyed as a separate stratum in the Ionian Sea, resulting in low percentage effort (and encounters) across the areas of high sperm whale density. Considering all the available data on sperm whale distribution and resighting rates along the Hellenic Trench and the surveys that covered the entire eastern Mediterranean, it is reasonable to believe that the entire eastern Mediterranean sub-population amounts to very few hundreds of individuals.

Photographic re-captures and site fidelity

The very high resighting rate of sperm whales within the study area (53% of all photo-identified individuals were sighted in more than 1 year) often in several consecutive years and in some cases extending over many years, all suggest strong site fidelity to the Hellenic Trench. To explain these high resighting rates, most of the observed sperm whales should either move along the Hellenic Trench for most of their time, or predictably return to it during the summer period with varying degrees of site fidelity depending on their age and sex. In the only other known and studied area inhabited by social units in the Mediterranean Sea – the waters east and south of the Balearic Islands – 52 sperm whales (mostly social groups) were photo-identified from 2003 to 2007, but only seven (13%) of them were resighted in different years (Luke Rendell, pers. comm.).

The rate of resighting in at least one different year was 60% higher for members of social units than for males. The resighting rate for social units themselves was 80%. Only male sperm whales have been matched photographically between the eastern and western basins (Frantzis *et al.*, 2011), and the coda (i.e. communication sounds) repertoires of social units have been shown to also vary between the western and eastern basin (Drouot *et al.*, 2004b; Rendell *et al.*, 2007). Frantzis *et al.* (2011) hypothesized that many females and their social units may never move between Mediterranean basins. The present results further support this hypothesis. The observation of a female sperm whale that was first observed as newborn along the Hellenic Trench being resighted in the same area 15 years later with its first offspring (Figure 6) is also in line with this idea.

The lower resighting rate of males (36%) and shorter 'residency' could be explained by greater dispersal. Their resighting mainly in consecutive years and subsequent absence in future years indicates short- to medium-term (from weeks to a few years) residency or repeated passages along the Hellenic Trench. The observed resighting rate of males, however, is comparatively much higher than in the Gulf of California, which is also an area inhabited by social units. In a 7 year study by Jaquet and Gendron (2009), only one out of 18 males (5.6%) was resighted in different years, and only two males were resighted in the same season. Surprisingly, the recorded resighting rate of males along the Hellenic Trench is also higher than in the Ligurian Sea, which is an area inhabited by males in the Mediterranean. Only 9.1% (four out of 44) sperm whales were resighted in different years (Drouot-Dulau and Gannier, 2007), although resightings spanning 3–7 years have been recorded (Drouot-Dulau and Gannier, 2007; Frantzis *et al.*, 2011). Even for highly resighted males in the Ligurian Sea, excursions to the Balearic Islands (Drouot-Dulau and Gannier, 2007; Rendell *et al.*, 2014) and one migration to the eastern Mediterranean (Frantzis *et al.*, 2011) suggest that male feeding and breeding needs are incompatible with fidelity to one site.

Group size

Males segregated from social units were either solitary or part of temporary and very small, loose aggregations, as in several male habitats around the world (Lettevall *et al.*, 2002). The most common occurrences (81% of male encounters) were singletons and loose pairs, with larger groups being rare. This is similar to observations made in the western Mediterranean basin (Pavan *et al.*, 2000; Drouot *et al.*, 2004a; Notarbartolo di Sciara *et al.*, 2006; de Stephanis *et al.*, 2008). Encounters with pairs were almost as common (or more common if photo-identification data were used) as with singletons along the Hellenic Trench, in contrast to observations in the open ocean, where encounters with pairs usually account for less than one-third of encounters with solitary males in both male and female habitats (Lettevall *et al.*, 2002). This higher 'sociality' of males along the Hellenic Trench might be related to the possibility that the males studied were on average younger (and consequently more social) than in studies in the open ocean. The mean male group size (with no use of photo-identification data) along the Hellenic Trench is almost identical to the mean group size estimated for male aggregations in the north-western Mediterranean Sea (Drouot *et al.*, 2004a; 1.87 and 1.84, respectively, with a range 1–5 for both areas).

In four out of five geographical areas inhabited by sperm whale social units outside the Mediterranean the mean social unit size ranged between 11 and 12.5 individuals (Antunes, 2009; Jaquet and Gendron, 2009). The mean group size of social units in the Hellenic Trench is much smaller (8.2), although higher than in the Gulf of Mexico (5.2). The mean aggregation or 'group' size in these studies ranged between 7.4 and 31.3 individuals. The only aggregation formed by more than one social unit along the Hellenic Trench had a group size (12) within the range of social units' group size. As was the case also in the Azores (Antunes, 2009), the groups of whales encountered at sea typically correspond to single social units, possibly including very few temporary visitors.

The small size of social units and the scarcity of large aggregations made up of more than one social unit might possibly be related to the absence of predators (i.e. killer whales) in the eastern Mediterranean (Notarbartolo di Sciara and Demma, 1994) and the extreme oligotrophy of this area (Walle *et al.*, 1993; Notarbartolo di Sciara *et al.*, 2008). Both of these factors would favour smaller group sizes (Jaquet and Gendron, 2009).

Population structure

The Hellenic Trench appears to be critical sperm whale habitat used by both sexes and all age classes for all aspects of the species' biological cycle. Mature, maturing and immature male and female feeding, probably breeding and calving are all taking place on the same ground and there are no indications of preferred feeding or breeding areas within it. Sex ratio in sperm whales is about equal at birth (Best *et al.*, 1984) and expected equal for sperm whale populations when the areas inhabited both by social units and males (i.e. warm-temperate waters plus high latitudes) are considered. If the Hellenic Trench was only a social unit habitat, the sex ratio should be biased towards females. The observed balanced sex ratio is consistent with both social units and males segregated from them sharing the same habitat at least during summer. It is also compatible with the hypothesis of a semi-closed local population in the eastern Mediterranean with low degree of exchanges.

Although solitary males have also been observed in other areas inhabited by social units; in the Atlantic, Pacific and Indian Oceans, the reported relative abundance of males segregated from social units has been much lower than in the Hellenic Trench (15.5%). In the Atlantic Ocean solitary mature males represented almost 10% of the total photo-identified sperm whales off Dominica (Gordon *et al.*, 1998), 5.9% in the Azores (45/762; Matthews *et al.*, 2001) and 0% in the northern Gulf of Mexico (Jaquet and Gendron, 2009). In the Pacific and Indian Oceans available relative abundances for mature males are 3.6, 3.2, 1.3, 0.6 and 0%, for Chile, the Gulf of California, the Galápagos and the Seychelles, respectively (Jaquet and Gendron, 2009). The higher male relative abundance along the Hellenic Trench may be explained by the presence of (a) feeding males that are not just short-term transients roving between social units, and (b) younger males observed in small groups (possibly 'bachelor groups'), which may have not been recorded as males in some earlier studies of oceanic populations, owing to their small size. The only other example of high male relative abundance in an area inhabited by social units comes from the Mediterranean as well.

Off the Balearics nine out of 42 (21.4%) sperm whales were apparently males photo-identified away from female groups (Luke Rendell, pers. comm.).

The fact that there were only five observations of short-term presence of males within social units suggests that summer is unlikely to be the main breeding season. On the contrary, the high number of newborns and an observation of a birth indicate that summer is the calving season with births peaking in July. If the length of gestation for Northern Hemisphere sperm whales is 15 to 16 months as proposed by Best *et al.* (1984), then the observed newborns should have been conceived from late winter to late spring. This is in agreement with whaling data from the North Hemisphere (Best *et al.*, 1984) and particularly the North Atlantic (Clarke, 1956), which suggest that breeding takes place between March and May. The timing of the breeding season is one possible explanation of the scarcity of large male sightings in his study, if such males approach the Hellenic Trench only during the breeding season. However, an alternative and likely explanation could be that mature sperm whales in the Mediterranean Sea are naturally smaller than in oceanic populations. The mean (11.4 m) and maximum (14.6 m) total lengths of 19 males segregated from social units were small in the present study. There are no known strandings of sperm whales larger than 15 m in the entire eastern Mediterranean during this and the last century (a report by Hirtz, 1921, of a large sperm whale in the Adriatic that was not measured by the author is considered unreliable). Studies in both Mediterranean basins also detected no sperm whales larger than 14 m (Pavan *et al.*, 1997; Drouot *al.*, 2004a). The mean total length (9.1 m) and total length range (8.6 and 9.5 m) of the nine largest females measured acoustically during this study, also suggest a smaller body size. The surprisingly elevated ages of some stranded small sperm whales (Frantzis *et al.*, 2003; unpublished data) also point to the same conclusions. Comparatively, male sperm whales of 15 m and over are common among strandings on both sides of the Atlantic Ocean (Goold *et al.*, 2002), despite the heavy historical whaling impact that targeted especially the large bulls. Furthermore, females above 10.5 m were very common in recent catches by whalers in the Azores (Clarke, 1956).

Sperm whales in the Gulf of Mexico were recently found to be significantly smaller than those in the Pacific (Jaquet, 2006). It has been suggested that cetacean populations occupying a small geographic range are of smaller individual size, because they do not migrate over large distances and thus large body size is not favoured (Brodie, 1975). Therefore, smaller size for Mediterranean or eastern Mediterranean sperm whales in comparison with conspecifics inhabiting the vast and productive oceanic grounds should not be a surprise. The absence of clear distinction between feeding grounds for segregated males and for social units in an extremely oligotrophic sea area with limited resources may also affect the individual size. Smaller size and smaller size difference between the two sexes would balance the increased trophic competition between mature males and social units.

CONCLUSIONS

There are few areas in the Mediterranean Sea that can be considered ‘hotspots’ for sperm whales. Even fewer (just two) are known social unit habitats, but it is upon these that the reproduction and the survival of this endangered population depend. Some important conclusions arise from this study:

a. The Hellenic Trench appears to be the core habitat for the eastern Mediterranean sperm whale sub-population, calving, nursing and very probably breeding occurs here.
b. This sub-population seems to be quite discrete and is likely to number very few hundreds of individuals; it is therefore very vulnerable.
c. Some features of the biology of sperm whales here differ from those of other well studied sperm whale populations. For example, both sexes use a limited area for feeding, breeding, calving and nursing with no obvious distant segregation at the scale that this occurs in typical oceanic populations.

Further surveys, especially between February and May, are needed to investigate seasonal patterns, with particular focus on the seasonality of breeding. In addition, specific analysis of the effect of environmental factors on the distribution, the estimation of the abundance through mark–recapture models and the study of social stability/fluidity of social units will consolidate our understanding of this population unit.

Of the sperm whales stranded along the Greek coasts 61% show marks from a collision with a large vessel (Panigada and Leaper, 2009; Frantzis *et al*., unpublished data), and it is clear that ship strikes are a serious acute threat. The patterns of sperm whale densities observed in this study, with a pronounced preference for waters close to the 1000 m contour and apparent lower densities further offshore suggest that, in this case, the problem could be greatly reduced by moving the shipping lanes a few kilometres further offshore.

Given the high calving mortality and the very small sub-population size suggested by this study and the mortality levels reported owing to ship strikes in the Greek Seas, the conservation status of the sperm whale sub-population in the eastern Mediterranean is poor and its survival uncertain. Immediate priority should be placed both on systematic monitoring of the population status and on implementing measures to reduce the mortality associated with ship strikes. Both goals, as well as the mitigation of new threats (such as seismic surveys and hydrocarbon exploration) that appeared recently in the region of the Hellenic Trench, can be served appropriately if a marine protected area for sperm whales is created along the Hellenic Trench, as was proposed by ACCOBAMS in 2007 (Anonymous, 2007; Resolution 3.22).

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