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Habitat use and preferences of cetaceans along the continental slope and the adjacent pelagic waters in the western Ligurian Sea

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Abstract

The physical habitat of cetaceans occurring along the continental slope in the western Ligurian Sea was investigated. Data were collected from two different sighting platforms, one of the two being a whale-watching boat. Surveys, conducted from May to October and from 1996 to 2000, covered an area of approximately 3000 km^2 with a mean effort of about 10,000 km year^{-1}. A total of 814 sightings was reported, including all the species occurring in the area: *Stenella coeruleoalba, Balaenoptera physalus, Physeter macrocephalus, Globicephala melas, Grampus griseus, Ziphius cavirostris, Tursiops truncatus, Delphinus delphis.* A Geographic Information System was used to integrate sighting data to a set of environmental characteristics, which included bottom gradient, area between different isobaths, and length and linearity of the isobaths within a cell unit. Habitat use was analysed by means of a multi-dimensional scaling, MDS, analysis. Significant differences were found in the habitat preference of most of the species regularly occurring in the area. Bottlenose dolphin, Risso's dolphin, sperm whale and Cuvier's beaked whale were found strongly associated to well-defined depth and slope gradient characteristics of the shelf-edge and the upper and lower slope. The hypothesis of habitat segregation was considered for Risso's dolphin, sperm whale and Cuvier's beaked whale. Canonical discriminant functions using depth and slope as predictors outlined clear and not overlapping habitat preferences for Risso's dolphin and Cuvier's beaked whale, whereas a partial overlapping of the habitat of the other two species was observed for sperm whale. Such a partitioning of the upper and lower slope area may be the result of the common feeding habits and suggests a possible competition of these three species. A temporal segregation in the use of the slope area was also observed for sperm whales and Risso's dolphins. Fin whales, and the occasionally encountered common dolphin and long-finned pilot whales showed a generic preference for the pelagic area. In contrast, striped dolphins were generically found in any type of physical habitat, in agreement with their known opportunistic feeding habits. Interannual and seasonal movements were observed in fin whales and in all the other regularly occurring species, indicating that changes in the environmental and climatological conditions have a remarkable influence on habitat use. Finally, a relationship between group size and

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habitat use was observed for the species known to forage in groups. This relationship suggests that these species respond to environmental variability either by moving within the study area or by behavioural changes that may reflect changes in the preference for prey items.

Keywords: Cetaceans; Habitat; Distribution; Physiography; Environmental factors; Western Ligurian Sea; Protected areas

1. Introduction

Several factors are known to influence the distribution of cetaceans. Environmental factors (i.e. physicochemical, climatological and geomorphological characteristics), biotic factors (i.e. prey distribution, predation, behavioural changes) and anthropogenic factors (human activities, pollution, etc.), play a role in structuring cetacean assortment of species (Borcard et al., 1992; Jaquet, 1996). However, the relative contribution of each of these factors in shaping spatially and temporally the distribution of the species is often hard to quantify. The difficulty of determining all the potentially relevant factors over consistent timescales, considering areas of several nautical miles, is very often the main reason for such a lack of knowledge.

Submarine topography, well known as one of the major forces driving the marine circulation, has been the subject of many habitat investigations (Hui, 1985; Kenney and Winn, 1987; Clarke, 1956, 1962; Best, 1969; Bannister, 1968; Whitehead et al., 1992) with the underlying assumption that the biodiversity of aquatic ecosystems increases directly with the complexity of the underwater topography. Habitat selection, in fact, may be considered a complex and dynamic function of the species requirements for food, mates, avoidance of predators/competitors and ability to move between habitat patches (Schofield, 2003). So differences in habitat uses are primarily the outcome of the different feeding habits, but they are also driven by other factors such as the presence of potential competitors or environmental changes. In this respect, evidence has been provided that climatic variations have influence on the species behaviour (Sutherland and Norris, 2002). Lusseau et al. (2004) found that ocean climate variation influences the grouping behaviour of two highly social cetacean species. Their findings suggest that climate variation may influence the species' social organisation through changes in prey availability. Investigating the link between climate variations, habitat selection and species behaviour is essential for the understanding of the causal link between large-scale climatic processes and population dynamics at the regional scale (Sutherland and Norris, 2002). In our study the spatial distribution of different cetacean species is discussed in relation to the hydrology and topography in an area located within the Ligurian Sea Sanctuary for Cetaceans. Special attention in this work was dedicated to the variability in space and time of the habitat preferences and to the study of the species group formations as a function of the habitat uses.

2. Materials and methods

2.1. Study area

The Ligurian Sea Sanctuary for Cetaceans, included within the Corso-Ligurian-Provençal Basin, northern Tyrrhenian and northern Sardinian Seas, is characterised by very high levels of primary productivity in contrast to the well-known generalised oligotrophy of the Mediterranean Sea (Barale and Zin, 2000; Viale, 1991). The high productivity has been related by some authors to the peculiar submarine topography, which is extremely complex and heterogeneous, and to the changeable wind and current regimes that characterise the area (Lacroix and Grégoire 2002; Gaudy and Champalbert, 1998; Macquart-Moulin and Patriti, 1996). In the absence of a large-scale geostrophic circulation, the physical oceonography of the Mediterranean is strongly influenced by dominant local and orographic wind fields (Millot, 1987). In the western Mediterranean, and especially during the winter season, the dominant winds are the "mistral" channelled down the Rhone valley. However, during the summer season the wind regime can be much more changeable, but still capable of strongly affecting the circulation.

The Ligurian sea supports an abundant biomass of Mediterranean krill, the euphausiid *Meganyctiphanes norvegica*, which constitutes a nodal prey item in many marine trophic chains (Casanova, 1970; Orsi-Relini and Cappello, 1992). All cetaceans regularly observed in the Mediterranean also can be found in this region, and they include fin whale (*Balaenoptera physalus*), sperm whale (*Physeter macrocephalus*), Cuvier's beaked whale (*Ziphius cavirostris*), long-finned pilot whale (*Globicephala melas*), bottlenose dolphin (*Tursiops truncatus*), Risso's dolphin (*Grampus griseus*), striped dolphin (*Stenella coeruleoalba*) and common dolphin (*Delphinus delphis*). Previous studies emphasised that cetaceans in this area are significantly more abundant than in all other seas surrounding Italy and in the rest of the western Mediterranean basin (Notarbartolo di Sciara et al., 1993; Forcada et al., 1996), and this is especially true for the fin whale (Notarbartolo di Sciara et al., 2003). The study area is approximately encompassed by the longitude of Cap Ferrat (7.33°E), close to the French/Italian border, to the longitude/latitude of Imperia (8.02° E; 43.80°N) and the 50-m and 2000/2500-m depth contours (see Fig. 1), and it includes a significant portion of the continental slope area. The presence of many submarine canyons at the boundary between neritic and oceanic domains creates conditions for the accumulation of migratory micronektonic species in the continental slope waters (Macquart-Moulin and Patriti, 1996). These authors showed that frequent strong gusts of seaward wind (mostly northwesterly but also northeasterly) along the Liguro-Provençal coast generate a strong offshore current in the superficial layers. A coastal upwelling is generally associated with this offshore current carrying off the shelf into deeper waters and the neritic bentho-pelagic species that stratify at the surface during the night. This periodic accumulation of pelagic zooplankton near the bottom above the slope, according to Macquart-Moulin and Patriti (1996) may constitute an abundant, although temporary, food resource exploited by the organisms related to the slope area.

2.2. Field methods

Shipboard visual surveys were conducted from 1997 to 2000, from June to September, on a 12-m engine-powered sailing boat. Sighting data were collected along roughly north-to-south transects. Transects did not follow a systematic design with random probability sampling but were designed as triangles to cross-depth contours as perpendicularly as possible and to cover as much of the area as possible, although it was not covered homogeneously (Fig. 2). Once the animals were located, transects were interrupted for periods ranging from a few hours to the whole day in order to collect data other than

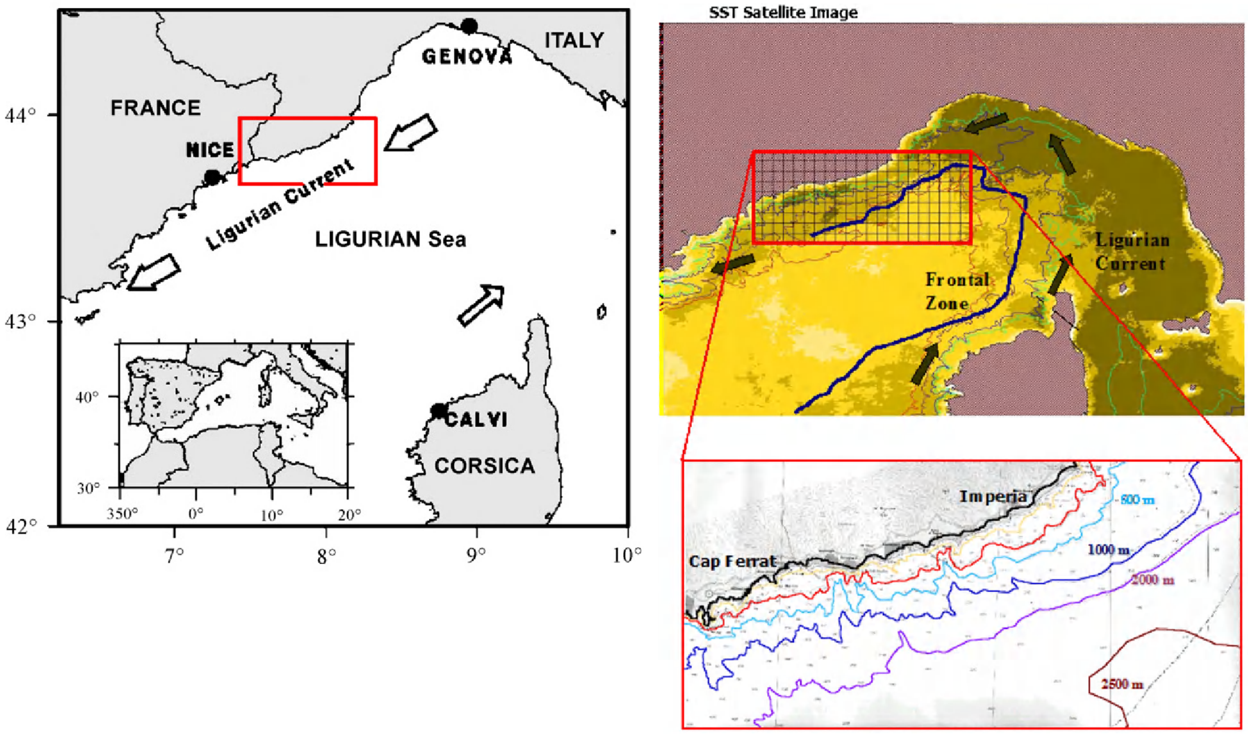


Fig. 1. Study area.

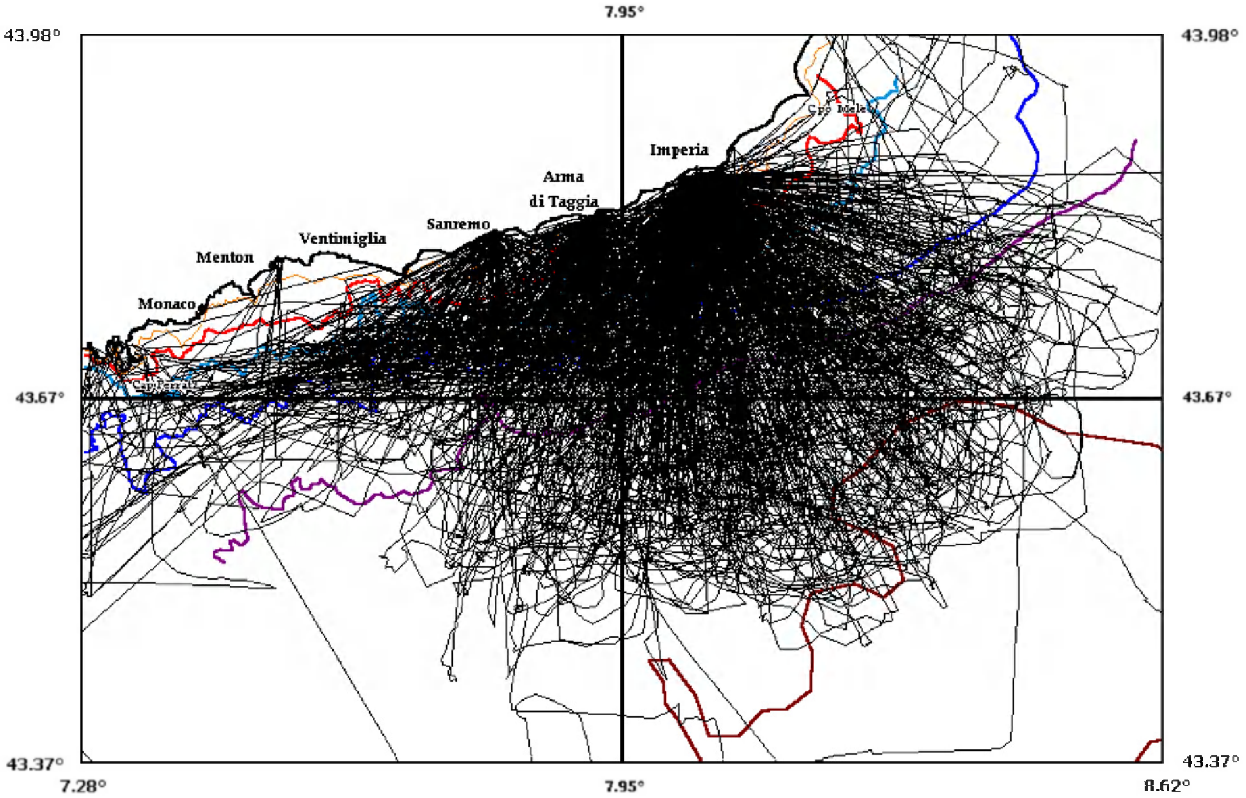


Fig. 2. Map showing the shipboard transects carried out from 1996 to 2000 in the research area.

presence/absence (e.g. photographic identification, behavioural and respiration pattern of focal species, tissue sampling for toxicological and molecular analysis of striped and Risso's dolphins). A "sighting" was defined as a group of animals of the same species seen at the same time showing similar behavioural characteristics and coordinated surfacing and diving patterns within approximately 400 m (1 km for fin whales and sperm whales) of each other.

To maintain consistent sighting effort a minimum of one observer was positioned at each side of the vessel. Observations were made in flat seas and calm weather, defined as "favourable conditions", and ceased when wind exceeded 3 on the Beaufort scale (wind speed: $5.4\,\mathrm{m\,s^{-1}}$). Searching and sea-state status were recorded every 60 min, or more frequently if changes in conditions occurred. Additional sighting data were obtained from a commercial 19-m whale-watching motorboat (Corsaro-bluWest). The sighting platform was placed approximately at the same height (i.e. about 4 m above the sea surface) for both the whale-watching and the sailing boat. Aboard the whale-watching boat, experienced observers (at least one trained biologist) guaranteed the reliability of the species identification and of the corresponding data collection. The whale-watching database covered 5 years of summer activity from 1996 to 2000 (June to September). In both the vessels, effort (course, speed, etc.), sea state and sighting data (i.e. position, species, group size, presence of calves, etc.) were recorded by means of a data logging system (IFAW- LOGGER Data Logging Software).

2.3. Data analysis: physical features

A GIS (ESRI Arcview 3.2) was used to divide the study area into 189 cells, each measuring 3×3 nautical miles, and also to integrate sighting data to a set of environmental characteristics (Table 1). The grid size chosen was large enough to avoid spatial autocorrelation. According to Legendre et al. (2002), the presence of spatial correlation may disturb tests of significance for correlation or regression, when both the animal response variable and the environmental predictor are spatially autocorrelated. Therefore, in order to test whether cells were spatially autocorrelated, and hence not independent, Moran's I, which is a global "measure of the correlation among

Table 1
Summary of the physical characteristics considered for every cell

Cell physical characteristics
Area between coast and the 50 m isobath (km^2)
Area between 50 and 100 m isobaths (km^2)
Area between 100 and 200 m isobaths (km^2)
Area between 200 and 500 m isobaths (km^2)
Area between 500 and 1000 m isobaths (km^2)
Area between 1000 and 2000 m isobaths (km^2)
Area between 2000 and 2500 m isobaths (km^2)
Length of the 50 m isobath (km)
Linearity of the 50 m isobath (km)
Length of the 100 m isobath (km)
Linearity of the 100 m isobath (km)
Length of the 200 m isobath (km)
Linearity of the 200 m isobath (km)
Length of the 500 m isobath (km)
Linearity of the 500 m isobath (km)
Length of the 1000 m isobath (km)
Linearity of the 1000 m isobath (km)
Length of the 2000 m isobath (km)
Linearity of the 2000 m isobath (km)
Length of the 2500 m isobath (km)
Linearity of the 2500 m isobath (km)
Minimum depth (m)
Maximum depth (m)
Bottom gradient (slope$_c$) (m/m)
Bottom gradient variability (Std. dev. (slope$_c$)) (m/m)

Note: linearity of isobath is computed as the ratio between the length of the isobath contained within the cell versus the total length comprised within the study area. Bottom gradient and bottom gradient variability computations are explained in Fig. 2.

neighbouring observations in a pattern" (Boots and Getis, 1988; Cliff and Ord, 1973), was computed for the animal response variable (i.e. the Habitat Score described later) year by year and for the whole study period (i.e. 1996–2000). Moran's I was computed using the MapStat extension to ArcView. Although Moran's I coefficients turned out to be slightly variable from species to species, all Moran's I statistics revealed spatial autocorrelations not significantly different from zero or extremely weak (Moran's I: mean 0.14, median 0.024, min −0.026, max 0.32).

Physical features considered for each cell are listed in Table 1.

As shown in Fig. 3 the sea bottom gradient (slope$_c$) was computed for each cell:

$$\mathrm{Slope_c} = \frac{[\mathrm{depth}_{\mathrm{isobath\ 1}} - \mathrm{depth}_{\mathrm{isobath\ 2}}]_{A_1}}{[\mathrm{mean}(a_1,\ldots,a_n)]}\left(\frac{A_1}{A_{\mathrm{tot}}}\right) + \frac{[\mathrm{depth}_{\mathrm{isobath\ 3}} - \mathrm{depth}_{\mathrm{isobath\ 2}}]_{A_2}}{[\mathrm{mean}(d_1,\ldots,d_n)]}\left(\frac{A_2}{A_{\mathrm{tot}}}\right), \quad (1)$$

where A_1 is the cell area encompassed within isobaths 1 and 2, A_2 is the cell area encompassed within isobaths 2 and 3, A_{tot} is the total area of the cell, $a_1,\ldots,a_n$ are minimum distances between the isobaths 1 and 2 (i.e. a minimum distance is calculated between every node of the two vectorial isobaths), and $d_1,\ldots,d_n$ are the minimum distances between isobaths 2 and 3 (again a minimum distance is calculated between every node of the two vectorial isobaths).

Consistently a slope$_c$ standard deviation, SD (slope$_c$), was computed as follows:

$$\mathrm{SD}\,(\mathrm{slope_c}) = \mathrm{SD}\left[\Delta\mathrm{depth}_{\mathrm{isobaths\ 1-2}}\left(\frac{1}{a_1}+\frac{1}{a_2},\ldots,\frac{1}{a_n}\right),\ \Delta\mathrm{depth}_{\mathrm{isobaths\ 2-3}}\left(\frac{1}{d_1}+\frac{1}{d_2},\ldots,\frac{1}{d_n}\right)\right], \quad (2)$$

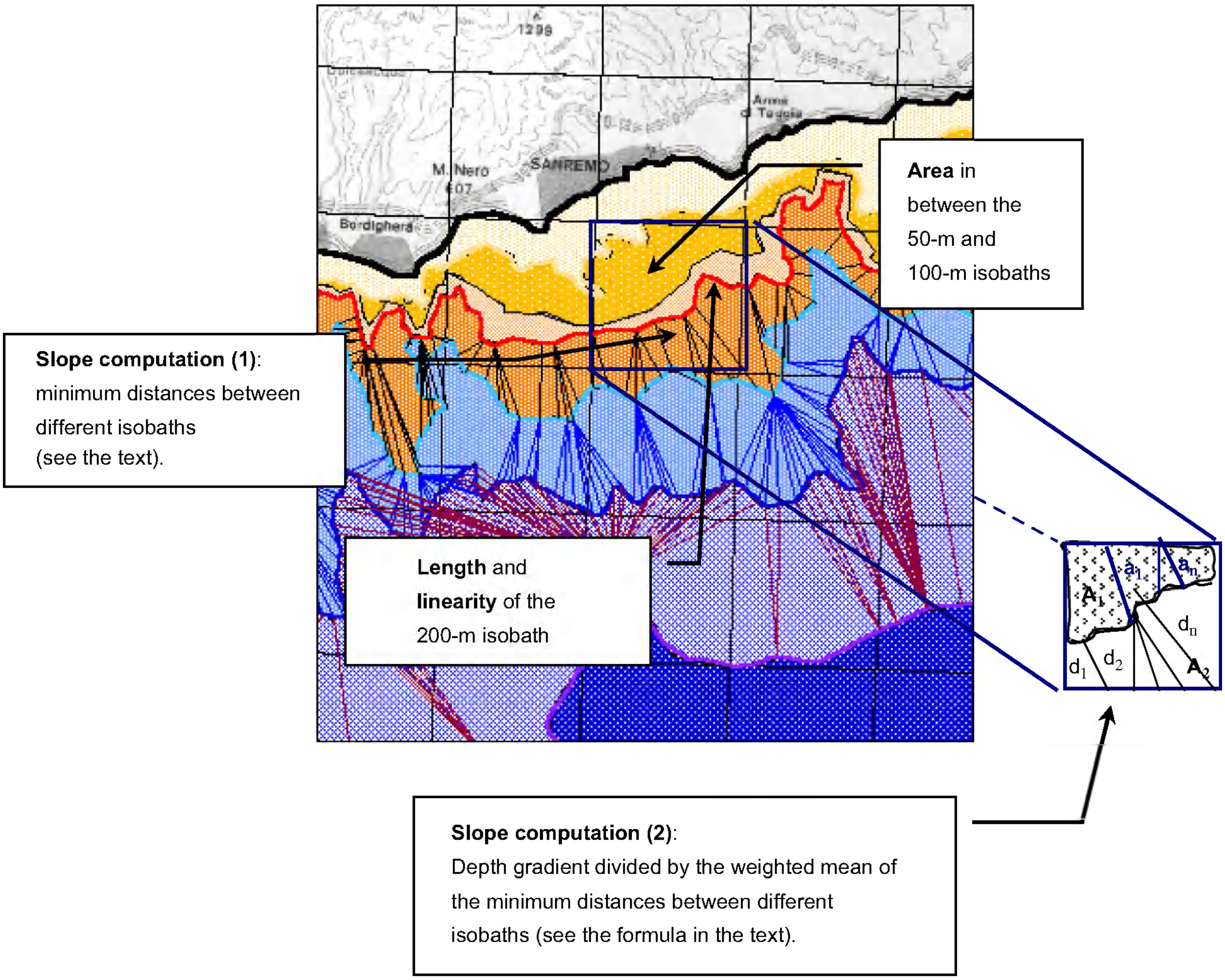
where $\Delta\mathrm{depth}_{\mathrm{isobaths\ 1-2}}$ is the depth difference between isobaths 1 and 2, $\Delta\mathrm{depth}_{\mathrm{isobaths\ 2-3}}$ is the depth difference between isobaths 2 and 3, $a_1,\ldots,a_n$ are the minimum distances between isobaths 1 and 2, and $d_1,\ldots,d_n$ are the minimum distances between isobaths 2 and 3.

2.4. Data analysis: wind speed and sea conditions

The daily time series of wind speed and sea conditions was acquired by the meteorological station located in Sanremo Portosole port. Wind speed in knots and sea conditions on a five-class scale is recorded every day in the morning, at noon and in the evening. In order to use all the data available, we coded the three series of sea conditions into a 12-class ordinal scale according to Table 2. These data were only used as proxy of the potential of zooplankton accumulation events in the slope area.

2.5. Data analysis: effort

Effort was evaluated in terms of kilometer of tracklines (Fig. 2) per cell unit for every year. Only the effort in "favourable conditions" (i.e. wind not exceeding 3 on the Beaufort scale) was considered. The tracks corresponding to the time spent with the same group of animals were also excluded from the effort amount. Table 3 shows the effort statistics for the two platforms: the whale-watching and the survey-dedicated boat. Since the effort was heterogeneous from year to year and the percentage of



Area in between the 50-m and 100-m isobaths

Slope computation (1): minimum distances between different isobaths (see the text).

Length and **linearity** of the 200-m isobath

Slope computation (2): Depth gradient divided by the weighted mean of the minimum distances between different isobaths (see the formula in the text).

Fig. 3.

survey vs. whale-watching data was also variable from year to year (whale-watching effort was around 51% of the total in 1997, but from 1998 it increased to 65–70% of the total), in order to allow comparison among the different years we used a cell-normalised effort index (i.e. $\mathrm{Effort_N}$). So we calculated an $\mathrm{Effort_N}$ for every field season by means of the following formula:

$$\mathrm{Effort}_{\mathrm{N}_{\mathrm{cell,year}}} = \frac{\mathrm{Effort_{cell}}}{\mathrm{Effort_{tot}}}, \quad (3)$$

where $\mathrm{Effort_{cell}}$ is the total effort amount (i.e. whale-watching + dedicated survey platform kilometers) calculated for a specific field season (i.e. the year) within a specific cell and $\mathrm{Effort_{tot}}$ is the effort amount (i.e. whale-watching + dedicated survey platform kilometers) totalled within the study area during the same field season (i.e. the year).

2.6. Data analysis: data set homogeneity

The homogeneity of the whale-watching and survey data sets was tested. A number of cells (N:30) were chosen within the study area where the effort amount of the two platforms was approximately the same. In these cells the sighting frequency (i.e. number of sightings divided by the effort amount) of the most common species (i.e. striped dolphin, *S. coeruleolaba*) was calculated independently by using either the whale-watching or the dedicated survey data set. The most encountered species was chosen in order to have a sample size large enough to detect a statistical difference between the whale-watching and the sailing boat. Therefore, striped dolphin sighting frequency was tested for the two platforms by means of the Wilcoxon signed-rank test for paired samples. The

Wilcoxon signed-rank test did not show any significant difference (T: 204, p-level >0.50) in the sighting capabilities of the two platforms since the striped dolphin median sighting frequency was 0.17 for the whale-watching boat (mean: 0.2602, median: 0.1717, SD: 0.287, SE: 0.052 sightings km^{-1}; N: 30) and 0.15 for the survey-dedicated boat (mean: 0.2227, median: 0.1467, SD: 0.2822, SE: 0.051 sightings km^{-1}; N: 30). In light of these results the two data sets were pooled together for the following analysis.

2.7. *Data analysis: Habitat Score*

Regression techniques are widely used to assess the habitat preferences of different species. Very often (Weir et al., 2001; Cañadas et al., 2002; Thiele et al., 2004; Panigada et al., 2005, Monestiez et al., 2006 among the others) as response variable a relative abundance index (e.g. a sighting frequency where number of sightings are calculated per unit of effort) is assumed. When such indexes of relative abundance are used, a sighting of a single animal may produce a maximum of preference in low effort cell units. These maxima of preference are outliers and may exert a very high leverage on the regression coefficients. In the present study the normalised index Habitat Score was used as a measure of habitat preference. The Habitat Score was defined for every species for different observation periods (i.e. the year or the month) according to the following formula:

$$\text{Habitat Score}_{N_{\text{cell, period}}} = \frac{(\text{no. animals}_{\text{cell}}/\text{max animals}_{\text{tot cell}}) \times (\text{no. sightings cell}/\text{max sightings}_{\text{tot cell}})}{\text{Effort}_{N}}, \tag{4}$$

where Habitat Score$_{N}$ is the cell-normalised index of preference with respect to a specific species and a specific period of analysis (i.e. the year or the month); no. animals$_{\text{cell}}$ is the species mean group size recorded in the specific cell; max animals$_{\text{tot cell}}$ is the maximum group size ever recorded in any cell of the study area during the considered period of analysis; no. sightings$_{\text{cell}}$ is the species sighting count recorded in the specific cell; max sightings$_{\text{tot cell}}$ is the maximum species sighting count recorded in any cell of the study area during the considered period of analysis and Effort$_{N}$ is the cell-normalised effort amount (see Eq. (3)).

Habitat Score ranges from 0 to 1 and takes into account both the number of sightings and the group size, adjusting both for effort. The advantage of considering both the number of sightings and the number of individuals is appreciable when Habitat Score is compared with the more widely used sighting frequency (i.e. number of sightings per kilometer). As previously explained, sighting frequency may generally lead to very high values when a single sighting occurs in a cell with low effort. Habitat Score smoothes such a bias, considering also the number of individuals. Fig. 4 shows a comparison between the sighting frequency and the Habitat Score. It can be observed that the higher sighting frequencies were found for cell units 99 and 78, where a sighting of a single individual was recorded with a very low effort. Habitat Score smoothes those two maxima and attributes the maximum of preference to cell 76, where the number of animals is higher. In the analysis presented in this study, Habitat Score was used either as index of the species' occurrence and preference or as a weighting factor for the cell units. When used as weighting factor, the normalised Habitat Score was applied with a multiplier in

Table 2
Sea condition scale

Morning	Noon	Evening	Sea conditions
QC	QC	QC	0
QC	QC	S	1
QC	QC	R	1.5
QC	S	S	2
QC	S	R	2.5
S	S	S	3
R	S	S	4
QC	R	R	4.5
R	R	S	5
ER	S	S	5.5
R	R	R	6
ER	R	S	6.5
ER	R	R	7
ER	ER	R	8
ER	ER	ER	9
ST	ER	ER	10
ST	ST	ER	11
ST	ST	ST	12

The original five-class scale (i.e. QC: quite calm, S: swell, R: rough, ER: extremely rough, ST: storm), recorded every day in the morning, at noon and in the evening was converted into an ordinal scale ranging from 0 to 12.

Table 3
Effort statistics for the two platforms

Field season	% Whale-watching effort	Total (km)	Effort (km)	Hours spent at sea on effort	Days at sea	
					Whale-watching	Survey
1996	100	3035	2671	243	44	–
1997	51	7557	6670	606	59	40
1998	71	8906	6838	622	73	62
1999	64	12874	7430	528	91	75
2000	68	7743	5807	675	88	74
Total		40115	29416	2674	355	251

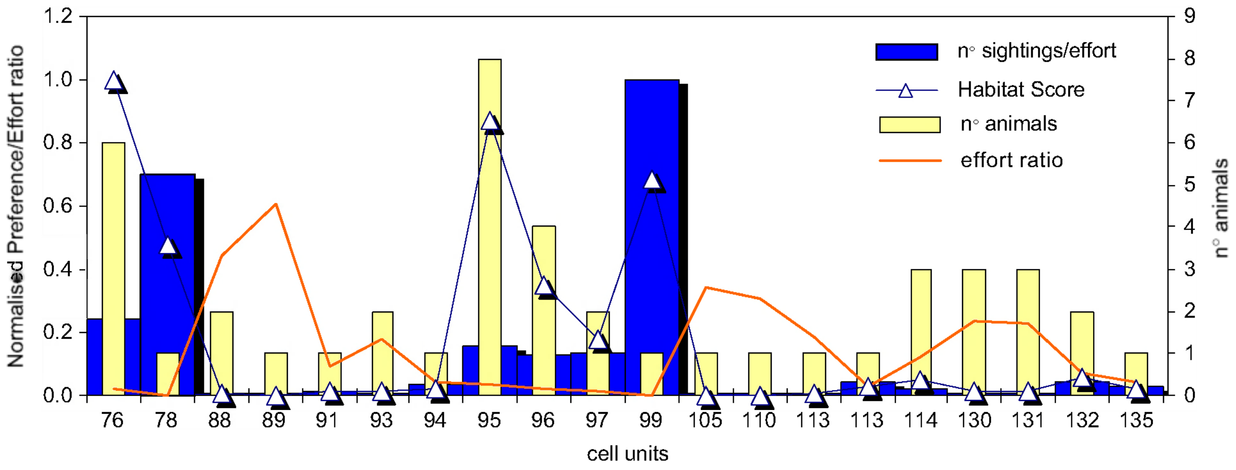


Fig. 4. Habitat Score ranges from 0 to 1 and takes into account both the number of sightings and the group size, correcting for the effort ratio. In such a way the Habitat Score smoothes the bias of a single individual sighting that may occur in a cell with a very low effort.

order to maintain approximately the original sample size of the unweighted data.

2.8. Analysis of the interspecific habitat preferences

In order to study the physical habitat similarities of the cell units, independently from their geographical position, a multi-dimensional scaling analysis (MDS, Clarke, 1993; Kruskal, 1964; Kruskal and Wish, 1978) was used. MDS analysis can be considered to be an alternative to factor analysis. In general, the goal of MDS is to detect meaningful underlying dimensions that allow the researcher to explain observed similarities or dissimilarities (distances) between the investigated objects. In factor analysis, the similarities between objects (e.g. variables) are expressed in the correlation matrix. With MDS one may analyse any kind of similarity or dissimilarity matrix. MDS analysis reproduces the cell distances in a "map" or configuration of a specified number of dimensions and attempts to satisfy all the conditions imposed by the rank order of distances in a distance matrix by placing similar cells close together in the ordination. The goodness of fit, or representativeness, of the MDS ordination is indicated by an S-stress value (Kruskal's S-stress), values of up to 0.2 generally indicating that plots may be interpreted sensibly (Clarke, 1993). An MDS was applied to the matrix of the cell physical characteristics (see Table 1). Being based on a factorisation, MDS enables to deal with the potential for multicollinearity of the physical habitat predictors. As distance metric, euclidean distance was used. The MDS algorithm minimised the raw normalised stress value up to an improvement less than 0.0001, which was assumed as the convergence criterion. Table 4 shows S-stress and fit measures (DAF, and Tucker's coefficient of congruence) of the MDS solutions. A smaller stress value, to a minimum of 0,

Table 4
Multi-dimensional scaling S-stress and fit measures

	Dimensionality				
	2	3	4	……	13
Raw normalised stress	0.0232954	0.0030792	0.0014194		0.000544
S-stress	0.0515501	0.0055841	0.0025599		0.000735
DAF, dispersion accounted for (DAF:1-raw stress)	0.9767046	0.9969208	0.9985806		0.999456
Tucker's coefficient of congruence ($DAF^{1/2}$)	0.9882837	0.9984592	0.99929		0.999728

DAF and Tucker's coefficient of congruence indicate how well the solution approximated the original proximities.

implies a better solution (stress can be seen as a residual variance), whereas larger fit values, to a maximum of 1, indicate a better solution. All the stress values obtained were lower than 0.07, indicating the excellent fit of the 2-dimensional (2D) solution. Consequently, the interspecific habitat preferences were analysed by using the 2D MDS plot.

2.9. Analysis of habitat use by species

The analysis was conducted in three parts: (a) by studying the occurrence of each species in time, (b) by evaluating the variability in time and space of the habitat uses and (c) by studying the relationship of habitat use and the species group size. All analyses were conducted with SPSS version 11.5.

3. Results

Surveys covered approximately an average of 10,000 km of search effort per year and resulted in a total of 814 sightings with certain identification including all the species occurring in the area. Striped dolphin (69.3%) and fin whale (14.6%) were the most frequently encountered species, followed by Risso's dolphin (6.3%), sperm whale (4.2%), and Cuvier's beaked whale (3.4%). Occasionally, encountered species were long-finned pilot whale (1%), bottlenose dolphin (1.2%) and common dolphin (0.1%).

3.1. Analysis of the interspecific habitat preferences

Thirteen MDS dimensions were extracted with a final S-stress (Kruskal, 1964) of 0.0007. Stress value improvements became negligible after the extraction of the fourth dimension. The first two dimensions accounted for 97.7% of the total stress and 82% of the cumulative improvement. Fig. 5 shows the plot of the first two MDS dimensions where definite clusters of points are visible. These clusters represent cells with similar physical characteristics. Particularly, the cells on the right quadrant (dashed line rectangle), characterised by depths greater than 2000-m and sea-bottom gradients lower than 0.05 m/m, can be considered as representative of the pelagic area, whereas the cells on the left upper quadrant (i.e. within the dotted circle), contained within the 1000–2000-m depth contours, and the cells within the bold red circle on the left side of the MDS biplot, encompassed within the 500–1000-m depth contours, are, respectively, representative of the lower and upper slope areas. Finally, cell units within the square on the right quadrant of the MDS biplot are all encompassed within the 200–500-m depth contours. As Fig. 6 suggests, with the exception of striped dolphin and fin whale, all the regularly encountered species appear to show clear preferences (Fig. 6a–d).

3.2. Depth and slope relationships

Table 5 shows the depth and slope statistics of the regularly encountered species. To test the preferences outlined by the MDS biplot, a canonical discriminant analysis (CDA, Afifi and Clark, 1996) was performed with depth and slope as explanatory variables. The CDA was applied to Risso's dolphin, sperm whale and Cuvier's beaked whale cell units. Every cell unit was weighted by the corresponding Habitat Score. Two canonical discriminant functions were found, but only the first was significant (Wilks' Lambda 0.57; $p < 0.0001$). Overall the two discriminant functions were able to correctly classify 62.7% of the three species sightings. Moreover, a leave-one-out cross-validation test was performed to check the accuracy of prediction controlling for

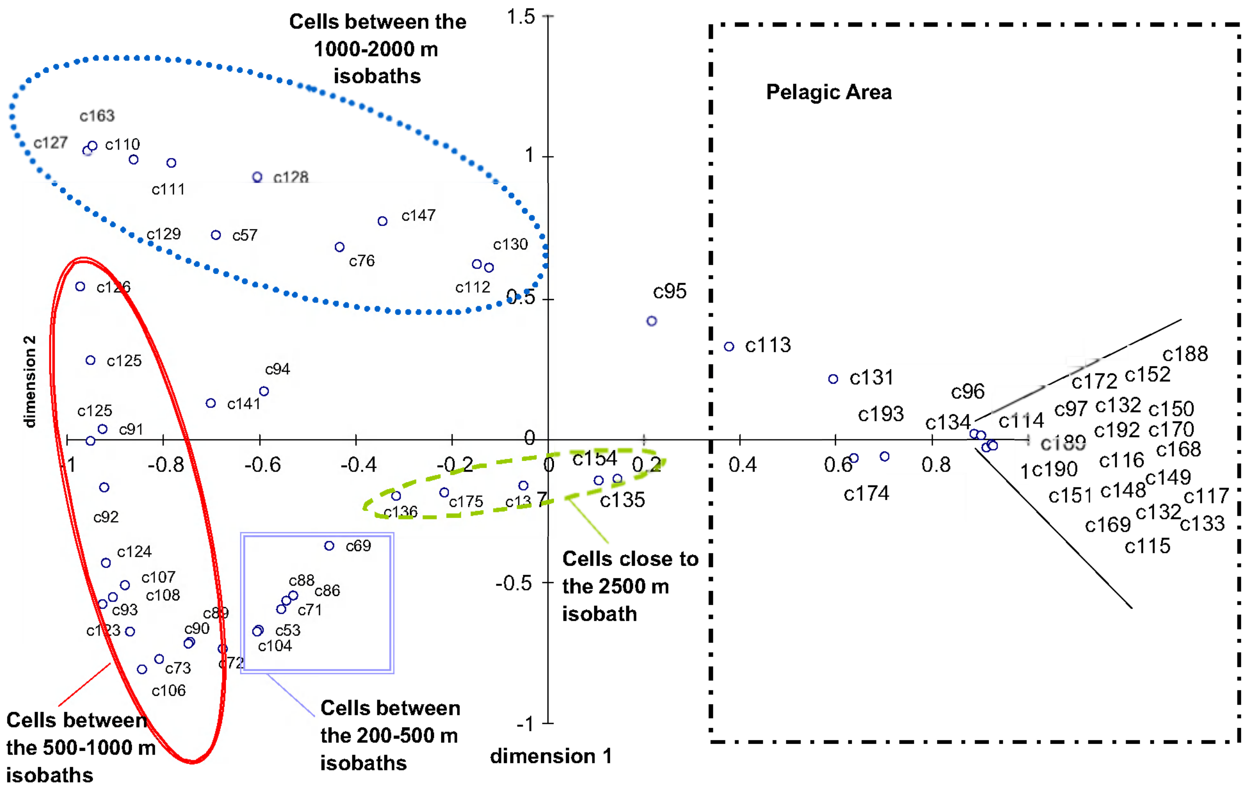


Fig. 5. MDS biplot. Definite clusters of points are visible. These clusters represent cells with similar physical characteristics.

overfitting (Efron and Tibshirani, 1993). With this test each case considered for the analysis was classified by the discriminant function derived from all cases other than that case. On the cross-validation data set, the percentage of the cases correctly classified was 61.6%, confirming that the model classification performances were stable. Since only the first canonical discriminant function proved to be significant, the model was able to discriminate just two out of the three groups of cells. The percentage of correct predictions, in fact, was extremely high for both Risso's dolphin (84.3%) and Cuvier's beaked whale (78.6%) cells while it was quite low (23%) for sperm whale cells (see Table 6). Sperm whales accounted for most of the mis-classifications (37.3%). The percentages of Risso's mis-classified as beaked whale (10%) and the vice versa (0.6%) were extremely low. The poor performance of the second canonical function is a consequence of the overlap of sperm whale's use of the habitat in the area of the other two species, which have, in contrast, well-defined and separate habitat preferences (see Fig. 7).

3.3. *Habitat use by species*

3.3.1. *Variability in time*

For this phase of the analysis the Habitat Score was used to study the species occurrence and to assess the interannual and monthly variability of the species' use of the study area. Being effort-biased and characterised by low sample sizes, October and May sightings were excluded from the analysis of the monthly occurrence.

3.3.1.1. Stenella coeruleoalba. Habitat Scores for striped dolphin were log-transformed to normality (Kolmogorov–Smirnov level of significance corrected by Lilliefors >0.05, *n*: 319). the log-transformed Habitat Scores were analysed by means of a two-way Anova (Sokal and Rohlf, 1995) testing both the effects of both the year and the month. No significant differences were found in striped dolphin annual occurrence (F_{year}: 1.49, $p > 0.20$), whereas significant differences were shown in the monthly occurrence (F_{month}: 3.69, $p < 0.05$). A Tamhane multiple comparison test, pooling all the years

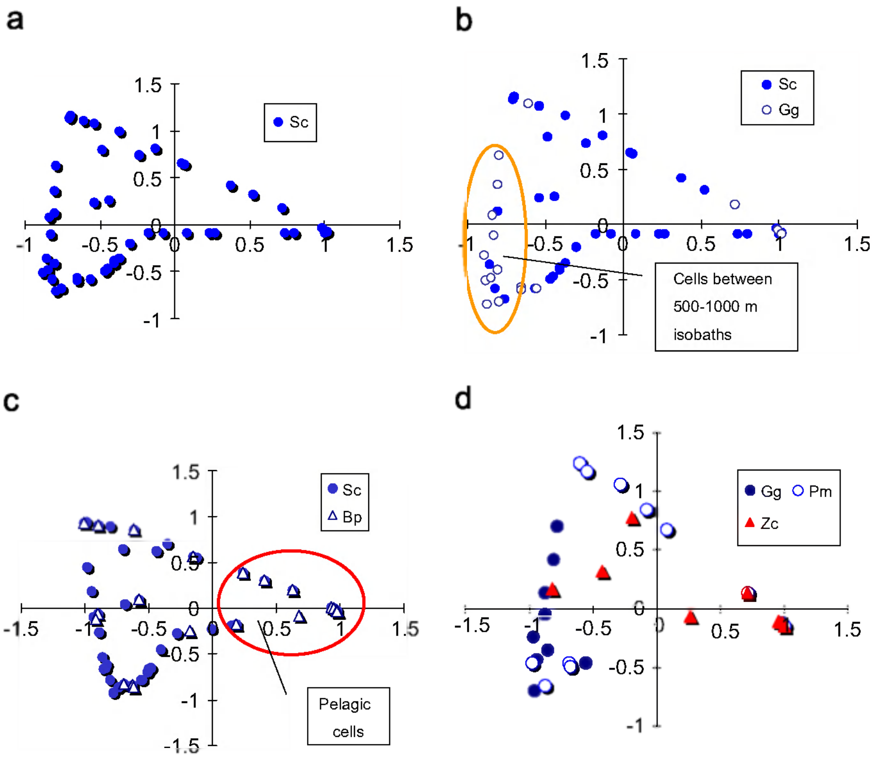


Fig. 6. MDS plots outlining the habitat preferences of different species. Symbols: Sc: striped dolphin; Pm: sperm whale; Bp: fin whale; Gg: Risso's dolphin; Zc: Cuvier's beaked whale.

together (1997–2000) from June to September, revealed that striped dolphin occurrence is higher in September than in August ($p<0.01$). Highly significant was also the interaction *year* $*$ *month* ($F_{\text{year}*\text{month}}$: 19.3, $p<0.001$), showing that the monthly occurrence pattern of striped dolphin changes in time. Particularly, Fig. 8a clearly shows that in 2000 striped dolphin occurrence in June was lower than in July and much lower than the occurrence in June recorded in all the other years. On the contrary in 2000 the July occurrence was much higher than within the preceding three years. Striped dolphin is the most frequently encountered species. Excluding the encounters that occurred within the same day, the median interval between two sightings of striped dolphin was 1 day, with 50% of the sightings (i.e. interquartile range, IQR) occurring between 1 and 3 days from a previous sighting (range: 1–18 days, Fig. 8c).

3.3.1.2. Balaenoptera physalus. Habitat Scores for fin whales were also log-transformed to normality (Fig. 8b) and tested by means of a one-way ANOVA (Sokal and Rohlf, 1995). Significant differences were found in the fin whale annual occurrence (F: 4.446, $p<0.01$, n: 92); particularly, fin whale occurrence in 2000 was significantly lower than in 1997 and in 1998 (Tukey HSD multiple comparison test $p<0.05$). One-way ANOVA applied to all the data pooled together showed significant differences also in fin whale monthly occurrence (F: 5.22, $p<0.01$, n: 88). Multiple comparison tests showed that fin whale occurrence is much lower in September (Tukey HSD, $p<0.05$) than in the preceding months.

3.3.1.3. Grampus griseus. Risso's dolphin occurrence did not change among the years (Kruskal–Wallis test *Habitat Score* vs. *year* χ^2: 0.484, $p>0.90$, n: 34) or among the different months (Kruskal–Wallis test for *Habitat Score* vs. *month* χ^2: 3.38, $p>0.40$, n: 41). Unlike striped dolphin, which is so frequently encountered that it could be considered a "resident" species in the study area, Risso's dolphin occurrence suggests a sort of "transient" use of the study area. The median interval between two sightings of Risso's dolphin, in fact, excluding the encounters occurring within the same day, is about

Table 5
Descriptive statistics of the distribution by depth (m) and slope (m/m) of the most frequent species

SPP	Min depth	Max depth	Mean depth	Slope (m/m)	Slope Std. dev.
Gg					
Mean	374.1	1100.1	821.8	0.130	0.015
Standard deviation	343.2	502.6	573.1	0.044	0.010
Minimum	50.0	500.0	275.0	0.024	0.000
Maximum	2000.0	2470.0	2470.0	0.211	0.045
Median	373.8	1000.0	714.0	0.129	0.014
SE	63.4	89.6	101.7	0.008	0.002
N	29	31	32	32	32
Pm					
Mean	1062.3	1734.6	1499.6	0.105	0.008
Standard deviation	748.3	584.9	696.1	0.072	0.010
Minimum	51.0	500.0	288.5	0.010	0.000
Maximum	2300.0	2410.0	2410.0	0.211	0.039
Median	1000.0	2000.0	1500.0	0.121	0.004
SE	161.4	118.1	138.8	0.014	0.002
N	21	25	25	25	25
Zc					
Mean	1722.1	2072.7	2060.3	0.059	0.002
Standard deviation	774.6	424.6	517.1	0.053	0.002
Minimum	795.0	1000.0	907.5	0.018	0.000
Maximum	2500.0	2500.0	2500.0	0.182	0.005
Median	2000.0	2130.0	2130.0	0.046	0.001
SE	276.4	138.0	139.1	0.014	0.001
N	8	9	14	14	11
Bp					
Mean	1747.8	2250.7	2179.2	0.054	0.003
Standard deviation	676.9	408.6	476.6	0.052	0.004
Minimum	44	266	155	0.008	2.7E-05
Maximum	2500	2500	2500	0.204	0.039
Median	2000	2470.9	2464.7	0.033	0.00069
SE	115.7	57.4	58.8	0.006	0.00054
N	34	51	66	66	56
Sc					
Mean	1140.7	1855.5	1779.2	0.076	0.00671
Standard deviation	811.0	640.5	742.0	0.061	0.00937
Minimum	30	266	155	0.009	2.7E-05
Maximum	2500	2550	2525	0.211	0.07382
Median	1000	2000	2105	0.046	0.00352
SE	69.2	47.6	50.0	0.004	0.00064
N	137	181	220	222	211

Gg: Risso's dolphin; Pm: sperm whale; Zc: Cuvier's beaked whale; Bp: fin whale; Sc: striped dolphin.

8 days, with 50% of the sightings (i.e. IQR) occurring between 2 and 17 days from a previous sighting (range: 1–45 days, Fig. 8c). So the median interval between two Risso's dolphin sightings is significantly longer (Mann–Whitney *U*: 756, $p<0.0001$; *n*: 85, Fig. 8c) than the median interval of two consecutive striped dolphin sightings. It is certainly true that striped dolphin is more sightable than Risso's dolphin because of the larger dimension of the groups and possibly because of the higher absolute abundance (there are still no reliable estimates available for Risso's dolphin abundance in this area, but preliminary results of a mark-recapture study suggest that Risso's dolphin abundance could be much lower than striped dolphin's, unpublished data). However, a sort of systematic "date fidelity" to particular dates was observed in Risso' dolphin encounters. Such a "date fidelity" supports the "transient use of the area" hypothesis. To test such "date fidelity", the 152 days of the

Table 6
Classification success of canonical discriminant functions

Confusion matrix	Species	Predictions			Total
		Gg	Pm	Zc	
Raw data	Gg	28	1	3	32
	Pm	8	6	11	25
	Zc	0	3	11	14
Percentage	Gg	87.3	2.8	10.0	
	Pm	32.9	23.0	44.2	
	Zc	0.6	20.8	78.6	
Cross validation	Gg	27	2	3	32
	Pm	8	6	11	25
	Zc	0	3	11	14
Percentage	Gg	84.7	5.3	10.0	
	Pm	32.9	23.0	44.2	
	Zc	0.6	20.8	78.6	

The number and percentage of cases correctly classified and misclassified are displayed. Cross-validation results are also displayed. Gg: Risso's dolphin; Pm: Sperm whale; Zc: Cuvier's beaked whale; Bp: fin whale; Sc: striped dolphin.

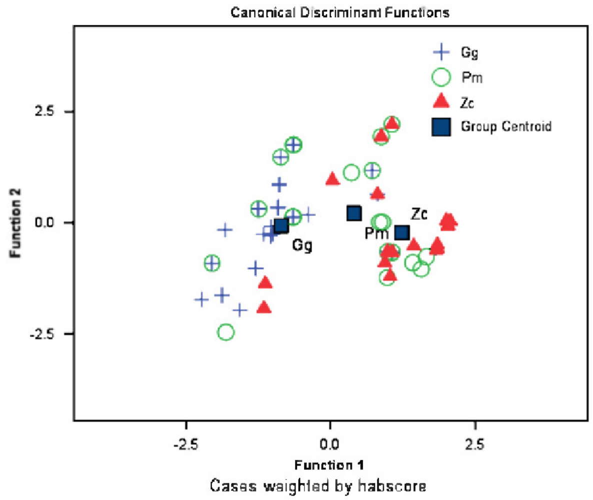


Fig. 7. Depth and slope preferences: biplot of the canonical discriminant functions (see the text for explanation) showing the separation of the habitat of Risso's dolphin (Gg) and Cuvier's beaked whale (Zc) and the overlapping of sperm whale (Pm) with the other two species.

typical research season (from June to October, see Fig. 8d) were grouped into 38 "4-day" intervals, and Risso's dolphin presence and absence were cross tabulated with the 38 "4-day" time intervals. Finally, a Monte Carlo randomisation test was applied. The Monte Carlo randomisation test showed a significant association (χ^2: 52.05, $p<0.05$ out of 10,000 randomisations) between Risso's presence and specific "4-day" intervals. Fig. 8d clearly shows that during the summer there are periods, like the end of June and the middle and the end of July, when Risso's dolphin encounters are more probable.

The "transient" use of the slope area could be a convenient strategy to exploit the temporary formation of food resources induced by the zooplankton accumulation typical of the slope area (Macquart-Moulin and Patriti, 1996). Therefore, in order to test the hypothesis of a relationship between the zooplankton accumulation events in the slope area and Risso's dolphin presence, a binary logistic regression analysis (Afifi and Clark, 1996) was applied to Risso's dolphin presence/absence data. The worsening of the sea conditions (Table 2) that was found correlated to the wind speed and, particularly, to the maximum value recorded during the three preceding days (r: 0.46, $p<0.001$), was used as a proxy for zooplankton accumulation events. Sea condition was in fact considered a proxy far more robust than the local measurement of wind speed for the formation of the coastal upwelling due to the offshore current carrying off the shelf into deeper waters. The logistic regression analysis revealed a direct positive correlation between Risso's dolphin presence and sea conditions, considering a time lag of either two or three days (Wald statistic >9, $p<0.01$, Table 7).

3.3.1.4. Physeter macrocephalus. No evidence of interannual or monthly variability was found in sperm whale occurrence (Kruskal–Wallis test for *Habitat Score* vs. *year* χ^2: 1.415, $p>0.74$, n: 21 and *Habitat Score* vs. *month* χ^2: 3.636, $p>0.30$, n: 19). The same 38 "4-day" time intervals used with Risso's dolphin were cross tabulated with sperm whale presence/absence. A Monte Carlo randomisation test revealed a lack of "date-fidelity" for sperm whale encounters (χ^2: 48.54, $p>0.05$ out of 10,000 simulated matrixes).

3.3.1.5. Ziphius cavirostris. Cuvier's beaked whale's occurrence did not vary among years (Kruskal–Wallis test for $HabitatScore * year$ χ^2: 8.394, $p>0.05$, df: 4, n: 20) or months (Kruskal–Wallis test for $HabitatScore * month$ χ^2: 6.99, $p>0.05$, df: 3, n: 23).

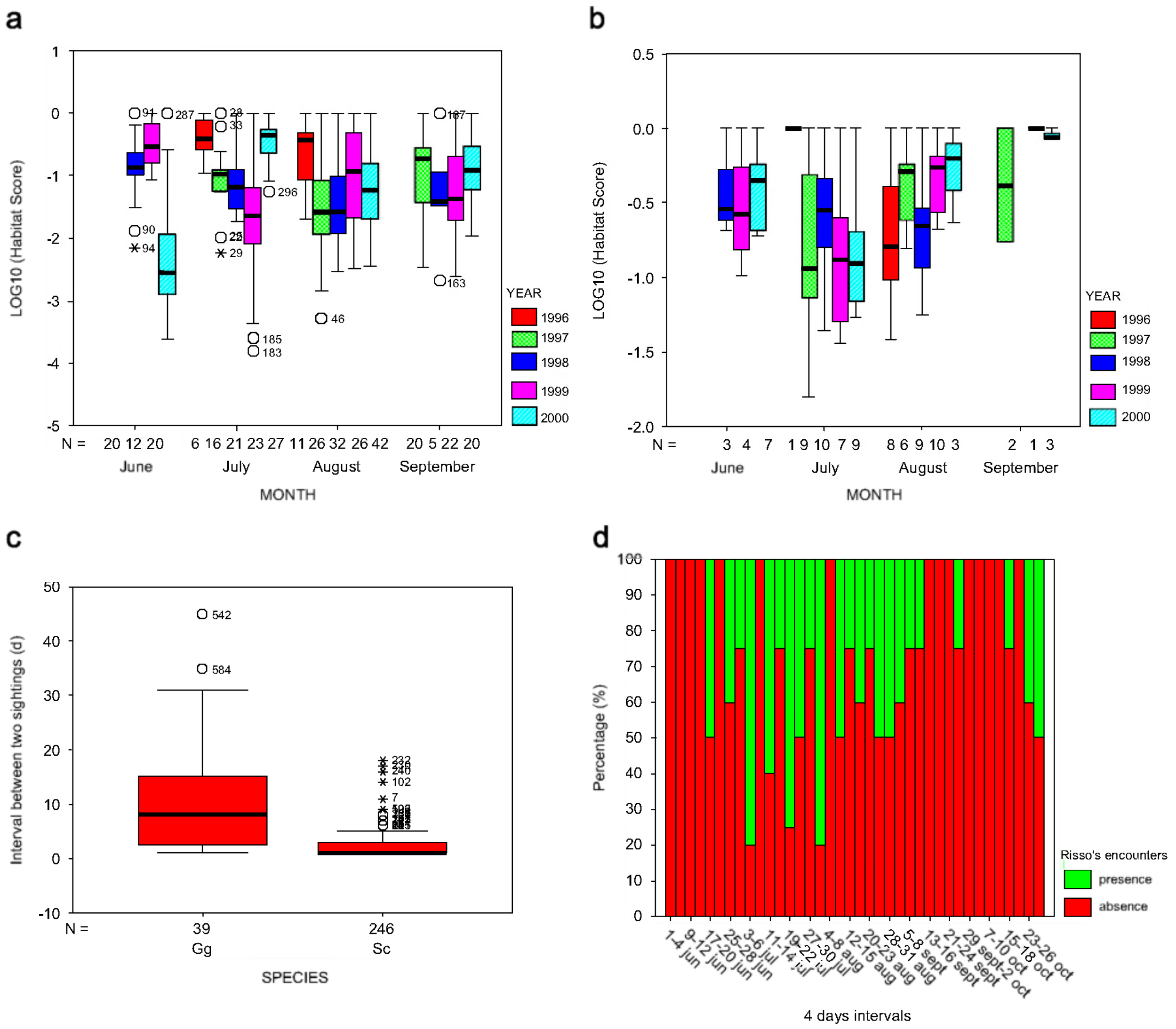


Fig. 8. Interannual and monthly occurrence (i.e. Log_{10} Habitat Score with confidence interval) within the study area: (a) striped dolphin, (b) fin whale; (c) Interval between two sightings of the same species: striped dolphin (Sc) vs. Risso's dolphin (Gg); (d) Risso's dolphin "time fidelity" the presence of the species in the area is mostly associated with specific dates (see the text).

3.3.2. Variability in time and space

For this part of the analysis cell centroid's latitude and longitude were used as dependent variables and the study area was divided into four quadrants that roughly divide the continental shelf-slope area from the pelagic area. Habitat Score was used either as an index of species occurrence in the four quadrants or as a cell weighting factor to test, by species, the spatial variability in time of the species habitat use (i.e. the variability in time of the mean centroid's coordinates of the species presence cells).

3.3.2.1. Stenella coeruleoalba. As already shown, striped dolphins did not reveal any particular preference for specific physiographic features within the study area (Fig. 6a). They appeared instead almost homogeneously distributed across the area. The MDS biplot evidence was confirmed by testing the Habitat Scores among the four quadrants. No significant differences were found in striped dolphin occurrence among the four quadrants (Kruskal–Wallis test Habitat Score vs. quadrant: χ^2: 4.86, $p > 0.05$; df: 3, n: 233). However, interannual variability was observed (Fig. 9). Significant differences

Table 7
Binary logistic regression results

Variables in the equation	*B*	SE	Wald	df	Sig.	Exp(*B*)	95.0% C.I. for Exp(*B*)	
							Lower	Upper
Sea conditions (3 days before)	0.239	0.065	13.562	1	0.000	1.270	1.118	1.443
Constant	−0.756	0.303	6.205	1	0.013	0.470		
Sea conditions (2 days before)	0.172	0.057	9.140	1	0.003	1.188	1.062	1.328
Constant	−0.597	0.226	6.975	1	0.008	0.550		

Risso's dolphin presence/absence was found correlated with the sea conditions recorded both two and three days before. *B*: unstandardised regression coefficient estimates. SE: standard error of the coefficient estimates. The Wald statistic and corresponding *p* values, the odds ratio, Exp(*B*) (i.e. the ratio change in the odds of the event of interest for a one-unit change in the predictor) and 95% confidence interval for Exp(*B*) are also shown.

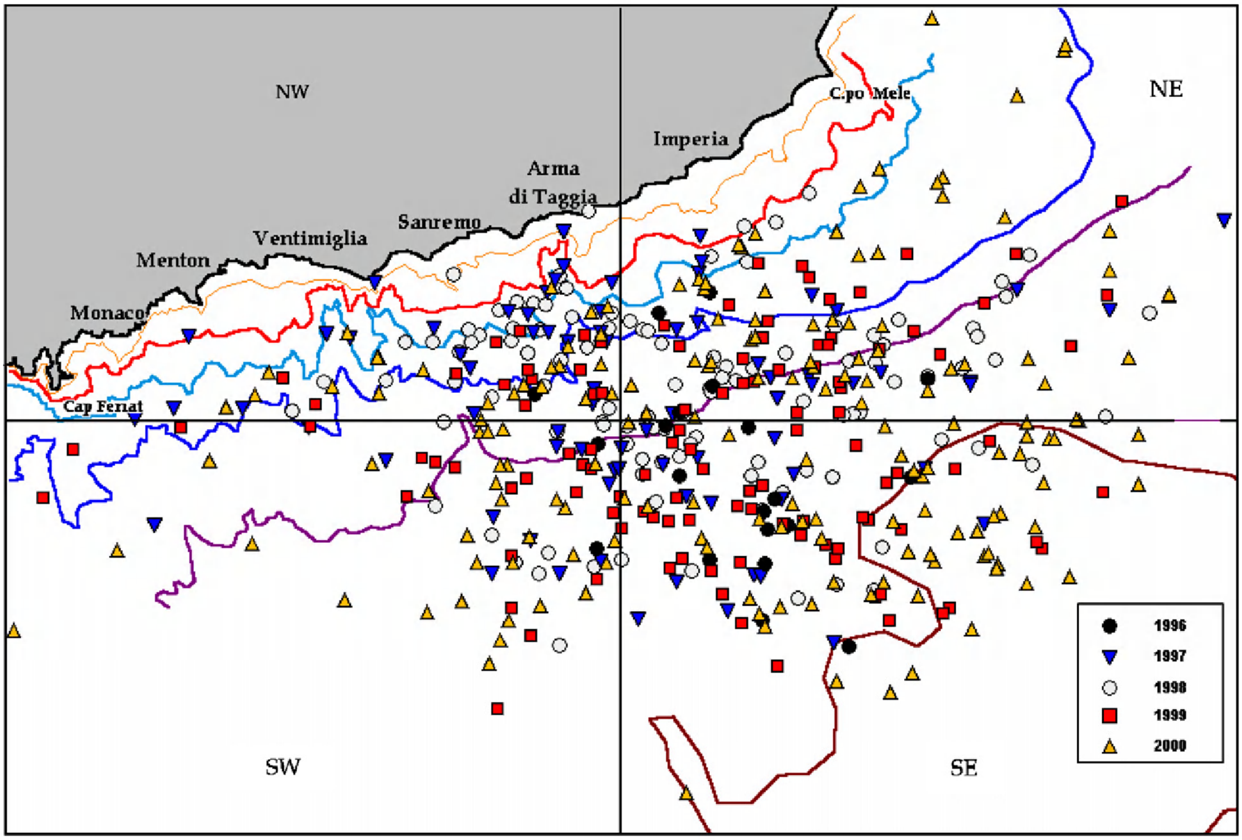


Fig. 9. Striped dolphin sighting distribution within the study area. Sightings from different years are shown with different symbols.

were found for both latitude (i.e. latitude of cell centroids; Kruskal–Wallis test χ^2: 23.5, $p<0.01$, *n*: 231) and longitude (i.e. longitude of cell centroids; Kruskal–Wallis test χ^2:13.2, $p<0.05$, *n*: 231) among different years. Moreover, a subsequent Kruskal–Wallis test, corrected for significance by Bonferroni's formula ($p<0.0125$) to account for the multiple comparisons, showed that striped dolphin distribution was approximately the same in terms of longitude every year with the exception of 1996, when striped dolphins were found more eastward than in 1998 ($p<0.001$); on the other hand, the latitudinal distribution was characterised by periodical north (years: 1997, 1998 and 2000) to south (years: 1996 and 1999) shifts. The mean latitude of striped dolphin encounters in the years 1996 and

1999 was significantly more to the south ($p<0.006$) than in the years 1997, 1998 and 2000. Moreover, to test the monthly use of the habitat, a Kruskal–Wallis test was applied to all the data pooled together independently from the year. Data from 1996, when no observations were available for months other than July and August, were excluded from this analysis. No evidence of monthly movements was found, considering both cell centroids' latitude (Kruskal–Wallis test χ^2: 1.86, $p>0.05$, n: 334) and longitude (Kruskal–Wallis test χ^2: 5.67, $p>0.05$, n: 334).

3.3.2.2. Balaenoptera physalus. Like striped dolphins, fin whales do not show any specific preference for physical habitat features (Fig. 6c) if not a generic preference for the pelagic area (depths greater than 2000-m and sea bottom gradients lower than 0.05 m/m). Most of the fin whale sightings occurred along the 2000-m depth contour (Fig. 10). An interannual and monthly variability of fin whale use of the habitat was also observed. Significant differences were found in fin whale distribution among the years (Kruskal–Wallis test: centroid's latitude: χ^2: 49.11, $p<0.0001$, centroid's longitude; χ^2: 48.68, $p<0.0001$ n: 86). Particularly, fin whale distribution was similar in 1996 and in 1999 (Bonferroni's $p>0.0125$), whereas significant differences (Bonferroni's $p<0.0125$) were found for all other years. Fin whale distribution in 1998 and in 2000 was, respectively, the easternmost and the westernmost (Bonferroni's $p<0.0125$, see Fig. 11a), whereas the longitudinal distribution observed in the remaining years was the same (Bonferroni's $p>0.0125$); on the other hand, fin whale distribution in 1997 and in 1998 was significantly shifted to north (Bonferroni's $p<0.0125$), towards the coast (Fig. 11b). However, in this respect, it should be noted that the mean distance from the coast in 1997 was significantly lower than in 1998 (Mann–Whitney U: 124, $p<0.001$, n: 36; Fig. 11c). No significant difference was found for the distance from the coast, when all the years were pooled together but excluding 1997 from the analysis (Kruskal–Wallis test: χ^2: 4.07, $p>0.25$, n: 95). A monthly pattern in fin whale distribution was also observed (Fig. 12a). In this respect, in order to avoid bias due to the low sample size of June and September distribution data, only the July/August period was investigated. A discriminant analysis (DA) was applied to the fin whale presence cells, using the month (i.e. July/August) as response variable and the centroid's latitude and longitude as predictors. Habitat Score was used also in this

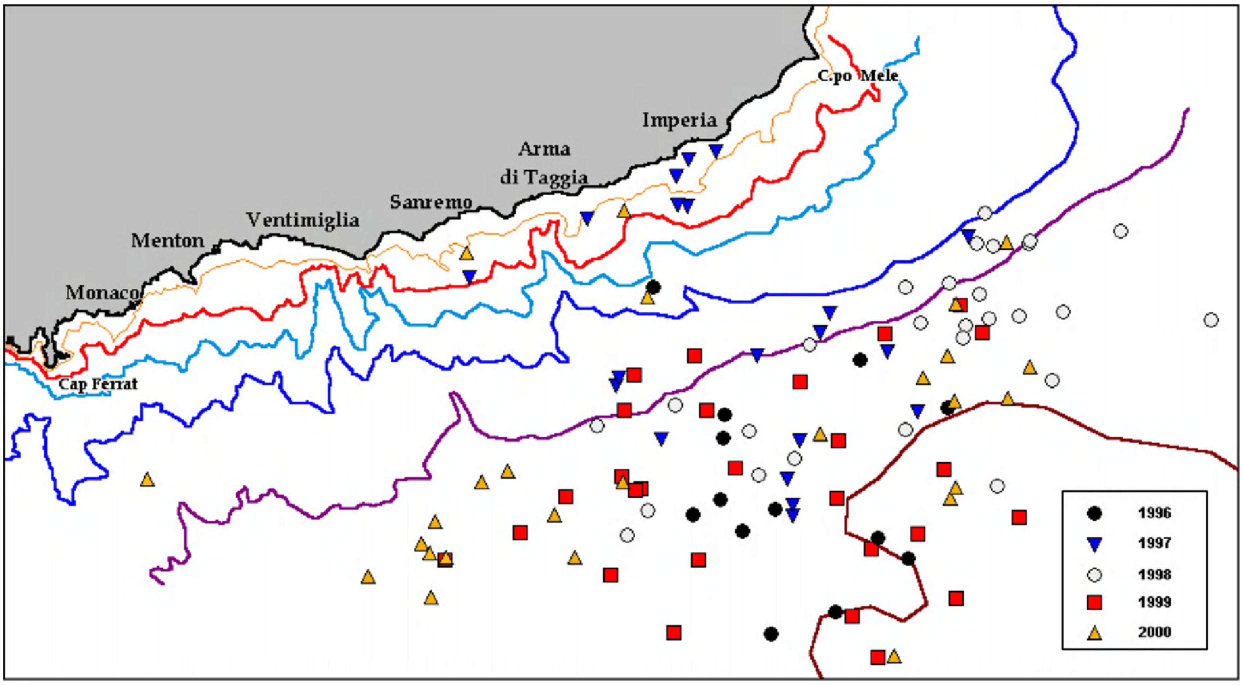


Fig. 10. Fin whale sighting distribution within the study area. Sightings from different years are shown with different symbols.

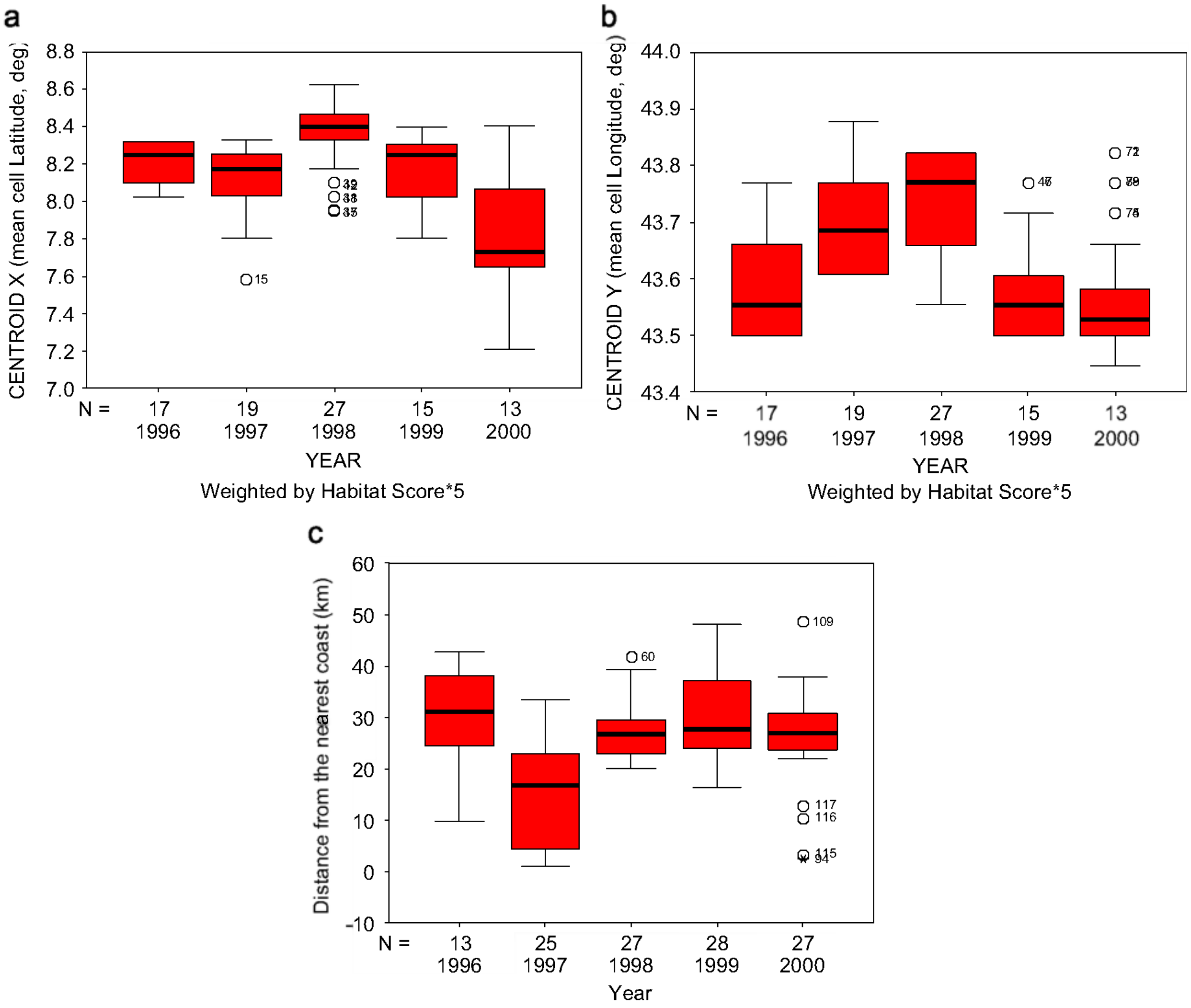


Fig. 11. Patterns in fin whale distribution: (a) longitudinal shifts among the years; (b) latitudinal shifts among the years and (c) variability of the mean distance from the coast among the years.

case as cell weighting factor. The DA showed that, independent of the year of observation, fin whale distribution in July is significantly more to the east than in August (Wilks' Lambda: 0.89 $p<0.05$, Fig. 12b). As the confusion matrix (Table 8) shows the discriminant function using latitude and longitude as predictors was able to correctly classify 67.9% of the original cases and 65.8% of the cross-validation data set.

3.3.2.3. Grampus griseus. Risso's dolphins are distributed on an area of well-defined physiographic characteristics (Fig. 6b) and particularly along the steeper sections of the upper continental slope (see Fig. 13). Risso's dolphin occurrence is significantly higher in the northwest quadrant, where the slope gradient is steeper than in the northeast quadrant (Mann–Whitney U: 28; Z: -2.356, $p<0.05$). No difference was observed in Risso's dolphin distribution among the years (Kruskal–Wallis test for *longitude * year* χ^2: 0.993, $p>0.80$, n: 33 and Kruskal–Wallis test for *latitude * year* (1998–2000) χ^2: 1.123, $p>0.50$, n: 26) except for 1997, when the southernmost sighting position was recorded (Kruskal–Wallis test for *latitude * year* (1997–2000) χ^2: 9.38, $p<0.05$, n: 33). However, a westernmost shift in Risso's dolphin distribution was observed in September with respect to July (Kruskal–Wallis test for *longitude * July*vs.*September* χ^2: 7.67, $p<0.0125$, n: 18).

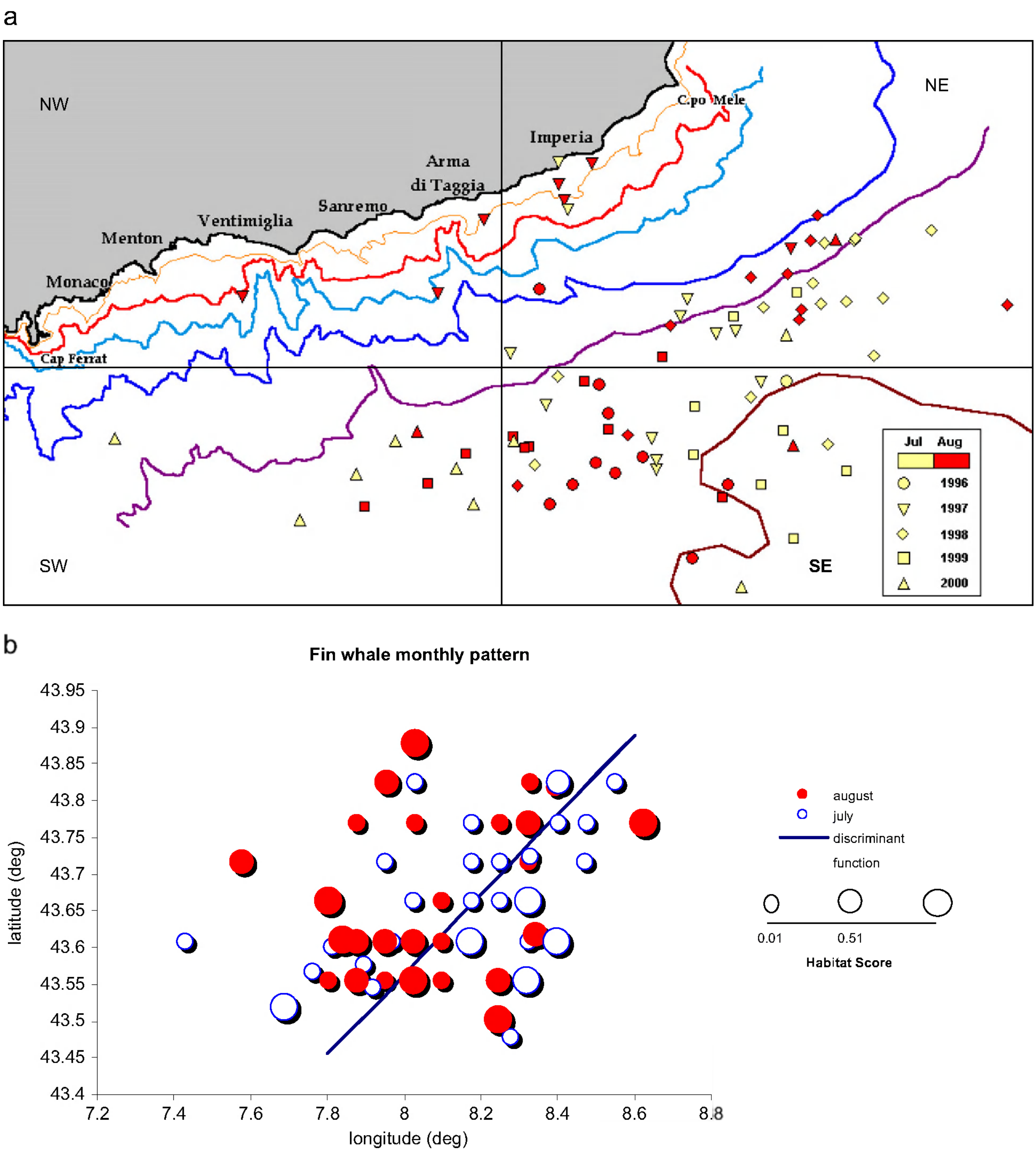


Fig. 12. Monthly pattern in fin whale distribution: (a) monthly sighting distribution within the study area (months are shown with different colours; years are shown with different symbols); (b) fin whale distribution pattern in July and August: July sightings are systematically shifted eastward with respect to August sightings. The discriminant function is also shown (see the text).

3.3.2.4. Physeter macrocephalus. Sperm whales occurred mostly along the continental slope, but were also encountered in the pelagic area (see Fig. 6d, Fig. 14). No difference was found among the four quadrants (Kruskal–Wallis test for *HabitatScore* quadrant*: χ^2: 1.227, $p>0.70$, n: 20). However, monthly and annual shifts in sperm whale distribution were observed in both longitude

(Kruskal–Wallis test for *longitude * month:* χ^2: 11.879, $p<0.01$, *n*: 18) and latitude (Kruskal–Wallis test for *latitude * year:* χ^2: 12.367, $p<0.01$, *n*: 18).

Z. cavirostris: Cuvier's beaked whales showed a well-defined preference for areas characterised by a definite depth and slope range (Fig. 6d). Beaked whales were encountered only in the eastern quadrants of the study area, with occurrence being approximately the same in the northeast and in the southeast quadrant (Mann–Whitney *U*: 20, $p>0.05$; *n*: 22, see Fig. 14). Monthly and yearly shifts in Cuvier's beaked whale distribution were also seen (Kruskal–Wallis test for *longitude * month:* χ^2: 8.696, $p<0.05$, df: 3, *n*: 24; *latitude * year:* χ^2: 20.609, $p<0.01$, df: 4, *n*: 24; *longitude * year:* χ^2: 15.136, $p<0.01$, df: 4, *n*: 24).

Table 8
Classification success of the discriminant analysis

	August	July	Total
Confusion matrix			
Cell count			
August	23	15	38
July	6	21	27
Percentage			
August	60.8	39.2	100
July	21.7	78.3	100
Cross validation			
Cell count			
August	23	15	38
July	7	19	27
Percentage			
August	60.8	39.2	100
July	26.8	73.2	100

The number and percentage of cases correctly classified and misclassified are displayed. Also cross-validation results are displayed.

3.3.2.5. Occasional species. The MDS biplot was used also for the occasionally encountered species, i.e. bottlenose dolphin (*T. truncatus*), long-finned pilot whale (*G. melas*), and common dolphin (*D. delphis*). As shown in Fig. 15, these species were seen in well-defined physical habitats. Bottlenose dolphins were always seen in shelf-waters (most of the sightings occurred within the 200-m depth contour), long-finned pilot whales were always seen in pelagic waters at depths deeper than 1000-m and common dolphins were always seen in the pelagic waters, associated with striped dolphin individuals. Because of the small sample size, the habitat use of these species was not further investigated.

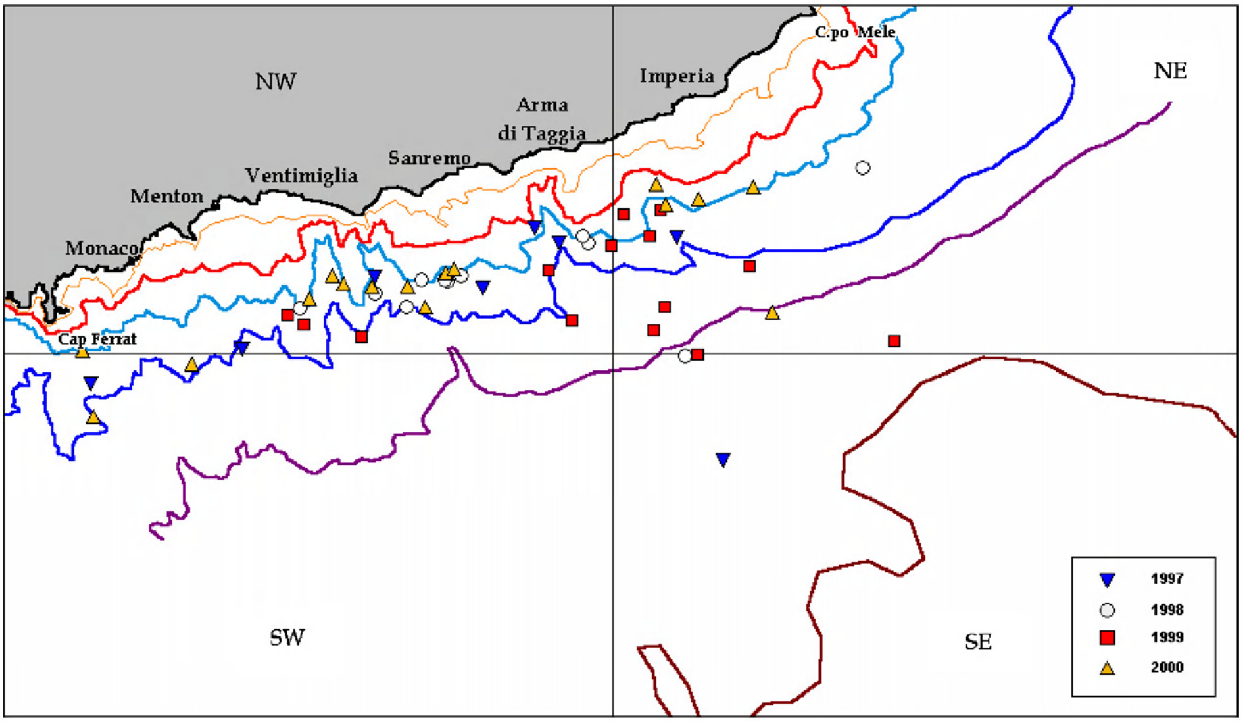


Fig. 13. Risso's dolphin sighting distribution within the study area. Sightings from different years are shown with different symbols.

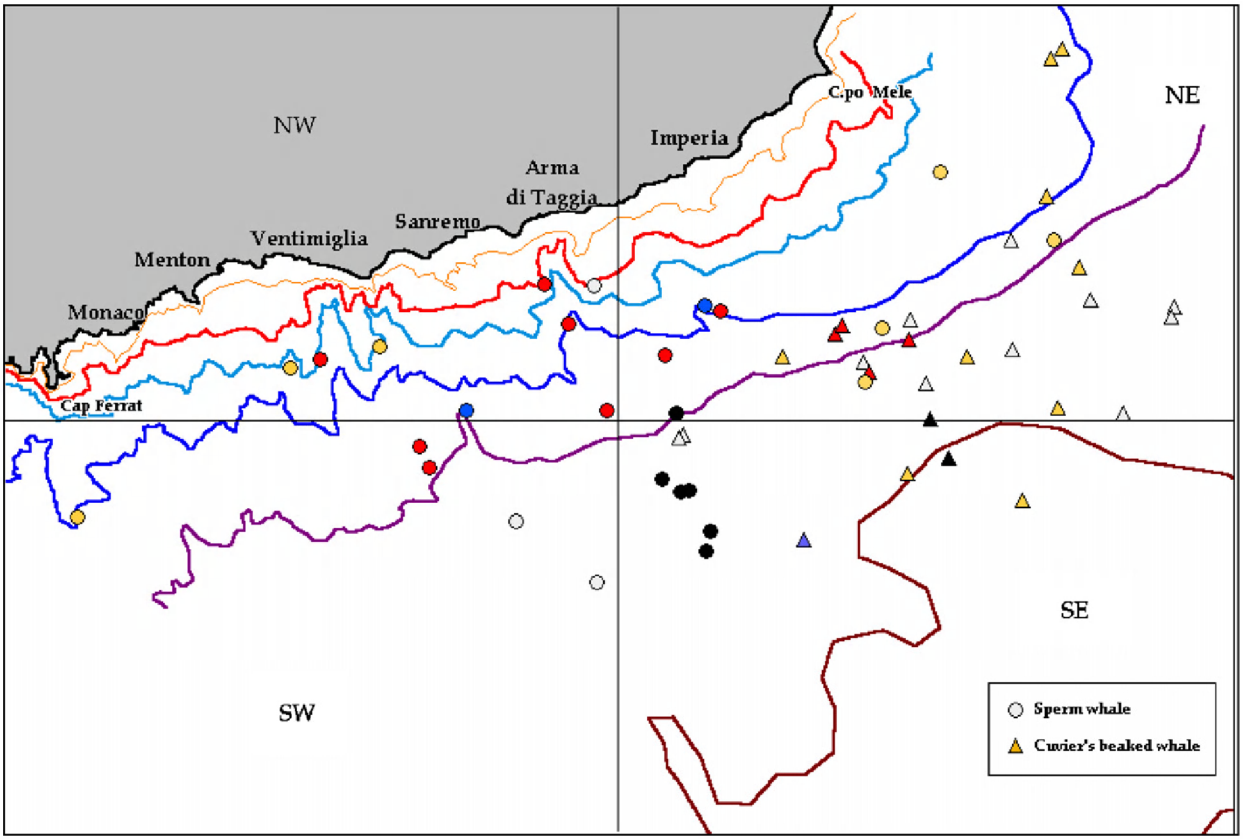


Fig. 14. Sperm whale (dots) and Cuvier's beaked whale (triangles) sighting distribution within the study area.

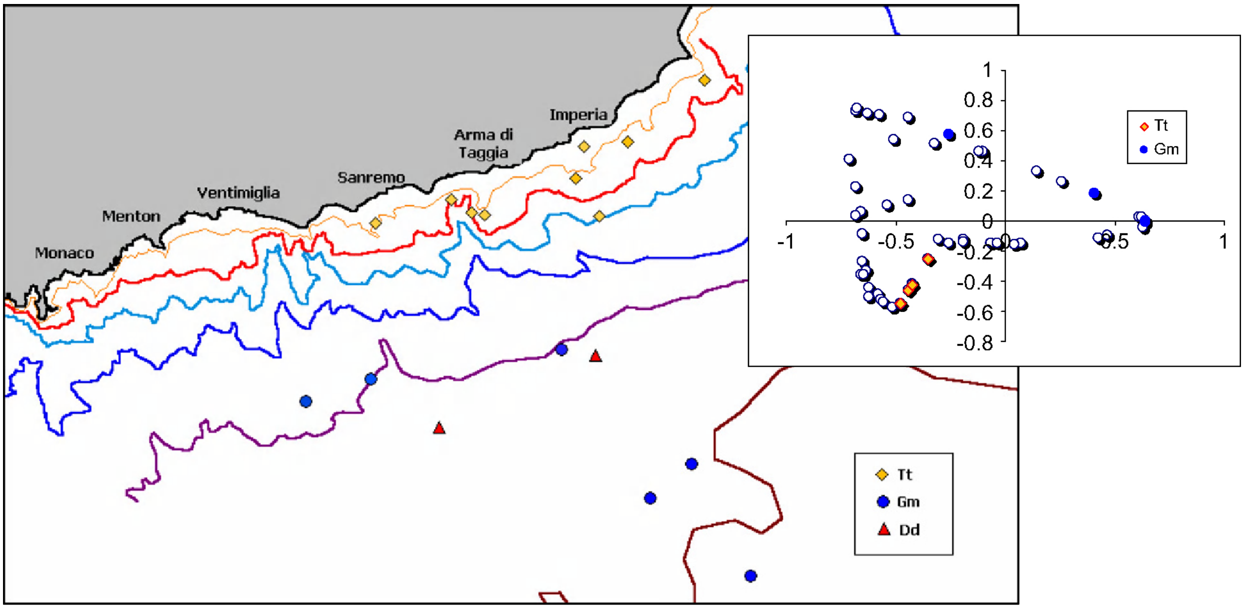


Fig. 15. Occasional species sighting distribution within the study area. Symbols: Tt: bottlenose dolphin, Gm: long-finned pilot whale; Dd: common dolphin. The MDS biplot is also shown for bottlenose dolphin (Tt) and long-finned pilot whale (Gm).

3.3.3. Relationship between habitat use and group size

As shown by Lusseau et al. (2004), climate variation may influence the species' social organisation through changes in prey availability. In the present analysis the relationship between habitat use and group size was investigated. Therefore, group sizes, weighted by Habitat Scores in order to consider both the effort and the habitat preferences, were studied to assess variability in time and space. For the assessment of spatial variability, differences in group sizes were studied either among the four quadrants or as differences in the spatial distribution (i.e. the variability in time of the mean centroid's coordinates of the species presence cells) of the different group formations.

3.3.3.1. Stenella coerulealba. Striped dolphin groups ranged from one to hundreds of individuals, with a median of 16 individuals (see Table 9). Fifty percent of the encountered groups (i.e. IQR) ranged from about 7 up to about 40 individuals (*n*: 389, see Fig. 16a). Group sizes were divided into five classes: 1–5, 6–10, 11–20, 21–30, 31–50 and >50 (see Fig. 16b). Group sizes smaller than 10 were not infrequent. Interannual (Kruskal–Wallis test: χ^2: 29.14, $p<0.0001$, n: 389) and monthly (Kruskal–Wallis test: χ^2: 23.50, $p<0.0001$, n: 389) differences in the mean dimension of the groups were observed. Particularly, in 1997 and 2000 striped dolphin groups were significantly smaller ($p<0.0125$) than in other years. Groups were also significantly smaller in September and July ($p<0.01$). Furthermore, significant differences were seen in the habitat use of the different group sizes in terms of both latitude (Kruskal–Wallis test: χ^2: 13.27, $p<0.05$, n: 367) and longitude (Kruskal–Wallis test: χ^2: 16.98, $p<0.01$, n: 367).

Table 9
Group size statistics by species

Species	Mean	Median	Std. dev.	Minimum	Maximum	Quartiles	(25°, 75°)
						25	75
Striped dolphin	26	16	30.4	1	240	7.2	37
Fin whale	1.9	1	1.2	1	6	1	3
Risso's dolphin	37	28	31	1	130	15	53
Sperm whale	2	2	1	1	4	1	4
Cuvier's beaked whale	4	4	2	1	8	2	6

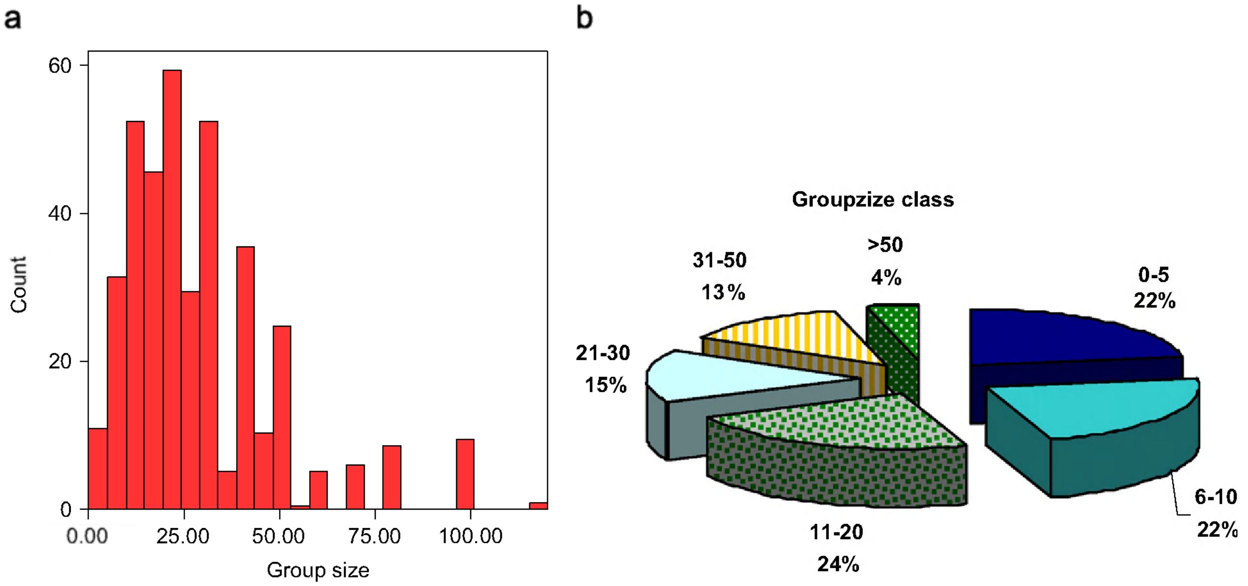


Fig. 16. Patterns in striped dolphin group size: (a) group size distribution and (b) frequencies of group size classes.

Smaller groups (i.e. from 6 to 20 individuals) were more frequently encountered eastward than larger groups (Kruskal–Wallis multiple comparison test, level of significance corrected by Bonferroni's formula $p<0.01$). These results suggest that striped dolphins may prefer certain areas for specific activities that require larger group sizes. In contrast groups of 1–5 individuals seem to be equally distributed within the study area. No significant difference was observed among the four quadrants showing that groups in the pelagic area are not larger than the others (Kruskal–Wallis χ^2: 4.168, $p<0.05$, n: 372).

3.3.3.2. Balaenoptera physalus. Fin whale groups were mostly of two individuals. The largest encountered group was of six individuals (Table 9). Significant differences were seen in fin whale group sizes among years and months (Kruskal–Wallis test for *groupsize* ∗ *year*: χ^2: 15.6, $p<0.01$, n: 86; Kruskal–Wallis test for *groupsize* ∗ *month*: χ^2: 15.4, $p<0.01$, n: 80). In 1996 the number of multiple encounters was significantly lower in 1999 than in 2000 (Bonferroni's $p<0.0125$); likewise, pooling all the years together, the number of multiple encounters was shown to be significantly higher in July than in August (Bonferroni's $p<0.0167$). No evidence of differential habitat uses was found for fin whale groups among the four quadrants (Kruskal–Wallis for *groupsize* ∗ *quadrant*: χ^2: 2.87, $p>0.40$, n: 107). Fin whale group sizes were subdivided into classes: groups made of one, two and more than two individuals. No difference was observed in the longitudinal distribution of these classes of group formation (Kruskal–Wallis test for *longitude* ∗ *groupsizeclass*: χ^2: 3.41, $p>0.181$, n: 86). However, groups larger than two individuals tended to be encountered significantly further south compared to single animals (Kruskal–Wallis for *latitude* ∗ *groupsizeclass:* χ^2: 11.25; Bonferroni's correction for multiple comparison: $p<0.0167$, n: 47).

3.3.3.3. Grampus griseus. Risso's dolphin's group sizes ranged from one single individual up to a hundred (Table 9). Group dimension did not change among the years except for 1997, when group sizes were significantly smaller (Kruskal–Wallis test for *groupsize* ∗ *year* χ^2: 12.01, $p<0.01$, n: 43). No monthly variation of the group dimension was observed (Kruskal–Wallis test for *groupsize* ∗ *month* χ^2: 4.69, $p>0.30$, n: 43).

3.3.3.4. Physeter macrocephalus. Sperm whale groups ranged from two to four individuals (Table 9). No difference was found in any of the four quadrants (Kruskal–Wallis test for *groupsize* ∗ *quadrant:* χ^2: 7.493, $p>0.05$, df: 3, n: 20). However, differences were seen among years and months (Kruskal–Wallis test for *groupsize* ∗ *year:* χ^2: 12.645, $p<0.05$, df: 4, n: 20; Kruskal–Wallis test for *groupsize* ∗ *month:* χ^2: 10.368, $p<0.05$, df: 3, n: 18).

3.3.3.5. Ziphius cavirostris. Cuvier's Beaked whale groups were generally made of four individuals, up to a maximum of eight individuals (Table 9). Group sizes were significantly higher in the northeastern quadrant (Mann-Whitney U:0.00; $p<0.01$), but differences were also seen among the years (Kruskal–Wallis test for *Group size*year:* χ^2:21.76, $p<0.05$, df:4, n:24); in 1999 larger groups were seen than in other years.

4. Discussion

Physiography controls the currents in the Liguro-Provençal basin. The "Liguro-Provençal-Catalan Current" follows the continental slope and during summer creates a stable themal front (Millot, 1999). This thermal front, although showing seasonal and interannual variations, runs very close to the 2000-m depth countour (Bèthoux and Prieur, 1983; Sournia et al., 1990). Many submarine canyons (a typical feature of the western Ligurian Sea) at the boundary between the neritic and the oceanic domains, due to the changeable wind and current regimes off the coast, greatly influence the ecology the upper slope area (Macquart-Moulin and Patriti, 1996). Our results suggest that physiography plays a role also in partitioning the distribution of cetacean species. Among the eight species examined in our study, three of them—bottlenose dolphin, Risso's dolphin and Cuvier's beaked whale—showed well-defined and not overlapping depth and slope preferences. Bottlenose dolphins, in fact, were encountered mostly in the shelf-edge area (Fig. 15), whereas Risso's dolphins and Cuvier's beaked whales were, respectively, found in the area of the upper (Fig. 13) and the lower slopes (Fig. 14). Sperm whales, although not infrequently encountered in pelagic waters, showed a high preference for the upper and lower continental slope. Fin whales, striped dolphins and the occasionally encountered long-finned pilot whales and common dolphins were not associated with any specific physiographic features, although there was a generic preference for the pelagic area (see Figs. 9–15). Nevertheless, the observed variability in interannual and monthly distribution of fin whales and striped dolphins suggests a relationship with the Ligurian thermal front and its variability, and consequently, although indirectly, a relationship with physiography.

Our results are consistent with what was found for the same species by Baumgartner et al. (2001) and Davis et al. (1998, 2002) in the Gulf of Mexico and by Waring et al. (2001) in the northeastern US shelf-break. More interestingly, our results are consistent with the findings of the other authors that have investigated the Mediterranean area. Cañadas et al. (2002) found in the northeastern Alboran Sea the same relationship with depth and slope for bottlenose dolphin, Risso's dolphin, sperm whale and Cuvier's beaked whale. However, these authors were not able to outline a habitat partitioning among the deep-water species (i.e. Risso's dolphin, sperm whale and Cuvier's beaked whale). Regional differences between the two different study sites might exist and be the cause of this lack of partitioning, but it should be mentioned that the method these authors used for the slope computation (i.e. the depth was derived from nautical charts, and the slope was the gradient between the minimum and maximum depths within the cell) is far less accurate than ours and could be ineffective in outlining the species differences. Gannier et al. (2002), considering the whole Mediterranean basin, found that sperm whales have the same preference for both the continental shelf-break and the open sea; no statistical significance could be demonstrated between the two habitats, confirming that sperm whales may be found either in continental slope waters or in a more pelagic domain. Our results are consistent with their conclusions. Monestiez et al. (2006) studied cumulative count data of fin whales over the summers of 1993–2001 to map their relative abundance by a modified kriging method. Littaye et al. (2004) studied the relationship between fin whales and satellite-derived environmental conditions in the northwestern Mediterranean Sea, using summer data over the period 1998–2002. Although these authors focused their analysis on much larger areas, their findings appear consistent with ours.

Panigada et al. (2005) studied the fin whale distribution in the Ligurian Sea during the 1990–1999 decade. They underlined the preference of fin whales for the offshore area (i.e. at depths deeper than 2000-m, more than 23 km from the nearest coast). However, their effort was dedicated mainly to the offshore portion of their study area, with very limited time spent in coastal areas. In this respect, our study clearly shows that the encounters of fin whales in continental slope waters are not infrequent. Most of the fin whale sightings occurred along the 2000-m depth contour (Fig. 10) in an area strongly influenced by the Liguro-Provençal thermal front. Fin whales showed also a periodic east-to-west pattern in their movements during the July–August period (Fig. 12). Such a pattern suggests once more a relationship with the counter-clockwise circulation of the "Liguro-Provençal-Catalan Current" Striped dolphins were encountered in almost every habitat available in the study area, although their distribution was found to respond to the environmental variability.

All the species known to be almost exclusively teutophagic (i.e. Risso's dolphin, sperm whale and Cuvier's beaked whale) were shown to be related to areas of the upper and lower slope. This is consistent with the hypothesis that they feed mostly on meso- and bathy-pelagic cephalopods, usually found in steep slope areas (Riedl, 1991; Quetglás et al., 2000). The competition for prey could be another issue to consider. Habitat selection, in fact, can be seen as a complex and dynamic function of the species requirements for food, mates, avoidance of predators/competitors, and ability to move between habitat patches (Schofield, 2003). Interspecific competition has been shown to directly affect habitat selection in fishes (Hixon, 1980; Larson, 1980; Munday et al., 2001). Although the information about the dietary habits of cetaceans is quite scarce for the Mediterranean Sea, on the basis of the few available data on stomach contents, it could be speculated that Risso's dolphin (Bello and Bentivegna, 1996; Kenney et al., 1995; Gannier, 1995; Würtz et al., 1992; Clark and Pascoe, 1985), Cuvier's beaked whale (Blanco and Raga, 2000; Blanco et al., 1997; Carlini et al., 1992; Podestá and Meotti, 1991) and sperm whale (sample of faeces collected by the authors, unpublished data) may compete with each other since they feed mostly on the same species: *Histioteuthis bonnellii* (Histioteuthidae), *H. reversa* (Histioteuthidae), *Todarodes sagittatus* (Ommastrephidae), *Ancistroteuthis lichtensteini* (Onychoteuthidae), *Heteroteuthis dispar* (Sepiolidae).

It is well known that competition for the food resource may lead to spatial or temporal segregation of habitats (Begon et al., 1986). The temporal segregation, in fact, may facilitate the coexistence of competing species through avoidance of direct confrontation or reduction of overlap of resource exploitation. The temporal patterns we observed in Risso's dolphin and sperm whale occurrence in the upper slope area may fit this habitat segregation hypothesis. Risso's dolphin's presence in the upper slope area, in fact, was characterised by a sort of regularity or "time fidelity". No regularity was found in sperm whale occurrence in the same area. Moreover, as it was shown by CDA (Table 6), sperm whales, accounting for most of the misclassifications (37.3%) of Risso's dolphin and Cuvier's beaked whale, coexist in the habitat of the other two species (Fig. 7). The sperm whales' use of different habitats is known.

Jaquet (1996) reviewing a variety of sperm whale habitat studies that seemed to have contradictory conclusions, attributed the discrepancies to the difficulty of defining the appropriate spatial and temporal scales. Our results suggest that interspecific competition in the western Ligurian Sea could be added to the factors shaping sperm whale distribution. On the other hand, Cuvier's beaked whales were found to be less mobile and more strongly associated with the lower slope area contained within the Genoa canyon, and these results are consistent with those of Moulins et al. (2007) in the same area. It is interesting to observe that similar partitioning of the habitat has been observed between sperm whales and Cuvier's beaked whales on the northeastern United States shelf-edge (Waring et al., 2001), and between sperm whales and northern bottlenose whales, *Hyperodon ampullatus* in the Gully on the Scotian Shelf (Whitehead et al., 1992; Gowans and Whitehead, 1995).

As already mentioned, in the western Ligurian Sea, many submarine canyons at the boundary between neritic and oceanic domains create the conditions for the accumulation of migratory micronektonic species in the continental slope waters. Macquart-Moulin and Patriti (1996) showed that pelagic species such as euphausiids, hyperids and mysids, during their upward migration and their nocturnal accumulation at the surface, are transported by surface currents generated by winds blowing landwards and then trapped in slope waters during their downward morning migrations. So this periodic pattern of concentration of pelagic zooplankton near the bottom above the slope may provide an abundant food source for organisms living in the slope area, and it could also be the reason for the occasional presence of fin whales over the upper slope (Fig. 10). It could be speculated that moving up and down along the slope area may be a convenient strategy for some species regularly occurring in this area to exploit the temporary food resource generated by the wind-driven accumulation of zooplankton and zooplankton feeders. The correlation found between Risso's dolphin presence (i.e. the species with the most regular pattern of occurrence in the upper slope area) and the sea conditions recorded during the preceding days supports this hypothesis. Fin whales, which in 1997 were observed close to the coast and well beyond the 2000-m depth contour, could have been attracted to this area by a similar zooplankton accumulation due to wind-induced currents of that kind. It is noteworthy that in 1997 also striped dolphins showed a similar response to the environmental variation, shifting their distribution northward and getting much closer to the coast than in other years.

All the species regularly occurring in the study area were found to be influenced by the interannual variability of the environmental conditions, showing marked shifts in their distribution during the time period considered. However, fin whales and striped dolphins, being much less related to the sea bottom biocenosis and feeding mainly on the organisms inhabiting the first hundreds of meters below the surface, appear to be the species more influenced by the environmental variability. Striped dolphins are known to have opportunistic feeding habits (Blanco et al., 1995; Pauly et al., 1998 Wurtz and Marrale, 1991; Pulcini et al., 1992), and, based on the present study, it could be speculated that they are less mobile than fin whales. The north-to-south shifts observed in striped dolphin distribution appear to be a response, in terms of short-range movements, to the environmental changes.

Sperm whales and Cuvier's beaked whales, being preferentially found in the lower slope area, may be more dependent on the deep circulation occurring in the canyons than on the environmental variability of the thermal front and of the upper layers. Finally, it should be remarked that a relationship between group size and habitat use was also found for almost all the species. Particularly, specific group sizes were found associated with certain areas (e.g. striped dolphins) or with certain years (e.g. striped dolphin and sperm whales). Such differences in group size may reasonably reflect a change in the animal preference for prey of the kind described also by Lusseau et al. (2004). Changes in the prey may require, in fact, a behavioural change for animals known to forage in groups. All these elements suggest that these species may respond to the environmental variability either with relative movements within the study area or with changes in their preference for prey items. On the other hand, concerning fin whales, the fact that larger groups (i.e. larger than three individuals) have been observed mostly beyond the 2000-m depth contour may be simply explained by the patchiness of their main prey in the offshore area (*M. norvegica*, Labat and Cuzin-Roudy, 1996), which causes the whales to aggregate while feeding on the same patch.

5. Conclusions

Cetacean assemblages studied during the summer months (from June to September) in the period 1996–2000 support the hypothesis that physiography plays a major role in partitioning the habitat uses of the different species in the western Ligurian Sea. Among the studied species, bottlenose dolphin, Risso's dolphin, sperm whale and Cuvier's beaked whale were all found associated with well-defined depth and slope gradients showing very clear preferences for specific physical habitats, respectively, the shelf-edge, the upper slope and the lower slope. In addition, Risso's dolphin, sperm whale and Cuvier's beaked whale showed a sort of habitat segregation of their habitats. Such partitioning is probably the outcome of the common feeding habits—the three species are mostly teutophagic and they probably feed on the same prey items—and it could be the effect of the interspecific competition. Sperm whales, in fact, are characterised by a habitat use that partially overlaps the uses of the other two species, and their movements between the upper and lower slope could be a sort of temporal segregation that may facilitate the coexistence of the competing species.

Fin whales, common dolphins and long-finned pilot whales were not found associated with specific physiographic features with the exception of a general preference for the pelagic area (i.e. depths greater than 2000-m and sea bottom gradients lower than 0.05 m/m). However, fin whales, not infrequently, have been encountered within the 2000-m depth contour in the upper slope and occasionally even in continental shelf-waters. Striped dolphins were generically found in any type of physical habitat, consistent with their known opportunistic feeding habits. Striped dolphin distribution suggests a higher site fidelity compared with the other species, even though small-scale interannual movements have been observed. As interannual and seasonal movements have been shown for fin whales and most of the regularly occurring species, it can be concluded that environmental changes (e.g. changes in the pattern of surface currents, in the wind strength and direction or in the sea-surface temperature) have a significant influence on the species use of the habitat. In this respect, a relationship was found between the group size and the habitat use of many of the species. Specific group sizes were found associated with certain areas (e.g. striped dolphins) or with certain years (e.g. striped dolphin and sperm whales). These findings suggest that some species may respond to the environmental variability either by moving within the study area or with behavioural changes (i.e. changes in the group formations) that may reasonably reflect changes in prey items.

Further investigations on a finer scale and with a more comprehensive data collection on the environmental conditions (i.e. weekly SST and ocean colour image data, vertical water column profiles, daily data on wind strength and direction, etc.) would provide important elements for a better understanding of the habitat preference and ecology of the cetacean species in the western Ligurian Sea, creating the opportunity for a sounder management of the Sanctuary area.

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