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Seasonal variation of striped dolphins, fin- and sperm whales' abundance in the Ligurian Sea (Mediterranean Sea)

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In order to investigate seasonal changes in cetacean relative abundance, a series of surveys were conducted between the French mainland and Corsica. From February 2001 to February 2004, thirty similar transects were conducted monthly, using the same dedicated boat and a consistent sampling protocol, including visual observation and passive acoustic sampling. A total effort of 5759 km was sampled, conducted at the same speed and in good sighting conditions. Relative abundances of striped dolphins (*Stenella coeruleoalba*) and fin whales (*Balaenoptera physalus*) were determined using standard line-transect methodology. The relative abundance of striped dolphins peaked in May and September ($>1.3\times10^{-2}$ ind.km^{-1}), while a consistent minimum value ($<0.6\times10^{-2}$ ind.km^{-1}) was obtained from December to April. A maximum relative abundance of fin whales occurred in August with 5.6×10^{-2} ind.km^{-1} and decreased to almost zero from November to January. For sperm whale (*Physeter macrocephalus*), a long diver species, frequency and abundance indices were determined using acoustic sampling. The highest acoustic relative abundance was observed from August to October, with more than 2×10^{-2} ind.km^{-1}. Environmental parameters (sea surface temperature and chlorophyll) were computed for the sampling area from remote sensing imagery and pooled on a monthly basis, to correlate with relative abundance indices of the three species.

INTRODUCTION

The Ligurian basin is characterized by a frontal system, which provides a high level of primary production, peaking in March–April. Field hydrological studies and remote sensing data have outlined a frontal area parallel to the mainland coast (Sournia et al., 1990) and to Corsica (Goffart et al., 1995). In summer, this area is well known to be attractive for a large number of cetaceans (Forcada & Hammond, 1998; Gannier, 1999), particularly striped dolphins (*Stenella coeruleoalba*) and fin whales (*Balaenoptera physalus*). Six other species inhabit this area: the sperm whale (*Physeter macrocephalus*), the Cuvier's beaked whale (*Ziphius cavirostris*), the long-finned pilot whale (*Globicephala melas*), the Risso's dolphin (*Grampus griseus*), the bottlenose dolphin (*Tursiops truncatus*) and the common dolphin (*Delphinus delphis*). Since 2002, Italy, Monaco and France have formally created the International Sanctuary for Marine Mammals, a protected area of 87,492 km^2 (Figure 1). Abundance of the two most common species were estimated after 1990, when a morbillivirus epizootic strongly affected the striped dolphin population of the Mediterranean Sea (Aguilar & Raga, 1993; Gannier, 1999). In the Ligurian Sea, summer abundance estimates of 27,000 striped dolphins were computed in 1992 (Forcada et al., 1996) and in 1996 (Gannier, 1998). The fin whale population was estimated to be 901 individuals, with a summer density of 0.015 ind.km^{-2} for the Ligurian–Provençal basin (Forcada et al., 1995; Gannier, 1997). To date, no estimate of absolute abundance is available for sperm whale, although higher relative abundances were found in the Gulf of Lions and the Ligurian Sea compared to the Ionian and Tyrrhenian Seas (Gannier et al., 2002).

Although seasonal samplings were conducted in the Ligurian (Gannier, 1999) and Tyrrhenian Seas (Marini et al., 1996), or more recently for the waters off Spain (Gomez de Segura et al., 2006), little is known about seasonal patterns of the most common species in the Mediterranean Sea. To date, the most notable finding for the Ligurian Sea is that fin whale and striped dolphin are present year-round, with an increased occurrence in summer (Clark et al., 2002; Gannier, 1999). In view of this lack of knowledge and the conservation scope of the Mediterranean Sanctuary, we dedicated a three-year study to investigate seasonal trends of cetaceans frequenting the area. More specifically, the objectives of this study were to assess seasonal variations in relative abundance and to relate these seasonal changes to environmental variables. This paper presents the results for the three main species occurring in the area: the striped dolphin, the fin whale and the sperm whale.

MATERIALS AND METHODS

Visual survey

From February 2001 to February 2004, dedicated surveys were conducted monthly, along two parallel transect lines, located between the French mainland and Corsica (Figure 1). Transects were covered during a two-day round trip with good meteorological conditions (i.e. wind less than or equal to 3 Beaufort), using the same 13 m motorboat and

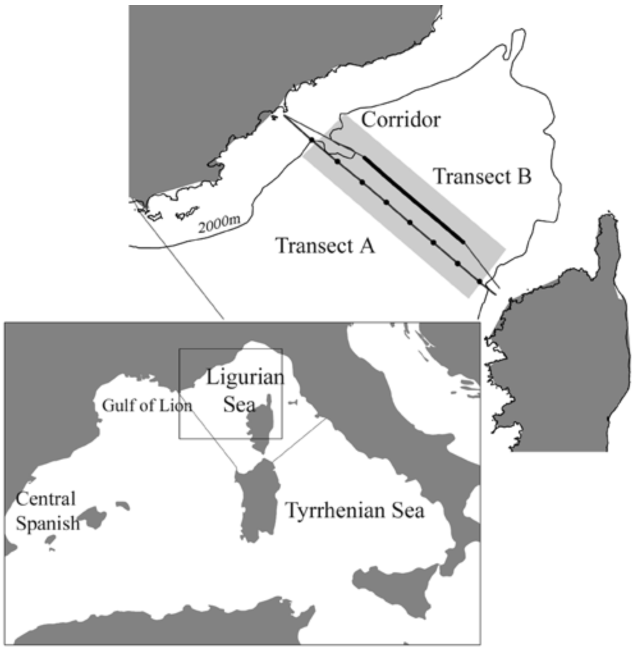

Figure 1. Map of the study area and transects conducted at 22 km.h^{-1} (simple line) and 13 km.h^{-1} (bold line). Locations of acoustic listening stations are shown as black dots and environmental parameters were averaged on the dashed corridor.

a consistent observer crew. Three experienced observers, seated with eyes 4 m above the water surface, searched the frontal sector (–90° to +90° relative to the bow) with the naked eye and were rotated every hour.

During the first day, transect A (160 km) was conducted at a speed of 22 km.h^{-1} (12 knots) between Cap d'Antibes (43°32'N 07°07'E) and Pointe de la Revellata (42°36'N 08°37'E, Figure 1). The next day, a shorter (74-km) anti-parallel transect (B), located 11 km apart north-east from the former, was surveyed at lower speed (13 km.h^{-1}). The purpose of transect B was to estimate the loss of sightings when sampling at a higher speed. The survey required the trip from Antibes to Corsica to be undertaken within one day, which could only be achieved at a relatively high speed of 22 km.h^{-1}. This effort, at lower speed, was not included in this study. However, to increase on-effort survey, the observation protocol was maintained, weather and day light permitting, when cruising at 22 km.h^{-1}, before reaching and after having left transect B. Transects were attempted when good weather was forecast, with a minimum lag of 17 days (Table 1).

The vessel position (from GPS) and environmental parameters such as wind force (on Beaufort scale estimated by observers) were recorded on an hourly basis (and at each sighting). For each sighting the bearing angle was measured by hand compass and the radial distance to the detection was measured with reticulated binoculars 7×50 and/or by the naked eye. Binocular measurements represent 55% of sightings for striped dolphins and 45% for fin whales. The survey was generally conducted as passing mode transects. However, in some cases where animals were detected at less than one kilometre from the vessel, they were approached to confirm species' identification, school size and composition. After such occasional approaches, the transect line was joined with a convergent course to minimize potential repeating of sightings. School size was estimated by combining each observer estimation of the minimum, maximum and average number of individuals.

Visual data analysis

Striped dolphin and fin whale sightings were initially analysed applying standard line-transect methods (Buckland et al., 2001). However, insufficient monthly effort was available for absolute abundance estimates to be computed. Therefore, indices of relative abundance, expressed in number of individuals per unit of effort (ind.km^{-1}), were computed monthly, using Distance 4.1® software. Transects surveyed at 22 km.h^{-1} were divided into 18.5 km samples (10 n.m.) for striped dolphins and into 37 km samples (20 n.m.) for fin whales, to account for changes in wind conditions along the track. Only effort performed in wind ≤3 Beaufort was considered. Sighting data were truncated at perpendicular distances of 1200 m for striped dolphin, and 2500 m for fin whale, thereby excluding 4 sightings for each species.

Relative abundance index (RAI, expressed in individuals per km) was computed as:

$$RAI = \left(\frac{n}{L}\right) \cdot \bar{s}$$

with *n*: the number of sightings, *L*: the effort in km (*n*/*L* represents the encounter rate) and $\bar{s}$: the mean school size.

Stratification on Beaufort was applied to test the effect of wind condition on encounter rate and mean school size and Z-tests were carried out on pooled data to assess the significance of the relationship (Buckland et al., 2001). The three Beaufort classes considered were '0–1', '2' and '3'.

Acoustic survey

Acoustic sampling was applied to assess sperm whale occurrence. A mono hydrophone (Magrec, HP 60MT) connected to a digital audio tape recorder was used. Two minute recording sessions were conducted at 8 acoustic stations, located 18.5 km (10 n.m.) apart along transect A (Figure 1). During these sessions, the vessel's propeller was de-clutched (in 2001) or the engine turned off (in 2002 and 2003). The hydrophone was estimated to be more than 7 m deep, after underwater observation (Gannier et al., 2002). A qualitative assessment of the strength of sperm whale clicks and underwater noise was recorded from 0 (absent) to 5 (high) following a previous method (Gordon et al., 2000). All recordings were listened to in the laboratory to double-check signal levels and estimated numbers of whales. As the exact number of whales could not be reliably determined when more than 3 whales were vocally active in the area, 3 was the maximum school size allocated by acoustic sampling (Gannier et al., 2002). On 16 occasions, acoustic detections were followed by a visual sighting, within 1 to 40 min. The distance between acoustic stations where sperm whales were heard and subsequent sightings, were used to estimate a potential range of distance to the animal for each signal level. Estimation of the maximum distance, takes into account a whale displacement of 2.7 km.h^{-1} (Drouot et al., 2004b). The estimated distances ranged from 0 km, for the maximum signal level (5), to 15 km, for a signal level of 2 (no distance estimates for signal level of 1). A signal level of

Table 1. *Sampling date and effort (in km) conducted at 22 km.h^{-1} with good sighting conditions (Beaufort ≤3) and distribution of global effort achieved per month according to three Beaufort strata.*

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
2001	–	11–12		2–3 27–28	25–26	23–24	25	12–13		25–26		4–5	
Effort		74		261	227	158	158	221		158		148	1405
2002	5–6	2–3		16–17	16–17	19–20	22–23	16–17	17–18		28	21–22	
Effort	296	209		121	209	250	256	251	208		158	176	2133
2003	–	8–9	26–27	23–24	30–31	16–17	13–14	6–7	18–19	11–12		19–20	
Effort		158	158	158	253	208	192	201	226	250		155	1959
2004	–	3–4											
Effort		255											255
Total	296	697	159	541	689	616	607	673	435	408	158	480	5759
Beaufort 0–1	230	125	140	216	442	371	390	340	337	231	74	148	3044
Beaufort 2	66	424	19	232	126	198	141	201	98	158	37	165	1865
Beaufort 3		148		93	121	47	76	132		19	47	167	850

3 corresponds to a whale located at a maximum distance of 7 km from the vessel. Based on these distance estimates, and considering a whale displacement of 2.7 km.h^{-1}, detections with a signal level of 3 or more made on two consecutive stations (18.5 km apart), were considered as being from two distinct whales (or different acoustic sequences). However, when two consecutive acoustic stations showed a click level lower than 3 (the whale being at more than 7 km away from the boat), we considered that the same whale was being recorded (same acoustic sequence). After having sorted all acoustic stations into sequences, the minimum number of whales heard was determined. Only stations with a noise level less than 4 were considered for analysis. A survey unit consisted of an 18.5 km (10 n.m.) transect section centred on a listening station. For each survey unit, we computed the acoustic sequence frequency (AF), defined as the number of acoustic sequences per kilometre of effort, and the acoustic relative abundance (ARA), defined as the minimum number of whales heard km^{-1} (Gannier et al., 2002), with a reasonable certainty of not reconsidering the same animal.

Environmental parameters

Remote sensing data were used to assess seasonal variations in environmental conditions. The ocean colour (chlorophyll pigment concentration) from Nasa SeaWifs (with agreement of Goddard DAAC) and sea surface temperature (SST) from Pathfinder sensor (PODAAC NASA/NOA) were extracted with Wimsoft®6.25 software. For both of these parameters, monthly values were computed using successive periods of 8 d. Data were extracted and averaged on a corridor of 5760 km^2 (130×44.5 km) around both transects (Figure 1), for waters deeper than 2000 m (>17 km from shore). The relationships between the occurrence of the three studied species and environmental parameters were investigated by plotting each species abundance indices (encounter rate, RAI or ARA) against log-transformed SST and chlorophyll concentration. The Pearson correlation coefficient was then computed.

RESULTS

Over the 3 y (37 consecutive months), 30 journeys were carried out, representing a total effective effort of 7770 km on correct sighting conditions (Beaufort ≤3), including 5759 km at 22 km.h^{-1} (Table 1). Six different species were observed and a total of 492 groups were detected, including 478 on-effort sightings. Striped dolphins and fin whales accounted for 69% and 26% of the sightings, respectively. Both sperm whales and Risso's dolphins represented 2% and long-finned pilot whales 1% of the sightings (Table 2). Additionally, bottlenose dolphins were only observed off-effort, in coastal waters off Corsica. All pelagic species were observed year-round, excepting the pilot whale, which was only recorded between July and September.

Monthly efforts conducted at 22 km.h^{-1} and accumulated over three years averaged 480 km (SD=194). A minimum of 158 km of effort was obtained in March and November, while more than 600 km was achieved in February and from May to August (Table 1). The Beaufort 0–1 class represented between 18 and 88% of the effort achieved per month, with a total of 3044 km achieved over the three years. The Beaufort 2 and Beaufort 3 classes totalled 2715 km (Table 1).

Striped dolphin

A total of 216 on-effort sightings of striped dolphins were recorded. A significant decrease in encounter rates was observed from Beaufort 0–1 class, with 5.1×10^{-2} ind.km^{-1} (Figure 2A), to Beaufort 2 and 3, with 2.6×10^{-2} and 1.3×10^{-2} ind.km^{-1} respectively (Z-test: Z>2.1, P<0.03). Therefore, to minimize the bias induced by poor sea state conditions, monthly encounter rates were computed using effort conducted in Beaufort 0–1 only. Striped dolphin schools ranged from 1 to 140 individuals. Mean school size decreased from 19.2 to 14.0 with increasing Beaufort classes (Figure 2A). However the differences among the three classes were not significant (Z-test: Z<1.62; P>0.10), thus the mean school size was computed without stratification. When considered

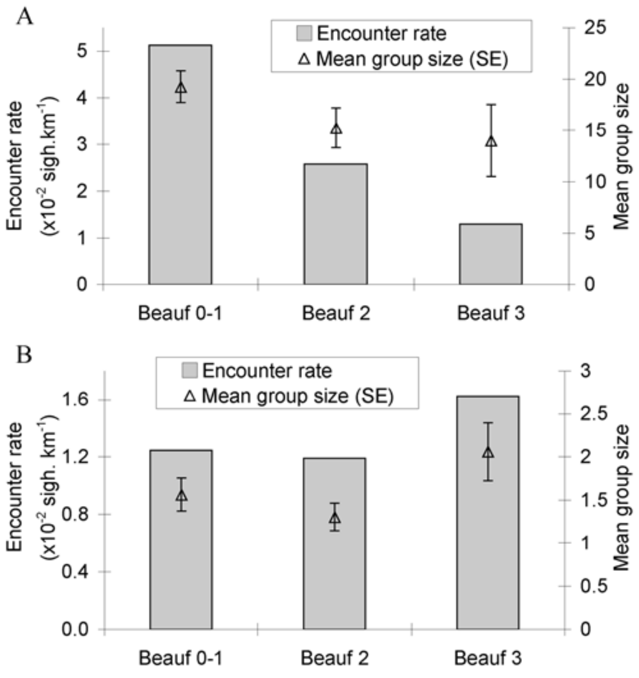

Figure 2. Encounter rate (×10^{-2} sighting.km^{-1}) and mean group size (±standard error) distribution on Beaufort classes, for (A) striped dolphin and (B) fin whales.

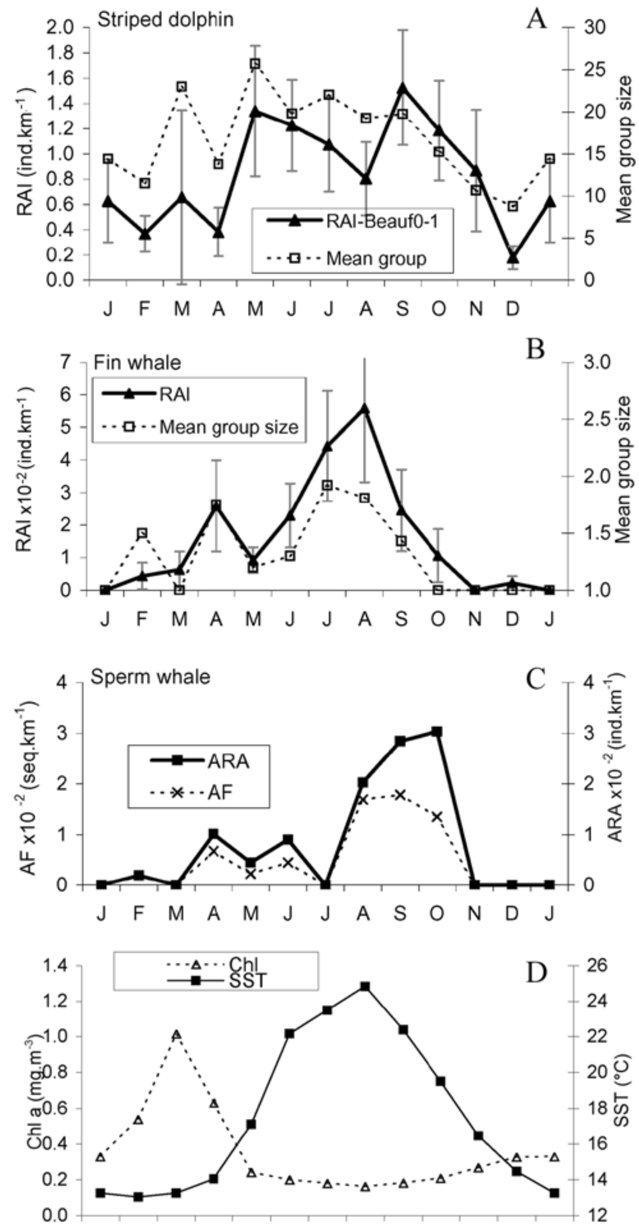

Figure 3. Monthly variation of: relative abundance index (RAI, individual.km^{-1}) and mean group size for: (A) striped dolphin; (B) fin whale; (C) acoustic sequence frequency (AF, sequence. km^{-1}) and acoustic relative abundance (ARA, ind.km^{-1}) for sperm whale; (D) monthly average of chlorophyll concentration (mg.m^{-3}) and sea surface temperature (°C).

monthly, mean school size was not consistently correlated to Beaufort classes.

Monthly school sizes clearly increase in summer, peaking in May (25.7 individuals on average). Minima occur in November, December and February (Figure 3A), and were significantly lower than the school sizes observed during the warm season (May to September; Z-test: Z>2.71, P<0.01).

We observed that monthly encounter rates estimated on Beaufort 0–1 conditions were about 1.4 times greater than those estimated on pooled Beaufort classes (r^2=0.986, P=0.000). On the Beaufort 0–1 class, encounter rates were relatively consistent from January to April, with less than 4.4×10^{-2} sighting.km^{-1} (Figure 3A), and peaked in June (6.2×10^{-2}) and in September–November (>7.7×10^{-2} sighting. km^{-1}). Relative abundance indices (RAI) ranged between 1.8×10^{-1} and 6.6×10^{-1} ind.km^{-1} from December to April, and peaked in May and September (13.4 and 15.2×10^{-1} ind.km^{-1}), despite a lower mean school size. These maxima differed significantly from the December and February indices (Z-test: Z>2.18, P<0.04).

Fin whale

After a truncation at 1,200 m, a total of 76 on-effort sightings of fin whales were retained for the analysis. Beaufort conditions did not show a significant effect on either encounter rate, or mean school size (Z-test: Z<1.3, P>0.21; Figure 2B). The only significant difference was found between the mean school size of the Beaufort 2 and 3 classes (Z-test: Z=2.05, P=0.05) and seems not to be related to sighting conditions. Fin whale school size ranged from 1 to 5 animals and peaked in July and August with an average of 1.9 and 1.8 individuals per school, respectively.

Encounter rate and RAI showed similar seasonal trends (Figure 3B). Minima (<0.22 ind.km^{-1}) were observed between November and January, and were significantly different from summer maxima. A first peak of abundance occurred in April, with 2.6×10^{-2} ind.km^{-1}, followed by an increase of up to 5.6×10^{-2} ind.km^{-1} in August. A strong decrease succeeded this maximum in autumn (Figure 3B).

Sperm whale

Sperm whales were acoustically detected on 16% of the 217 acoustic stations performed in low underwater noise on transect A. Their presence was recorded almost throughout

Table 2. *Sightings of cetaceans recorded from February 2001 to 2004.*

	Number of sightings		School size	
	Total	On-effort*	Range	Mean (±SD)
Striped dolphin	334	330	1–140	18.0 (17.3)
Fin whale	126	123	1–5	1.5 (0.9)
Pilot whale	7	7	1–25	14.6 (7.8)
Risso's dolphin	10	9	1–30	9.0 (9.9)
Sperm whale	12	9	1–9	2.3 (2.4)
Bottlenose dolphin	3	-	2–5	3.67 (1.5)

the year, except in January, July and November. The acoustic sequence frequency (AF) remained lower than 7×10^{-3} seq. km^{-1} from November to July (with a slight increase in late spring), and increased notably in August–October, to a level around 17×10^{-3} seq.km^{-1} (Figure 3C). The acoustic relative abundance (ARA) varied similarly, with a first peak in spring (4 to 10×10^{-3} ind.km^{-1}), and a consistent increase from August to October, where a maximum of 30×10^{-3} ind. km^{-1} was reached (Figure 3C).

Environmental parameters

Monthly SST in the area described a bell-shape curve, characterized by a peak in August (24.8°C) and a colder temperature from January to March (13°C, Figure 3D). Only slight differences in temperature were observed between the three studied years. Mean phytoplankton biomass consistently reached maximum values in March (Figure 3D) and decreased to minimum values in summer, although intensity and bloom duration varied during the three years.

Occurrence of striped dolphins, fin- and sperm whales tend to increase with SST (Pearson r>0.607, P=0.036), while opposite trends are observed with chlorophyll concentration for the 3 species. The most significant correlation was observed between fin whale encounter rate and log-transformed temperature (Pearson r=0.826, P=0.001). It is however important to point out that a time lag of 2 months occurs between maximum temperature and maximum occurrence of sperm whales in the area. A significant correlation was also found between striped dolphin and log-transformed chlorophyll RAI (Pearson r=–0.651, P=0.022).

DISCUSSION

The central part of the Marine Mammal Sanctuary is well known for its high summer density of striped dolphins and fin whales (Forcada & Hammond, 1998; Forcada et al., 1995; Forcada et al., 1996; Gannier, 1998), while sperm whales seem to favour the Gulf of Lions, compared to the Ligurian Sea (Gannier, 1999; Gannier et al., 2002). Seasonal changes in the area are poorly known and this study provides valuable quantitative data on seasonal abundance variation of the three main species: striped dolphins, fin- and sperm whales, inhabiting the Ligurian Sea. These dedicated surveys represent the first monitoring of the Marine Mammal Sanctuary, conducted monthly in a consistent way over three consecutive years, and including winter periods (50% of our sampling effort was collected between September and May). Nevertheless, the previous study of Gannier (1999), conducted from 1988 to 1995 in the Ligurian Sea, and opportunistic transects (>200) conducted year-round in the Tyrrhenian Sea between September 1989 and 1992 (Marini et al., 1996), represent valuable sources of comparison for ours results.

Striped dolphin

Summer periods can be compared to several studies conducted in the area. Previous mean school sizes (19 to 22 individuals) observed between June and August (Forcada et al., 1995; Gannier, 1998; Gannier, 1999) were consistent with our results. However, relative abundance estimates computed in previous years were consistently lower. Relative abundance indices obtained by Gannier (1998, 1999) in 1996 and 1998, ranging between 0.67 and 0.79 ind.km^{-1} were slightly lower than our estimates, while in 1991 notably lower values (0.47 ind.km^{-1}) were obtained by Forcada & Hammond (1998). The enhanced values obtained in this study, could reflect an increase in the striped dolphin population in the area after the epizootic mortality. Indeed, in the early 90s, striped dolphins of the Mediterranean Sea were strongly affected by a morbillivirus epizootic (Aguilar & Raga, 1993). Such a hypothesis of an increased striped dolphin population after the epizootic was also suggested by Gomez de Segura et al. (2006) in the central Spanish Mediterranean Sea. Comparison with the results of Forcada & Hammond (1998) showed that encounter rates, however, were similar, which tends to suggest that the increase in striped dolphin density since the 90s should be assigned to an increased occurrence of larger groups (rather than an increase in group numbers). These variations in density estimates could also be explained by differences in field protocols (plate-form, speed, …) and/or data processing (stratification on sea state, school size, …). However, we also observed during these 3-y surveys, a tendency for summer relative abundance to increase from 2001 to 2003 (Laran, 2005). It seems unlikely that this increase is to be assigned to the creation of the Marine Mammal Sanctuary in 2002, as conservation measures implemented since its creation, in 2002, have been relatively faint.

The rest of the year represents a more difficult season to survey, and to date, despite the need of better understanding seasonal trends to implement appropriate management strategies in the Sanctuary, no results based on continuous sampling are available for the area. Stratification on Beaufort condition and computation of our abundance index on Beaufort 0–1 class throughout the year seems to provide appropriate estimates. Significant differences between striped dolphin encounter rates obtained on Beaufort strata were also observed by Forcada & Hammond (1998).

Seasonal trends in school size and relative abundance observed by Gannier (1999) are consistent with our results with minimum relative abundance observed in December, February and April. However, the homogeneous effort achieved throughout the year in this study results in a finer temporal scale, which allows us to demonstrate a definite increase in striped dolphin abundance from May to

October. Our first peak in May differs from the low index (0.19 ind.km^{-1}) observed in spring by Gannier (1999), and suggests a first increase of striped dolphin occurrence in the Sanctuary area before summer, followed by a slow decrease from May to August and a second peak four months later, in September. This trend was consistent over the 3 y surveyed. This result could be explained by a migration pattern with striped dolphins crossing our sampling area for a first time in May and a second time in September. Possible migrating areas could be the Tyrrhenian Sea, where striped dolphin sightings (number of individuals not mentioned) dominate between January and July (Marini et al., 1996). A second potential area could be the Central Spanish Mediterranean Sea where density appears to be maximal from October to March (Gomez de Segura et al., 2006).

Gannier (1999) observed that water temperature clearly increases from May, and suggested that this factor could affect striped dolphin distribution. Our peak of abundance in May also supports this hypothesis. However, we also observed a decrease of abundance in our study area in August, when water temperature is at its highest. This might reflect a possible displacement of some pods to other warm areas (no significant decrease of school size) before their return in September.

Fin whale

Our summer school sizes, ranging from 1.3 to 1.9 individuals, are in agreement with the range of 1.2 to 1.6 previously found in the area (Forcada et al., 1995; Gannier, 1997). Aggregation of whales peaked in July and August with more than 1.8 whales observed per school on average, probably due to the higher availability of food in the Ligurian Sea. Decreasing school size at the end of summer was also mentioned in previous studies (Gannier, 1999).

Relative abundance indices computed in previous studies ranged between 2.8×10^{-2} ind.km^{-1} for the Corsican shelf (Gannier, 1997) and 9.13×10^{-2} ind.km^{-1} for the western Mediterranean Sea (Forcada et al., 1996). Our intermediate results of 4.4 and 5.6×10^{-2} ind.km^{-1} in July and August are consistent with the estimate of Gannier (1997) for the off shore stratum (5.3×10^{-2} ind.km^{-1}).

Overall, as previously observed by Forcada et al. (1995, 1996), stratification on Beaufort categories did not produce any significant difference of fin whale encounter rates and school sizes. The slightly larger encounter rate and mean school size observed on Beaufort 3 could be explained by a reduced effort (850 km) in this class, compared to other classes (>1800 km).

This study demonstrates seasonal variations in fin whale relative abundance and confirms that the species never entirely leaves the Ligurian Sea (Clark et al., 2002). In winter, relatively low abundances of fin whale are observed in agreement with the relative abundance of 2.6×10^{-3} ind.km^{-1} obtained by Gannier (1999). A first peak of whales occurs in April (2.6×10^{-2} ind.km^{-1} on average), following the phytoplanktonic bloom observed in March. However, from 2001 to 2003, a strong inter-annual variation in abundance estimates and in the timing of the peak of maximum occurrence were observed (Laran, 2005). These results are opposed to the low value (0.5×10^{-2} ind.km^{-1}) reported in spring by Gannier (1999). Relative abundance reaches highest values in summer, which corresponds to the feeding period for the species. Our results are consistent with the summer estimates of Gannier (1999), with 4.1×10^{-2} ind.km^{-1} from June to September, although our monthly resolution allows us to distinguish a clear peak in August. In the Central Tyrrhenian Sea, Marini et al. (1996) observed a continuous occurrence of fin whales with maximum values observed in April–May and September–October. This could suggest a northern movement of fin whales during summer months (June–August), from the Tyrrhenian Sea to the Ligurian Sea feeding ground. As observed in the Ligurian Sea, Marini et al. (1996) also reported minimum occurrence of fin whales in November and December. These results suggest a movement of whales to other, perhaps warmer, regions in winter, when feeding ceases to be their predominant activity. These movement patterns would be consistent with the seasonal migration scheme observed in the Atlantic Ocean. Nevertheless, some scientists have suggested that, rather than global migration routes, fin whales in the Mediterranean Sea follow an aggregation-dispersion scheme: they aggregate in specific, relatively small, productive areas in summer, to meet their feeding requirements, and disperse over wider geographical areas during the rest of the year (without heading to specific wintering grounds, Notarbartolo et al., 2003). Winter global distribution and movement patterns still need to be confirmed in the Mediterranean Sea.

Fin whale density in the Ligurian Sea is comparable to nearby oceanic areas, such as the north-eastern Atlantic (Goujon et al., 1994) or Central Bearing Sea (Moore et al., 2002). About 3,600 fin whales were estimated for the western Mediterranean Sea, by Forcada et al. (1996) with a density of 2.41×10^{-2} ind.km^{-2}, while Gannier (1997) obtained a lower estimate of 1.99×10^{-2} ind.km^{-2} for the Ligurian pelagic area and Forcada et al. (1995) 1.55×10^{-2} ind.km^{-2}. A decrease of the fin whale encounter rate from 1995 to 1999 was mentioned by Panigada et al. (2005). Our study tends to support these lower values, with a maximum RAI 38% lower than the estimates computed in 1991 (Forcada et al., 1996). This decrease in whale abundance observed over the last years is a cause for great concern and raises major conservation issues. In fact, intense traffic activity occurs in the Ligurian Sea in summer, when fin whales happen to concentrate in the area, which could lead to a drastic impact on the population through direct mortality (collision with vessels) and habitat degradation. Furthermore, this study displays a marked relationship between whale abundance and temperature throughout the year. Therefore, climate changes and global warming should be considered as major issues susceptible to affect krill density and consequently the fin whale population in the area.

Sperm whale

For the purpose of the analysis, the effect of the thermocline on signal reception was assumed as null, considering sperm whale diving depth and strength of the clicks. Therefore, our results, and particularly sperm whale distance-estimates, should be considered carefully, being aware that reception is also affected by water column stratification (maximum in summer).

Acoustic sampling appeared as an efficient tool to assess seasonal trends in sperm whale abundance. Our mean acoustic relative abundance (ARA) of 9.0×10^{-3} ind.km^{-1} obtained in June was consistent with the previous acoustic results of Gannier et al. (2002), who obtained 7.8×10^{-3} ind. km^{-1} in the Ligurian Sea. Concerning seasonal variations, previous surveys reported the absence of sperm whale between October and May in the area (Gannier, 1999), and from October to April in the Tyrrhenian Sea (Marini et al., 1996). Our continuous sampling demonstrates for the first time that sperm whales occur throughout the year in the Ligurian Sea, with a maximum abundance from August to October. Moulins & Würtz (2005) point out an occasional presence of a large social unit in December in the area, which is consistent with the two sightings of young whales performed during our surveys in September and December 2003. Thus, while mean school size was estimated to be 1.3 individuals in the north of 41°N parallel (Drouot et al., 2004a), larger social group appear to frequent the area during the cold season. In this study, the acoustic determination of the number of individuals (limited to 3 individuals) could have induced a bias leading to an under-estimation of sperm whale numbers. When combining visual and acoustic sampling, seasonal patterns, including a low occurrence period from January to July and a favoured period from August to December, are even more clear-cut (Laran & Gannier, 2006).

CONCLUSION

Compared to previous studies, our large number of surveys conducted all year round, from 2001 to 2004, allowed more accurate results to be obtained. The study thereby enhanced the knowledge on seasonal occurrence of striped dolphin, fin- and sperm whales in the International Sanctuary for Marine Mammals. In particular, this survey allowed us to estimate fin whale and striped dolphin relative abundance indices throughout the year, and acoustic sampling produced consistent results on variation of sperm whale occurrence.

This study demonstrates that the 3 main species inhabit the Marine Mammal Sanctuary area the whole year round. The striped dolphin, fin- and sperm- whales are consistently less abundant in winter (from December to March) in the area, suggesting that the 3 species undertake seasonal movement patterns. Striped dolphin occurrence increases before the start of the summer, with a second peak later in September. Fin whale shows a first peak in spring, following the phytoplanctonic bloom, and a definite increase of abundance during the summer months. Sperm whale shows a sharp increase in abundance later in the season, from August to October. These patterns were consistent over the 3-y survey. This study, by providing new information on seasonal trends in cetacean abundance, represents a useful reference for development of future management plans for the Mediterranean Marine Mammal Sanctuary. For example, periods of lower potential interactions between cetacean and human activity, such as vessel traffic and drift-net fishing, could be scheduled.

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REFERENCES

Aguilar, A. & Raga, J.A., 1993. The striped dolphin epizootic in the Mediterranean Sea. *Ambio*, **22**, 524–528.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L., 2001. *Introduction to distance sampling: estimating abundance of biological populations*. New York: Oxford University Press.

Clark, C.W., Borsani, J.F. & Notarbartolo di Sciara, G., 2002. Vocal activity of fin whales, *Balaenoptera physalus*, in the Ligurian Sea. *Marine Mammal Science*, **12**, 286–295.

Drouot, V., Gannier, A. & Goold, J.C., 2004a. Summer social distribution of sperm whales (*Physeter macrocephalus*) in the Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, **84**, 675–680.

Drouot, V., Gannier, A. & Goold, J.C., 2004b. Diving and feeding behavior of sperm whales (*Physeter macrocephalus*) in the Northwestern Mediterranean Sea. *Aquatic Mammals*, **30**, 419–426.

Forcada, J. & Hammond, P.S., 1998. Geographical variation in abundance of striped and common dolphins of the western Mediterranean. *Journal of Sea Research*, **39**, 313–325.

Forcada, J., Notarbartolo di Sciara, G. & Fabbri, F., 1995. Abundance of fin whales and striped dolphins summering in the Corso-Ligurian Basin. *Mammalia*, **59**, 127–140.

Forcada, J., Aguilar, A., Hammond, P.S., Pastor, X. & Aguilar, R., 1996. Distribution and abundance of fin whales (*Balaenoptera physalus*) in the Western Mediterranean during summer. *Journal of Zoology*, **238**, 23–34.

Gannier, A., 1997. Estimation de l'abondance estivale du Rorqual commun *Balaenoptera physalus* (Linné, 1758) dans le bassin Liguro-Provençal (Méditerranée nord-occidentale). *Revue d'Ecologie (Terre et Vie)*, **52**, 69–86.

Gannier, A., 1998. Une estimation de l'abondance estivale du Dauphin bleu et blanc *Stenella coeruleoalba* (Meyen, 1833) dans le futur Sanctuaire Marin International de Méditerranée nord-occidentale. *Revue d'Ecologie (Terre et Vie)*, **53**, 255–272.

Gannier, A., 1999. Les cétacés de Méditerranée: nouveaux résultats sur leur distribution, la structure de leur peuplement et l'abondance relative des différentes espèces. *Mésogée*, **56**, 3–19.

Gannier, A., Drouot, V. & Goold, J.C., 2002. Distribution and relative abundance of sperm whales in Mediterranean Sea. *Marine Ecology Progress Series*, **243**, 281–293.

Goffart, A., Hecq, J.H. & Prieur, L., 1995. Contrôle du phytoplancton du bassin Ligure par le front Liguro-Provençal (secteur Corse). *Oceanologica Acta*, **18**, 329–342.

Gomez de Segura, A., Crespo, E.A., Pedraza, S.N., Hammond, P. & Raga, J.A., 2006. Abundance of small cetaceans in waters of the central Spanish Mediterranean. *Marine Biology*, **150**, 149–160.

Gordon, J.C.D., Matthews, J.N., Panigada, S., Gannier, A., Borsani, F.J. & Notarbartolo di Sciara, G., 2000. Distribution and relative abundance of striped dolphins, and distribution of sperm whales in the Ligurian Sea cetacean sanctuary. *Journal of Cetacean Research and Management*, **2**, 27–36.

Goujon, M., Forcada, J. & Desportes, G., 1994. Fin whale abundance in the eastern north Atlantic, estimated from French program MICA-93 data. 8th Annual Conference of the European Cetacean Society, 1994, 81–83.

Laran, S., 2005. *Variations spatio-temporelles du peuplement de cétacés en Mer Ligure (Méditerranée nord-occidentale) et relations avec les conditions environnementales*. PhD thesis, Free University of Brussels (V.U.B.), Belgium.

Laran, S. & Gannier, A., 2006. Variation saisonnière de la présence du cachalot (*Physeter macrocephalus*) dans le Sanctuaire Pelagos (Mer Ligure). *Mésogée*, **61**, 71–77.

Marini, L., Consiglio, C., Angradi, A.M., Catalano, B., Sanna, A., Valentini, T., Finoia, M.G. & Villetti, G., 1996. Distribution, abundance and seasonality of cetaceans sighted during scheduled ferry crossing in the Central Tyrrhenian Sea: 1989–1992. *Italian Journal of Zoology*, **63**, 381–388.

Moore, K.E., Waite, J.M., Friday, N.A. & Honkalehto, T., 2002. Cetacean distribution and relative abundance on the central-eastern and the southeastern Bering sea shelf with reference to oceanographic domains. *Progress in Oceanography*, **55**, 249–261.

Moulins, A. & Würtz, M., 2005. Occurrence of a herd of female sperm whales and their calves (*Physeter macrocephalus*), off Monaco, in the Ligurian Sea. *Journal of the Marine Biological Association of the United Kingdom*, **85**, 213–214.

Notarbartolo di Sciara, G., Zanardelli, M., Jahoda, M., Panigada, S. & Airoldi, S., 2003. The fin whale *Balaenoptera physalus* (L. 1758) in the Mediterranean Sea. *Mammal Review*, **33**, 105–150.

Panigada, S., Notarbartolo di Sciara, G., Zanardelli Panigada, M., Airoldi, S., Borsani, J.F. & Jahoda, M., 2005. Fin whales (*Balaenoptera physalus*) summering in the Ligurian Sea: distribution, encounter rate, mean group size and relation to physiographic variables. *Journal of Cetacean Research and Management*, **7**, 137–145.

Sournia, A., Brylinski, J.M., Dallot, S., Le Corre, P., Leveau, M., Prieur, L. & Froget, C., 1990. Fronts hydrologiques au large des côtes Françaises: les sites-ateliers du programme Frontal. *Oceanologica Acta*, **13**, 413–438.

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