J. Mar. Biol. Ass. U.K. (2007), **87**, 187–193
Printed in the United Kingdom

doi: 10.1017/S0025315407054689

SST fronts and the summer sperm whale distribution in the north-west Mediterranean Sea

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The relative distribution of sperm whales (*Physeter macrocephalus*) and sea surface temperature (SST) fronts have been studied in summer in the north-western Mediterranean Sea. We used passive acoustic data (778 samples) obtained offshore during dedicated surveys between 1999 and 2004 and Pathfinder/Modis remote sensing data to compute front maps and to calculate mean distances from sperm whale detections (N=132) to SST-fronts. Mean distances from sperm whale acoustic detections to SST-fronts were significantly lower (10.4 km) than from other acoustic samples to those fronts (17.0 km). The same result was obtained when calculating distances from sperm whales to the North Balearic Front surface signature. If sperm whales are commonly observed along the continental slope, we showed that offshore individuals were located close to SST-fronts. This bimodal distribution in the north-western Mediterranean is linked to sperm whale feeding strategy, demonstrating ecological opportunistic behaviour in this high level predator.

INTRODUCTION

Habitat studies allow us to understand species integration in an ecosystem and to define critical habitats, such as preferred zones for feeding, breeding or nursing. Such studies show that sperm whale (*Physeter macrocephalus*, Linnaeus 1758) distribution is influenced by several environmental factors which seem to increase its main prey abundance, cephalopods in many areas and occasionally fish (Rice, 1989; Smith & Whitehead, 1993; Clarke, 1996). Nursery schools are usually restricted to warmer waters (Rice, 1989; Whitehead, 2003) and may favour slope areas, such as in the Mediterranean Sea (Drouot, 2003).

Steep topography is found in continental slope areas, canyons or sea-mounts, and appears to be favourable to cephalopod biomass (Childerhouse et al., 1995; Jaquet, 1996; Waring et al., 2001; Jaquet & Gendron, 2002). Hydrological features may concentrate sperm whale prey as well: upwellings enhance the surface trophic web and concentrate more passive preys in deeper layers (Smith & Whitehead, 1993; Rendell et al., 2004), while downwellings drive oxygen and organic substances into deep water leading to trophic web development (Berzin, 1971). Consequently, frontal zones, which include upwelling and/or downwelling, improve the high trophic level biomass (Hamazaki, 2002; Whitehead, 2003).

Our study area is the north-western basin of the Mediterranean Sea (Figure 1), which features very steep continental slope near the coast of Provence and Riviera, off Minorca (Balearic Islands) and north-western Corsica: in these regions, depths reach about 2000 m less than 30 km offshore. On the contrary, the Gulf of Lions continental shelf extends over 100 km, a similar topography being observed off the western coast of Sardinia, with a continental shelf of nearly 50 km.

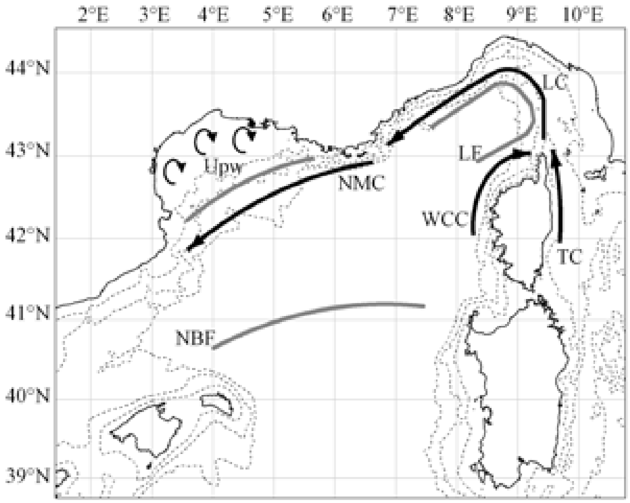

Figure 1. Topographic and hydrodynamic features in the north-western Mediterranean Sea: 200 m, 1000 m and 2000 m contours (dashed lines), upwellings (Upw), currents (black arrows: WCC, Western Corsican Current; TC, Tyrrhenian Current; LC, Ligurian Current; NMC, North Mediterranean Current) and fronts (grey lines: LF, Ligurian Front; NBF, North Balearic Front).

Two main thermal fronts are known in the north-western basin (Figure 1): (1) between the north Mediterranean current and the colder upwelled waters of the Gulf of Lions; and (2) the permanent North Balearic Front (NBF), between modified Atlantic waters from the Algerian basin and the

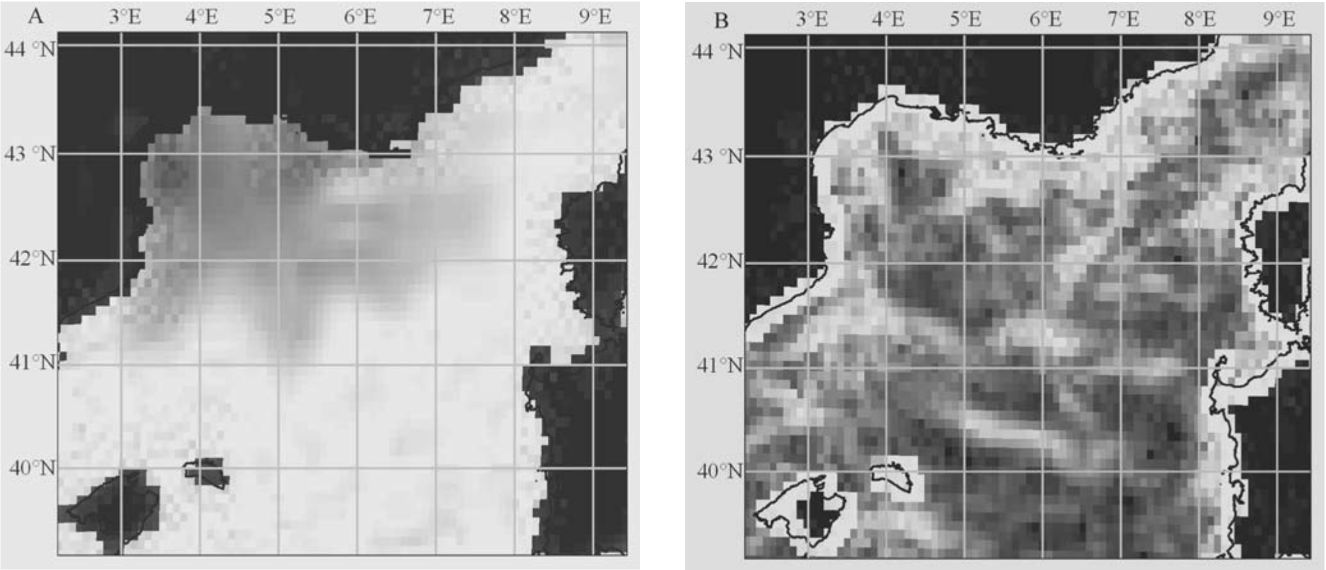

Figure 2. Transformation of a sea surface temperature (SST) map into temperature gradient map, example of survey week 2004-w24. (A) original SST map; (B) temperature gradient map with frontal zones.

colder waters of the Liguro–Provençal basin (Le Vourch et al., 1992; Millot, 1999). On the other hand, the Ligurian Sea presents a permanent geostrophical front, the Ligurian Front, mainly forced by the cyclonic circulation, itself a consequence of dense water formation in winter (Sournia et al., 1990).

In the western Mediterranean Sea, the relationship between sperm whale distribution and topography has been studied near the Spanish, French and Balearic coasts (Cañadas et al., 2002; Gannier et al., 2002; Drouot, 2003; Drouot et al., 2004). The Ligurian Front does not seem to influence sperm whale distribution, since sightings tend to be homogeneous in the Ligurian Sea, perhaps in relation to the local dome structure (Gordon et al., 2000; D'Amico et al., 2003).

During surveys in the western basin between 1999 and 2004, acoustic detections of sperm whales were consistently made away from any topographic feature, but close to the location of the NBF, as supposed from on-board sea surface temperature (SST) measurements. In this region, Viale (1991) noticed that sperm whale 'abundance' was three times higher than elsewhere in the Mediterranean Sea. To further investigate this aspect of sperm whale distribution, we have analysed relationships between sperm whale acoustic observations and SST features obtained from satellite data sets.

MATERIALS AND METHODS

Field methodology

Dedicated surveys were conducted during summers between 1999 and 2004 from a 12 m motor-sailing boat (for details see Gannier et al., 2002). A cruise speed of 11 km h^{-1} (6 knots) was adopted and every two nautical miles (3.7 km) along the survey track, one-minute acoustic sampling was done with a dual-channel towed hydrophone, and SST was measured with the hull-mounted probe. Sperm whales were acoustically detected from the distinctive regular click patterns emitted during their feeding activity (Teloni, 2005). Visual sightings as well as vocalizations of other species were systematically noted on a dedicated log-book and later converted into a computer database. When sperm whale clicks were heard, time of detection, boat position obtained from GPS, sea state, signal and overall noise levels were noted: signal and noise were given a level index of 0 to 5 (signal) or 1 to 5 (noise). Sounds were recorded on a digital audio tape whenever the signal level exceeded 3. Once acoustically detected, sperm whales were not systematically approached, since during off-shore surveys emphasis was placed on sampling coverage.

Environmental data

The SST maps were obtained with satellite imagery Pathfinder (1999–2003) and Modis (2004), with a 9×9 km/pixel resolution. A weekly time-scale was chosen to avoid occasional cloudy daily maps. To obtain thermal fronts, the raw SST maps were transformed into temperature gradient files, using a maximum difference gradient as available in WimSoft© software (Figure 2). Frontal zones were defined whenever a difference higher than 1.2°C existed between two cells, corresponding to a SST gradient of about 0.1°C km^{-1} as measured on a diagonal between centres of adjacent cells. Le Vourch et al. (1992) used a 0.2°C km^{-1} gradient to define a thermal frontal zone in their multi-seasonal study of the Mediterranean Sea. A lower gradient value was preferred for our study, because SST contrast between different water masses may be lighter during summer and in open sea.

Data analysis

Whales were not located exactly from acoustic data due to inadequate field material (a field computer with Rainbow Click© software was only available from 2003 onwards). Hence, whale position was approximated with a circle of 8 km diameter centred on the boat position: 8 km was the effective hydrophone detection range for a sperm whale with moderate noise levels (Gannier et al., 2002). As a

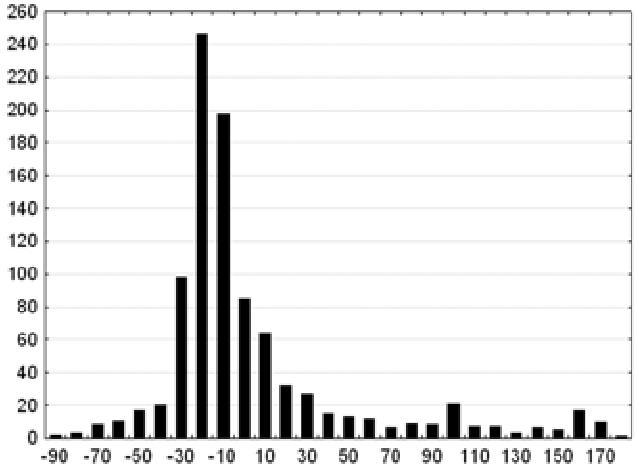

Figure 3. Distribution of sperm whale acoustic detection distances to the 2000 m isobath (surveys 1999–2004).

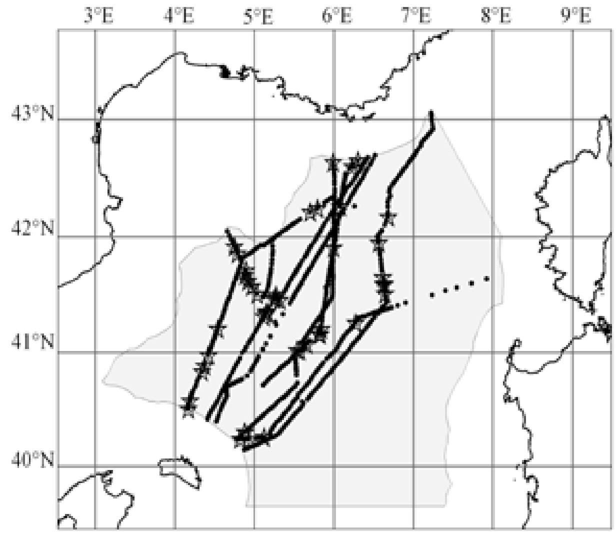

Figure 4. Acoustic samples (1999–2004) in the offshore zone (grey area): sperm whale detections (white stars) and other acoustic samples (black dots).

consequence, a single sperm whale could generate a series of five consecutive positive detections, sometimes more, leading to a trend for autocorrelation in data series. To overcome this problem during our analysis, we considered acoustic sequences rather than a single positive event (Gannier et al, 2002). A detection sequence was defined as a series of positive contacts eventually including one negative sample. This data conversion had to deal with different cases: (1) a single whale detection sequence including one negative datum (i.e. no click) due to the whale surfacing pattern; (2) multiple detections caused by changes in boat course in attempts to approach a whale; and (3) a detection sequence from a whale cluster (2 whales or more) causing an extended positive detection series (up to 17 positive contacts in a row). Cases (1) and (2) were dealt with by keeping only the highest signal level detection in a positive samples series (for example, in survey of week 24 in 2001, 2001-w24, a series of seven positive samples with signal levels 1-1-3-4-2-1-1 was replaced by one 0-0-0-1-0-0-0 sequence). Cases (3) were processed accordingly, keeping only the maximum signal levels in a positive sample series (for survey 2001-w24, a series of 11 positive samples with signal levels 1-1-2-4-4-3-4-2-4-2-2 was replaced by sequence 0-0-0-1-0-0-1-0-1-0-0).

In order to study the influence of open-sea fronts, we sorted samples into one continental slope data set (not used for the study) and one offshore set. When plotting distances from sperm whale detections to the slope limit, i.e. the 2000 m isobath (Figure 3), we observed that the number of acoustic detections decreased by half between the classes [10;20] and [20;30], and stayed at a low level beyond this distance, therefore 20 km was chosen as a boundary between slope and offshore data.

Table 1. *Survey names and dates with acoustic sample size (N_0), number of sperm whale acoustic detections (N_1) and sequences (n1).*

Sample name	Date	N_0	N_1	n1
1999-w22	18–25 June 1999	91	23	7
1999-w26	20–27 July 1999	63	9	4
2001-w24	4–11 July 2001	81	21	5
2001-w26	20–27 July 2001	124	11	5
2002-w24	4–11 July 2002	87	20	5
2002-w25	12–19 July 2002	97	21	8
2003-w24	4–11 July 2003	81	9	4
2004-w25	12–19 July 2004	22	18	7
All Years		646	132	45

We calculated the distances between each acoustic sampling location and the frontal zone with a Geographical Information System (ArcGIS 8©); when a detection was located right in the frontal zone, the null value was assigned to the distance. This task was done with: (1) every superficial front occurring in the study area during the week of survey and (2) with the NBF, which was identified from large scale water masses visible on the western Mediterranean SST map.

All statistical results were obtained with Statistica 6.1© software. The normality of distance-to-front variables was controlled with a Lilliefors test. The statistical comparison was carried out for every survey week separately, and then for all samples pooled. Distances from SST fronts to sperm whale acoustic detections ($\bar{d}_1$) were compared with distances to other (negative) acoustic samples ($\bar{d}_0$). We used a Mann–Whitney test whenever samples followed a non-normal distribution, and a *t*-test when a sample fitted a normal distribution. In our study, test *P*-values between 0.10 and 0.05 were considered as indicative of a trend.

RESULTS

A total of 778 acoustic samples was obtained in the offshore region, including 132 sperm whale detections which were all located in the sampling area, notably between latitudes 41°N and 42°N (Table 1, Figure 4). A total of 45 acoustic sequences was defined from the 132 acoustic detections. All distance distributions followed a non-normal distribution except the week 25 of 2004 (noted as 2004-w25, thereafter). The SST frontal situation varied from one year to the next with the possible occurrence of one structure in the south-central part of the study area, corresponding to the NBF, as in surveys 2001-w24 and 2002-w24 (Figure 5C,E), and/or of strong frontal areas off the Provençal coast of mainland

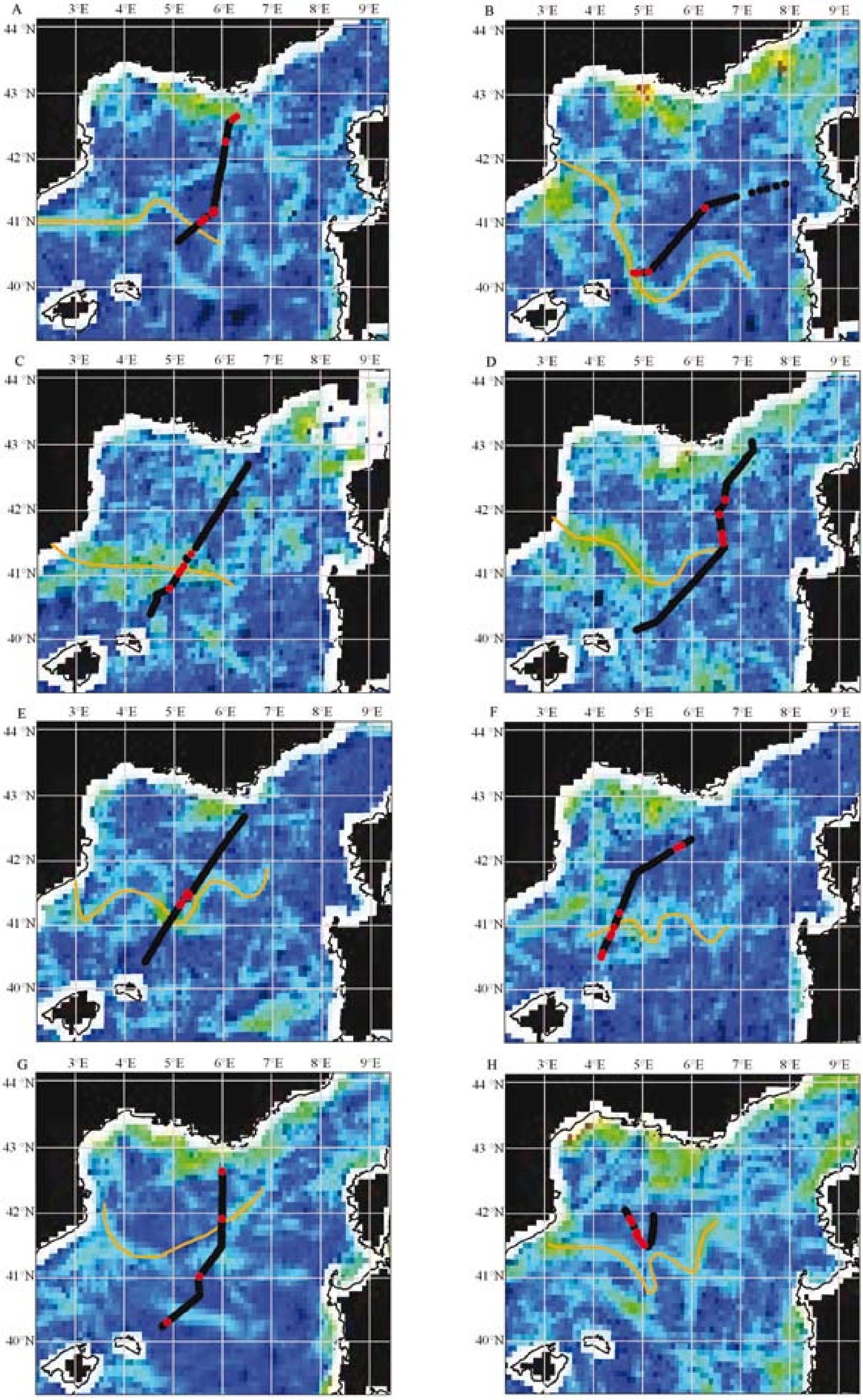

Figure 5. Sperm whale acoustic distribution as obtained during different survey periods (1999–2004) (red dots: sperm whales acoustic detections, black dots: other acoustic samples) and SST-fronts for the corresponding weeks (A, 1999-w22; B, 1999-w26; C, 2001-w24; D, 2001-w26; E, 2002-w24; F, 2002-w25; G, 2003-w24; H, 2004-w25). SST-front scale

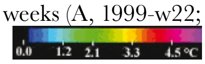

Table 2. *Distances from all SST-fronts to sperm whale acoustic detection ($\bar{d}_1$) and other acoustic samples ($\bar{d}_0$) for surveys 1999–2004.*

Survey	$\bar{d}_1$ ±SD	$\bar{d}_0$ ±SD	test *P*-value
1999-w22	18.32 ±19.2	15.79 ±16.7	0.94
1999-w26	9.45 ±12.9	29.34 ±18.5	0.0389
2001-w24	1.74 ±3.9	10.87 ±14.0	0.0636
2001-w26	0.87 ±1.9	8.52 ±11.7	0.1164
2002-w24	12.99 ±7.8	28.07 ±28.6	0.3541
2002-w25	14.81 ±27.1	28.23 ±25.7	0.0472
2003-w24	10.18 ±9.3	9.60 ±11.4	0.5473
2004-w25	7.83 ±6.7	11.35 ±5.6	0.1851
All surveys	10.36 ±15.4	17.05 ±20.2	0.0220

SD are standard deviations and *P*-values are for Mann–Whitney test.

Table 3. *Distances from North Balearic SST-fronts to sperm whale acoustic detection ($\bar{d}_1$) and other acoustic samples ($\bar{d}_0$) for surveys 1999–2004.*

Week	$\bar{d}_1$ ±SD	$\bar{d}_0$ ±SD	test *P*-value
1999-w22	97.71 ±89.4	103.26 ±75.6	0.825
1999-w26	41.67 ±47.9	91.81 ±37.2	0.0447
2001-w24	21.26 ±20.4	121.06 ±68.4	0.0006
2001-w26	55.34 ±39.7	107.17 ±71.4	0.0782
2002-w24	21.75 ±5.9	57.14 ±40.2	0.0570
2002-w25	60.72 ±71.9	99.50 ±61.2	0.0893
2003-w24	85.57 ±59.0	76.84 ±31.4	0.6630
2004-w25	62.25 ±27.0	61.49 ±27.5	0.955*
All surveys	61.14 ±61.9	93.66 ±62.7	<0.0001

SD are standard deviations and *P*-values are for Mann–Whitney test or *, Student *t*-test.

France, as in surveys 1999-w26 or 2002-w25 (Figure 5B,F). Alternatively, the SST situation in the central north-western basin could be more diffuse, such as in 2003-w24 (Figure 5G).

All frontal zones analysis

When all weekly samples were pooled, distances from sperm whale detections to SST fronts ($\bar{d}_1$) were significantly lower (Mann–Whitney test $P<0.0220$) than other acoustic samples ($\bar{d}_0$) with values of 10.36 and 17.05 km, respectively (Table 2).

For weekly situations, ($\bar{d}_1$) was lower than ($\bar{d}_0$) for six samples (Table 2): 1999-w26 (9.4 vs 29.3 km), 2001-w24 (1.7 vs 10.9 km), 2001-w26 (0.9 vs 8.5 km), 2002-w24 (12.9 vs 28.6 km), 2002-w25 (14.8 vs 28.2 km) and 2004-w25 (7.8 vs 11.3 km). For surveys 1999-w26 and 2002-w25, the distance differences were statistically significant, in relation to many visible SST-fronts (Figure 5B,F). For 2001-w24, the distance difference was indicative of a clear trend (Figure 5C). Finally, for surveys 1999-w22 and 2003-w24, we obtained ($\bar{d}_0$) marginally inferior to ($\bar{d}_1$) (Table 2), with distances of respectively 15.8–18.3 km (1999) and 9.6–10.2 km (2003).

North Balearic Front analysis

When the North Balearic Front was considered alone and all weeks were pooled, sperm whale detections were closer to the SST-front than other acoustic samples: ($\bar{d}_1$) (61.1 km) was significantly (Mann–Whitney test $P<0.0001$) lower than ($\bar{d}_0$) (93.7 km).

For six survey weeks, ($\bar{d}_1$) was inferior to ($\bar{d}_0$): 1999-w22 (97.7 vs 103.2), 1999-w26 (41.7 vs 91.8 km), 2001-w24 (21.2 vs 121.1 km), 2001-w26 (48.5 vs 107.2 km), 2002-w24 (21.7 vs 51.1 km), 2002-w25 (60.7 vs 99.5 km) (Table 3). Moreover, this difference was statistically significant for surveys 1999-w26 and 2001-w24, and indicative of a clear trend for 2001-w26, 2002-w24 and 2002-w25. Two weekly samples showed a ($\bar{d}_0$) inferior to ($\bar{d}_1$) (2003-w24 and 2004-w25), although in both cases the difference was quite marginal (Table 3).

The NBF seemed to have a strong influence on sperm whale distribution: about 70% of sperm whale detections (92 in 132) were in the vicinity of this offshore frontal region (Figure 5) and survey 2001-w24 showed a non-significant difference in the all front analysis, when the difference between ($\bar{d}_1$) and ($\bar{d}_0$) was significant for the NBF analysis.

In summary, the sperm whale detections were generally recorded closer to the frontal zones than other acoustic samples, and particularly to the NBF. However, this was not true for two weekly surveys: in 2003-w24, the NBF was not clearly defined, the two principal water masses of the western basin being separated by a rather wide transition region (Figure 5G). In 1999-w22, strong SST fronts were located in the continental slope zone, and appeared to attract sperm whales, and the NBF was not distinct along our survey track (Figure 5A).

DISCUSSION

Whichever the analysis (all frontal zones or North Balearic Front alone), SST fronts appeared to aggregate sperm whales in offshore waters of the north-western Mediterranean Sea: all years being pooled together, ($\bar{d}_1$) was significantly inferior to ($\bar{d}_0$). Moreover, the weekly situation showed the same trend, even if some samples did not show a significant difference, with the exception of two cases with ($\bar{d}_1$) superior to ($\bar{d}_0$).

In 2004-w25, the non-significant difference between ($\bar{d}_1$) and ($\bar{d}_0$) was probably related to our sampling scheme, which did not get across the north-western basin and did not cross the main offshore zone (Figure 5H). For surveys 1999-w22, 2002-w25 and 2003-w24, there was not a single SST-front between Atlantic modified waters and the Liguro–Provençal waters, clearly delimiting the NBF, but several smoother frontal zones. In these cases, sperm whales were not grouped around one SST-front but spread out over the north-western basin (Figure 5A,F&G), close to other SST-fronts, such as between the North Mediterranean Current and the colder waters of the Gulf of Lions (Figure 5A,F).

Several authors showed the influence of frontal zones on sperm whale distribution worldwide. In the Gulf of Mexico, more important concentrations of sperm whale were observed near cyclonic eddies (Biggs et al., 2000; Davis et al., 2002), as was pointed out in the presence of warm core rings in the Gulf Stream (Waring et al., 2001; Davis et al., 2002). In those studies, the largest sperm whale groups were observed at the limit between these medium-scale phenomena and adjacent waters, i.e. near a frontal zone between two different water masses. Hamazaki (2002) also showed an association between sperm whale distribution and frontal zones in the North Atlantic: his model predicted that sperm whale presence was correlated with stronger monthly frontal probabilities. In the Pacific Ocean, Jaquet (1996) highlighted the distribution of sperm whales around high primary production zones, particularly the Pacific equatorial divergence.

Frontal zones seem to favour other teutophageous species, such as beaked whales (*Mesoplodon* spp. and *Ziphius cavirostris*), pilot whales (*Globicephala melas*) and Risso's dolphin (*Grampus griseus*) in the North Atlantic (Hamazaki, 2002). Davis et al. (2002) showed that most sightings of the 'squid eaters' group (e.g. dwarf and pigmy sperm whales, pilot whales, Risso's dolphin, and Ziphiidae) occurred, over abyssal depths, at the steepest SST gradients, at the periphery of a cyclone zone and in a convergence zone, both forming fronts. Among other marine mammal species, southern elephant seals (*Mirounga leonina*) have an at-sea distribution following the Antarctic Circumpolar Convergence (Bradshaw et al., 2004).

In fact, conditions present in frontal zones (upwelling and/or downwelling) are certainly favourable to the development of cephalopod populations. Off Costa Rica jumbo squid (*Dosidicus gigas*) concentrations decrease with a decreasing intensity of upwellings during El Niño events (Ichii et al., 2002). In the Mediterranean Sea, sperm whales seem to feed mainly on Histioteuthidae (Astruc & Beaubrun, 2005). Mediterranean cephalopod species correspond to eastern Atlantic cephalopod species (Mangold-Wirz, 1963) and include all genera regularly preyed upon by sperm whales: Histioteuthidae, Ommastrephidae, Onychoteuthidae, Gonatidae, Pholidoteuthidae, Octopoteuthidae and Cranchiidae (Rice, 1989; Clarke, 1996; Whitehead, 2003). Those species should follow the same distribution trends as other cephalopod species around the world and then probably aggregate near frontal zones, hence the presence of sperm whales near the NBF.

In the north-western Mediterranean Sea, Viale (1991) pointed out the increasing sperm whales' presence near the NBF, but Drouot (2003) did not find a significant relationship between sperm whale distribution and SST. The latter study was based on surveys in the whole western basin and did not discriminate between continental slope and offshore data, which certainly reduced the apparent influence of SST among other environmental factors taken into account.

In the western Mediterranean Sea, it has been shown that sperm whales do not exclusively favour slope waters (Gannier et al., 2002): these authors showed that effort-corrected acoustic relative abundance did not vary significantly between slope (defined as areas within the 2000 m isobath) and offshore waters, with average values of respectively 1.48 and 0.95 whale/100 km. In the eastern Alboran Sea, Cañadas et al. (2002) showed that sperm whales pertained to the 'deep water' group of the local odontocete population. This modelling result was obtained from a fine-scale (2×2 km) analysis which was limited to physiographic variables (depth and slope). As a matter of fact, the area of study of Cañadas et al. (2002) did not practically extend into waters deeper than 1500 m, when our area of study is offshore and mainly over the abyssal plain of 2000–2800 m depth. Our offshore large scale distribution of whales may be mainly linked to oceanic water variables, such as the SST gradient, because our area of study lies in the Algero–Provençal basin which, contrary to the Tyrrhenian Sea, for example, does not include any distinct bottom topography feature.

A global model incorporating both physiographic and hydrological variables in a single approach could in principle describe the sperm whale distribution in both slope and open sea strata: a preliminary attempt was presented by Praca et al. (2006), using an Ecological Niche Factor Analysis. However, identifying a link between the offshore distribution and SST, a single hydrological variable, is clearly a noteworthy milestone before successfully describing the global sperm whale distribution in the western Mediterranean Sea with a multivariate model.

CONCLUSION

In offshore regions and away from any topographic singularity, hydrologic features such as thermal fronts appear to favour the sperm whale presence, perhaps due to trophic web development and subsequent availability of sperm whale food resources. We have shown that the North Balearic Front plays this role during summer in the north-western Mediterranean Sea, and that other frontal zones also seem to attract sperm whales. The SST fronts' influence on sperm whale distribution should also be investigated during other seasons and in other regions, in order perhaps to better explain the poorly known sperm whale movements across the western basin throughout the year. Further modelling should include both physiographic and oceanographic variables to better describe the global sperm whale distribution in the Mediterranean.

We thank all the volunteers from the GREC and CRC-Marineland for their participation in the field data collection. We thank the PODAAC of NASA Jet Propulsion Laboratory for allowing easy access to the Pathfinder and MODIS SST data archives. We thank the Ministère de l'Ecologie et du Développement Durable and the Conseil Régional de Provence–Côte d'Azur for having participated to the funding of our study in 2002–2006. For this work, Emilie Praca received a Leonardo da Vinci European grant. We thank two anonymous referees and the Editor for their helpful comments on the earlier version of the manuscript.

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Submitted 9 June 2006. Accepted 24 September 2006.