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ORIGINAL ARTICLE

Long-term presence and habitat use of Cuvier's beaked whale (*Ziphius cavirostris*) in the Central Tyrrhenian Sea

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Abstract

Cuvier's beaked whale (*Ziphius cavirostris*, G. Cuvier 1823) is a poorly known species and many international agreements have asked for a better understanding of its biology for conservation purposes. In the present study, systematic cetacean surveys were carried out from ferries along a trans-regional fixed transect in the Central Tyrrhenian Sea (Civitavecchia, Latium – Golfo Aranci, Sardinia), just outside the southeastern border of the Pelagos Sanctuary. This research provided long-term, consistent data on Cuvier's beaked whale during two research periods (1990–1992 and 2007–2011). The objective of the research was to compare the presence, distribution and habitat use of Cuvier's beaked whale between the two investigated periods. Summer data (June–September) from the two periods were compared in terms of frequency of sightings, group size and spatial distribution related to the main ecogeographical features. A presence-absence model (generalized additive modelling) was performed to predict habitat suitability in the two study periods. The results highlight long-term site fidelity of Cuvier's beaked whale in the Central Tyrrhenian Sea with encounter rates comparable to the ones reported for other key areas. Separate suitability models based on 1990s and 2000s data appeared to work for each individual time period but differences were evident between the two periods, indicating changes in habitat selection over time. Our findings of the study appear to expand the definition of suitable beaked whale habitat and underline how the temporal scale of the analysis can affect the results in habitat studies. Moreover, this research highlights the importance of the Central Tyrrhenian Sea marine region for Cuvier's beaked whale and the ability of continuous monitoring to identify changes in cetacean frequency and distribution, necessary for adaptive conservation management approaches.

Introduction

The Mediterranean Sea hosts one regular ziphiid species, the Cuvier's beaked whale (*Ziphius cavirostris*, G. Cuvier 1823) (Notarbartolo di Sciara & Birkun 2010), the most cosmopolitan of all of the beaked whale species (MacLeod *et al.* 2006; Allen *et al.* 2012). Globally, the species is listed as Least Concern by IUCN (Taylor *et al.* 2008), although the Mediterranean sub-population is listed as Data Deficient (Cañadas 2012). Beaked whales are difficult to detect and identify at sea mainly because of their elusive behaviour (Barlow *et al.* 2006); thus, they are poorly known and most information comes from stranding data (Podestà *et al.* 2006; Holcer *et al.* 2007; Öztürk *et al.* 2011). Mass stranding events have been related to navy sonar and seismic exploration (*e.g.* Frantzis 1998, 2004; Tyack *et al.* 2006, 2011; Filadelfo *et al.* 2009), which are considered major threats to Cuvier's beaked whale in the Mediterranean basin (Cañadas 2012). Other potential threats are the occasional risk of entanglement in gillnets (Reeves *et al.* 2013), ingestion of plastic debris (Allen *et al.* 2012; Cañadas 2012), ship noise (Aguilar Soto *et al.* 2006) and contamination by heavy metals (Storelli *et al.* 1999; Frodello *et al.* 2002). Several field campaigns in the Mediterranean have investigated some aspects of the ecology, distribution and habitat use of free-ranging individuals (Cañadas *et al.* 2002; Moulins *et al.* 2007; Rosso *et al.* 2007; Azzellino *et al.* 2008; Gannier & Epinat 2008; Tepsich *et al.* 2014) and an initiative for modelling high-use areas for Cuvier's beaked whale was undertaken under the Agreement on the Conservation of Cetaceans in the Black Sea, Mediterranean Sea and Contiguous Atlantic Area (ACCOBAMS) Ziphius initiative (Cañadas *et al.* 2011). Nevertheless, more information is needed and many documents under the ACCOBAMS agreement, as well as other EU Directives and national legislation, ask for a better understanding of the biology of this species for conservation purposes. According to the literature, the species is distributed in several key areas (Cañadas 2012), especially over and around canyons in the Eastern Ligurian Sea, the Alboran Sea and off Southwestern Crete. The same areas, based on evidence of threats and potential impact on the species, have also been recognized as important areas for conservation (MacLeod & Mitchell 2006). Other areas of distribution were recently recognized by analysing data on strandings in the Southern Adriatic Sea (Holcer *et al.* 2007) and in Israeli and Palestinian waters (Podestà *et al.* 2006; Kerem *et al.* 2012). Furthermore, based on regional scale (Marini *et al.* 1992; Gannier & Epinat 2008) and large-scale studies, Gannier (2011) confirmed the importance of the Central Tyrrhenian Sea as a favourable habitat for the Cuvier's beaked whale, in addition to the key areas listed by MacLeod & Mitchell (2006).

In the early 1990s, the first monitoring project on cetaceans took place in the Central Tyrrhenian Sea (Marini *et al.* 1996) along a fixed line transect (FLT) using the ferries running between Civitavecchia (Latium, Italy) and Golfo Aranci (Sardinia, Italy) as research platforms. In 2007 the research restarted along this FLT with the same protocol. Testing for the presence of cetaceans along the same transect over a 20-year time span, Arcangeli *et al.* (2013b) showed the regular occurrence of Cuvier's beaked whales in the area.

Different studies have reported changes in oceanographic parameters in the Mediterranean Sea over the last 20 years (Fuda *et al.* 2002; Rixen *et al.* 2005; Schröder *et al.* 2006, 2010), influencing food availability and resulting in potential changes of cetacean ranges and distributions (Gambaiani *et al.* 2009; MacLeod 2009). For *Balenoptera physalus* as an example, the FLT continuous monitoring in the Central Tyrrhenian Sea during 1990–1992 and 2007–2011 revealed a long-term change in habitat use and a direct correlation of inter-annual and intra-annual variability in chlorophyll concentration with the change in distribution of the species to be shown (Arcangeli *et al.* 2014). Comparison of the habitat selection of Cuvier's beaked whales over such a long period in an area characterized by complex bathymetry such as the Central Tyrrhenian Sea could enhance knowledge of the relationships between Cuvier's beaked whales' presence and habitat features, adding information on the definition of the species' favourable areas.

In this paper, we discuss Cuvier's beaked whale distribution in the Central Tyrrhenian Sea in relation to different environmental features that are known to have important influences on the biological processes of this species. Using data from the two research periods (1990–1992 and 2007–2011), the objectives of the study were to describe the habitat preferences of Cuvier's beaked whale over a long time period and obtain information that will be useful for driving further action on the conservation of this species (Hooker *et al.* 1999; Cañadas *et al.* 2002; Azzellino *et al.* 2008).

Material and Methods

Study area

Systematic surveys were conducted along a trans-regional fixed line transect in the Central Tyrrhenian Sea between Civitavecchia (Latium, Central Italian peninsula) and Golfo Aranci (Sardinia): the transect is about 220 km long and crosses several habitat types, such as continental shelf, slope, offshore waters with canyons, abyssal plain and sea mountains (Fig. 1). The 200-m isobaths run almost parallel along the coastlines of both Latium and Sardinia: the continental shelf is quite extended along the eastern side of the basin, with a ridge coming out from the wide shelf of Tuscany and crossing the study area southward. Along Sardinia the shelf is reduced and the water depth reaches 1000 m at about 15 km away from the coastline. The abyssal plain is found at around –1500 m depth and volcanic seamounts rise up to 600/800 m. Steep slopes are also present, defining a complex bottom topography.

Deep waters rich in nutrients reach the study area from the Eastern Mediterranean Sea and the Ligurian Sea, flowing towards the Gibraltar Strait. Surface circulation is instead influenced by the Atlantic current coming into the Tyrrhenian Sea from the south, generating a cyclonic gyre off the Sardinian coast; this is also

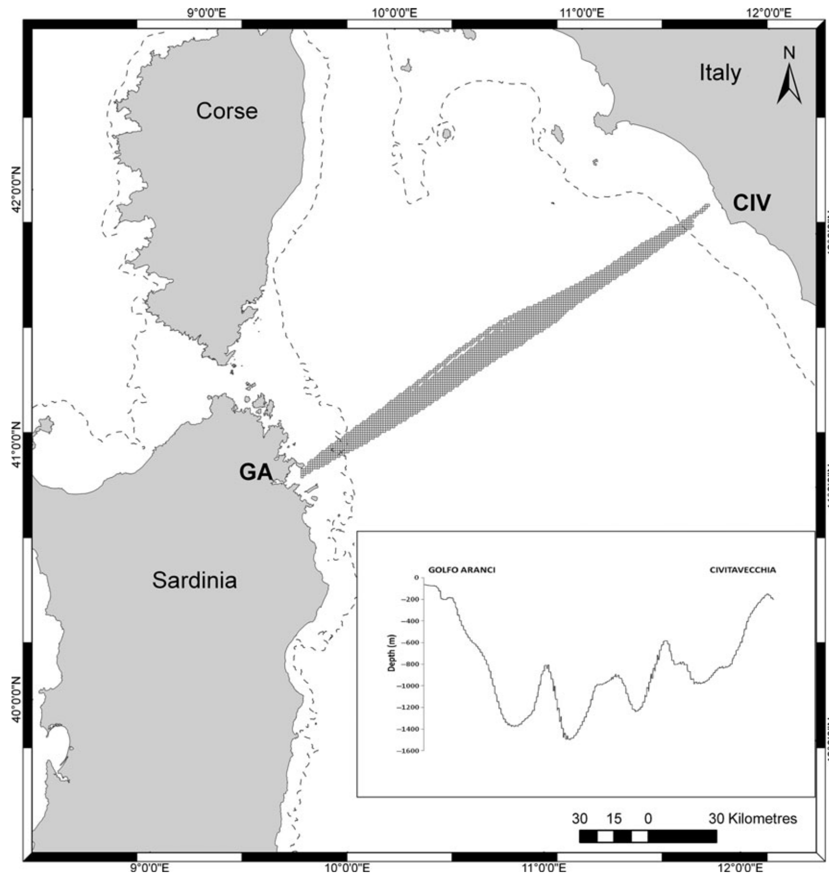

Fig. 1. Study area. In grey the area of the surveyed transects between Civitavecchia (CIV, central Italian peninsula) and Golfo Aranci (GA, Sardinia). Dotted line identifies the 200 m isobath. Bottom right: bathymetric profile of the transect.

maintained by the year-round jet wind blowing eastward from the Strait of Bonifacio, which enhances the vertical mixing of the water masses, inducing divergence and important upwelling/downwelling phenomena (Astraldi & Gasparini 1994). Summer upwelling was also described along the coast of Latium by Marullo *et al.* (1994) because of water stratification. A trend of increasing temperature and salinity in the intermediate and deep layer has been documented in the region since the late 1980s (Gasparini *et al.* 2005) and this process has been speeding up since the late 1990s (Schröder *et al.* 2006).

From a conservation point of view, the Central Tyrrhenian Sea was recently recognized as a Specially Protected Area of Mediterranean Importance under the protocol on Special Protected Areas and Biological Diversity in the context of the Barcelona Convention (UNEP 2010). In spite of its importance for conservation, this region falls just outside the southeastern boundary of the Pelagos Sanctuary and is exposed to heavy threats for cetaceans, such as high nautical traffic pressure, which increases in summer months (Vaes & Druon 2013), active navy sonar and seismic exploration (Cañadas 2012).

Field methods

Fixed line transects are routes set in advance, which can be repeatedly surveyed using any vessel that regularly travels along the same route. The use of ferries as observation platforms for dedicated surveys (*sensu* Donovan 2005) was first applied in the early 1990s along a fixed transect in the Tyrrhenian Sea (Marini *et al.* 1996) and, from 2007, along a network of fixed routes in the Mediterranean Sea (Arcangeli *et al.* 2013a). The method is particularly useful to monitor systematically long-term changes in cetacean occurrence through different habitat types, including open sea regions, because biases owing to spatial heterogeneity or to small sample sizes are minimized.

In this study, a fixed line transect in the Central Tyrrhenian Sea running from Civitavecchia to Golfo Aranci was surveyed almost twice a week from the beginning of June until the end of September during two research periods (from 1990 to 1992 and from 2007 to 2011). The same protocol was applied during the two periods to assure the consistency of the data collected, taking into account the meteorological conditions (observations carried out at Beaufort wind force state ≤3), speed and type of ferries (same type of ferries with range of mean speed 17–23 knots), experience of observers (only appropriately experienced and trained observers used in the programmes). At least two dedicated Marine Mammal Observers were located on each ship's command deck, conducting observational scans by the naked eye and binoculars (8×42 magnification), covering a 270° of visual range ahead of the ferry. Information regarding the route, speed and weather conditions were recorded at the beginning and at the end of the effort and each time a change occurred. During sightings, information about the time, ship's position, radial angle to the sighting, surface behaviour, direction of swimming, distance from the ship and group size of the species were recorded. A group was defined as more than one individual seen at the same time within few body lengths one to the other (Moulins *et al.* 2007).

Data analysis

Only data collected during the same season (from the end of May to the end of September) in both research periods (1990s: 1990–1992, 90 surveys; 2000s: 2007–2011, 160 surveys) were taken into account for the analysis.

Depth, slope, aspect northing and easting (facing direction of slope) and distance from the 200-m isobath were chosen for the analysis as these are usually considered the most important ecogeographical variables (EGVs) for predicting Cuvier's beaked whale presence (*e.g.* Cañadas *et al.* 2002; Moulins *et al.* 2007; Azzellino *et al.* 2008; MacLeod *et al.* 2008; Tepsich *et al.* 2014; Fig. 2). A depth map at 1-km^2 resolution was created from isobaths of the study area and slope and aspect maps were then derived from it using the Spatial Analyst tools in ARCMAP 10.1. The aspect parameter was converted into two linear components to be included in the analysis: aspect easting (sine of the aspect value) and aspect northing (cosine of the aspect value). Distance from the 200-m isobath (D200) was chosen because it was considered to be more descriptive than 'distance from shore' for deep-diving species and in order to avoid bias resulting from the variable extension of the continental shelf (Hooker *et al.* 1999; Praca *et al.* 2009). Thus, in order to gain data also on the continental shelf for the predictive maps (even if no sightings occurred there) the distance was considered both towards the coast and towards the open sea, with negative values assigned in continental shelf.

Spatial analysis was performed on a grid of 1×1 km resolution, this being the finest available scale for the EGV data (Claridge 2006; Hall *et al.* 2010; Gannier 2011). EGV values were extracted for the central point of each grid cell of the study area. The cell effort was calculated as the length travelled on effort for each cell in a total of almost 2000 km^2 of surveyed area.

Whale sighting data

Each ferry trip was considered as an independent statistical unit. Independency of the dataset was tested using the Spearman rank correlation and the autocorrelation test, assuming that the data between two successive outbound (or return) surveys, which had a minimum time interval of a week, were independent (Arcangeli *et al.* 2013b). Sightings per unit of effort (SPUE) was measured as the number of sightings per 100 km surveyed in good weather conditions (Evans & Hammond 2004; Wall *et al.* 2006).

Non-parametric statistical analyses (Kruskal–Wallis test and post-hoc Mann–Whitney test between each pair) were used to compare monthly and yearly variations in SPUE and group size between the two research periods. Analyses were performed using the program PAST 2.17 (Hammer *et al.* 2001).

Spatial analysis was studied using a Geographic Information System (ARCMAP 10.1 and Geospatial Modelling Environment) combining data from all months and years within the same research period. The distributions of sightings in the two research periods were first investigated using the Kernel smoother for point pattern analysis of occurrence-only data (Hengl 2009) to map areas of higher densities of sightings.

Habitat suitability analysis

Habitat preferences were first investigated for each variable in each time period separately. Values of each variable were extracted for the cetacean sightings positions and along the monitored transect as mean cell values. The range of values for each variable was divided into classes and the percentage frequency distribution of values in the sighting positions in the 1990s and in the 2000s were compared by graph and when possible by Chi-squared test, with the expected values along the monitored transect.

A species distribution model was then performed in order to account for any possible interactions between variables. A presence-absence model (generalized additive modelling, GAM; Hastie & Tibshirani 1990) was chosen to assess Cuvier's beaked whale habitat preferences as recommended by Praca *et al.* (2009) for data that are systematically recorded, collected within the same protocol and with an equal distribution effort across the investigated area. GAM was also chosen because it does not make any prior assumptions about the relationships and shape of the relationship between habitat features and species distribution (linear, sigmoidal *etc.*) and it is more flexible than other models (Guisan *et al.* 2002; Redfern *et al.* 2006; Hall *et al.* 2010).

Within each considered period, a subset of absence cells was randomly selected amongst those with highest

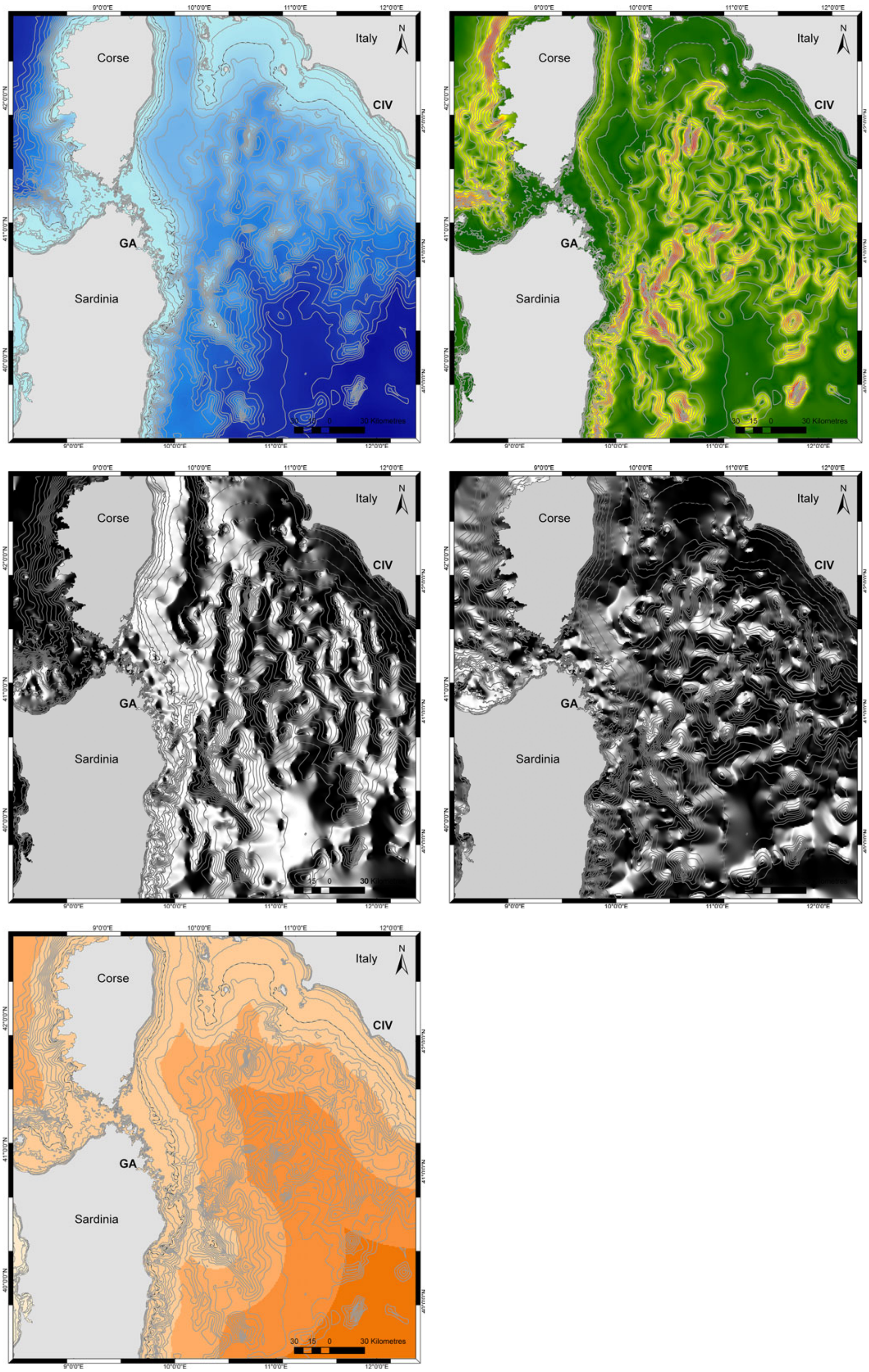

Fig. 2. Maps of the ecogeographical variables. Depth and Slope (top left and right), Aspect Easting and Northing (centre), Distance from 200 m isobath (down right). Dotted line identifies the 200 m isobath.

effort values along the transect, to prevent false absence bias, (>50 km, MacLeod *et al.* 2008; Arcangeli *et al.* 2013b). Moreover, to avoid bias because of a large number of cells with 'zero', a number of absence cells almost three times higher than the number of presence cells was selected for the analysis (Smith 2010). To check the representativeness of the selected cells we:

1 repeated the selection a number of times to check the consistency of the results;
2 checked for each parameter the similarity of data distribution of the all data and the subset with a Kolmogorov–Smirnov test;
3 performed the GAM analysis with a different number of selected cells to check the predictions coming from the different models.

Independency of the EGVs was tested before they were included in the analysis. The percentage of deviance explained and Akaike's information criterion (AIC) stepwise selection criteria were the main criteria used to test for the accuracy of the models.

The predictive abilities of the models were successively validated using an independent data set of Cuvier's beaked whale sightings and related survey effort that intersected the study area (surveys along the fixed line transects of Livorno-Golfo Aranci and Civitavecchia-Barcelona within the ISPRA monitoring network, Arcangeli *et al.* 2013a). In addition, we cross-validated the distributions predicted from each study period with data coming from the other period, in order to verify whether or not we obtained a better validation using contemporary data.

Model analysis and validation were performed using R 3.0.1 software (R Core Team 2013).

Results

Whale sighting data

The general results of the monitoring conducted during the two study periods are shown in Table 1. *Ziphius cavirostris* was recorded in each of the 8 years of the research, resulting in 3% of total cetacean sightings in the 1990s (n = 8) and 5% in the 2000s (n = 26).

Although all monitoring was conducted in conditions with a Beaufort scale of under 3, no detailed information on the sea state is available for the first investigated period. All Cuvier's beaked whale sightings during 2007–2010 occurred in Beaufort sea states of between 0 and 1. In 2011, three out of nine sightings were in Beaufort sea states equal to 2 and no sightings occurred in higher sea states.

SPUE showed different values, with a slight although not statistically significant increase during the latter survey period ($SPUE_{1990s} \pm SE = 0.043 \pm 0.02$; $SPUE_{2000s} \pm SE = 0.081 \pm 0.02$; Mann–Whitney test, $N_{1990s} = 90$, $N_{2000s} = 160$, $P > 0.05$).

Statistical comparison was performed within each research period to verify whether inter-annual variability occurred: in both the 1990s and 2000s no significant differences in SPUE between years were found (Mann–Whitney test, $P > 0.05$), indicating fairly consistent presence of the species in the study area.

The mean group size seen in the 1990s was 1.75 ± 0.16, slightly lower than in the 2000s (1.88 ± 0.24) but the difference was not statistically significant (Mann–Whitney test, $P > 0.05$). During the last research period, 81% of sightings consisted of groups of one or two individuals whereas in 2009 60% of recorded groups were composed of four or give animals. In 2010 groups of two or three animals were observed breaching.

Spatial distribution

The distribution of sightings was studied in the surveyed cells during the two research periods (Fig. 3) and kernel analysis was performed to identify the high sighting density areas (Fig. 4): in the 1990s two main areas were identified at 30–45 km away from the continental shelf whereas in the 2000s three different hot-spots were observed, only partially overlapping with the previously recognized areas as the sightings were more dispersed along the transect.

Habitat suitability analysis

The observed distribution of animals was investigated in relation to each variable in order to highlight habitat preferences. Mean depth values recorded in the sightings locations were similar during the two research periods, according to a bathymetric affinity for medium–high

Table 1. Whole dataset: study periods and general results of surveys along the fixed line transect in central Tyrrhenian Sea (Civitavecchia - Golfo Aranci, Italy).

Study period	Years	Season	Frequency of surveys	km of effort	No. of species	Total sight.	CBW sight.
1990s	1990–1992	June–Sept.	4–8 per month	16,750	7	344	8
2000s	2007–2011	June–Sept.	4–8 per month	28,874	8	640	26

CBW, Cuvier's beaked whale; sight., sightings; Total sight., all cetacean species sightings.

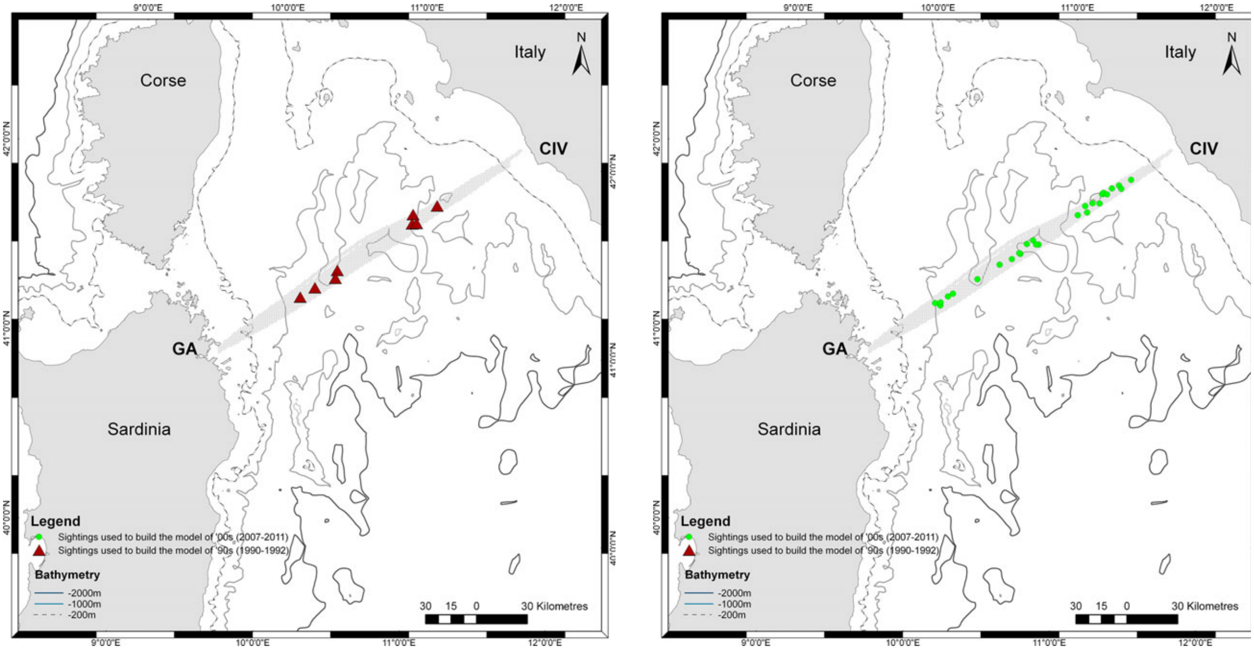

Fig. 3. Surveyed cells (in grey) and sighting locations for the 1990s (red triangles, left) and the 2000s (green dots, right).

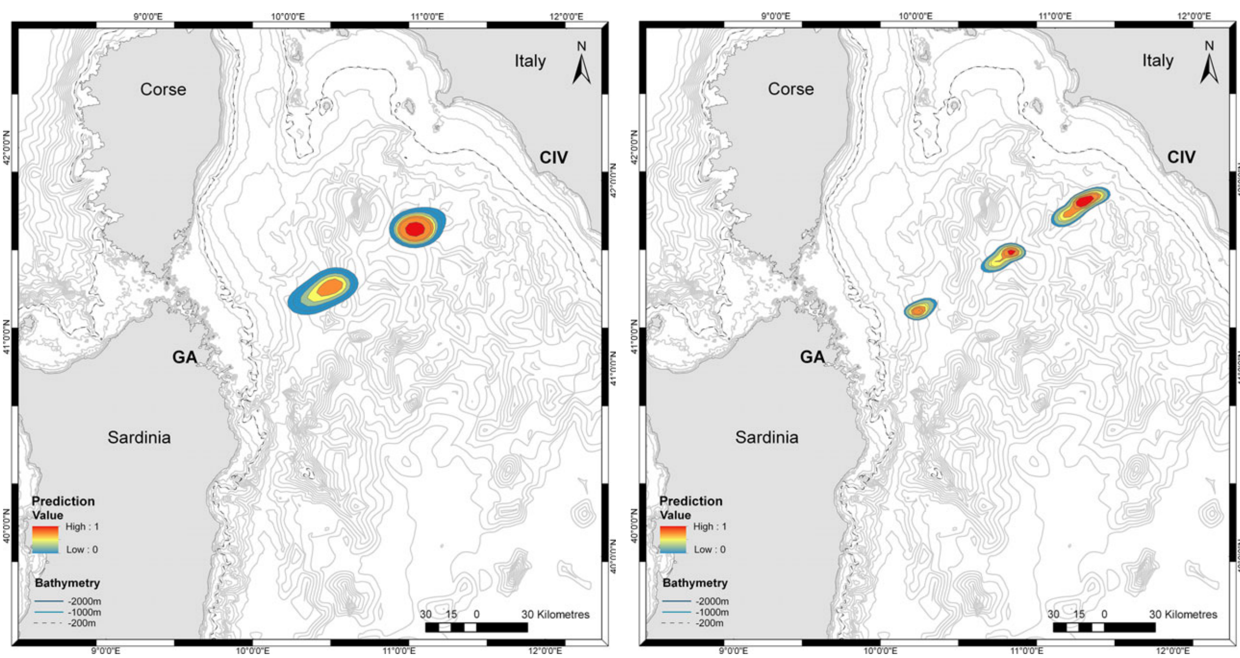

Fig. 4. Distribution of sightings in the 1990s (left) and in the 2000s (right) (Kernel parameters: adaptive Kernel; volume level = 0.70; smoothing factor, h = bcv2).

depths (mean 1990s = -1131 ± 75 m; mean 2000s = -989 ± 41 m). In the 2000s the distribution frequency of sightings differed significantly from the expected values (Chi-squared test, $P < 0.05$), with a peak for the 800–1000 m class, whereas in the 1990s two maximum, higher than the expected values, were recorded for the 1000–1200 m and 1200–1400 m classes (Fig. 5).

The distribution frequencies of sightings showed a marked difference between the two periods with respect to slope: mean slope was higher in the 1990s (77.35 ± 16.4 m·km^{-1})

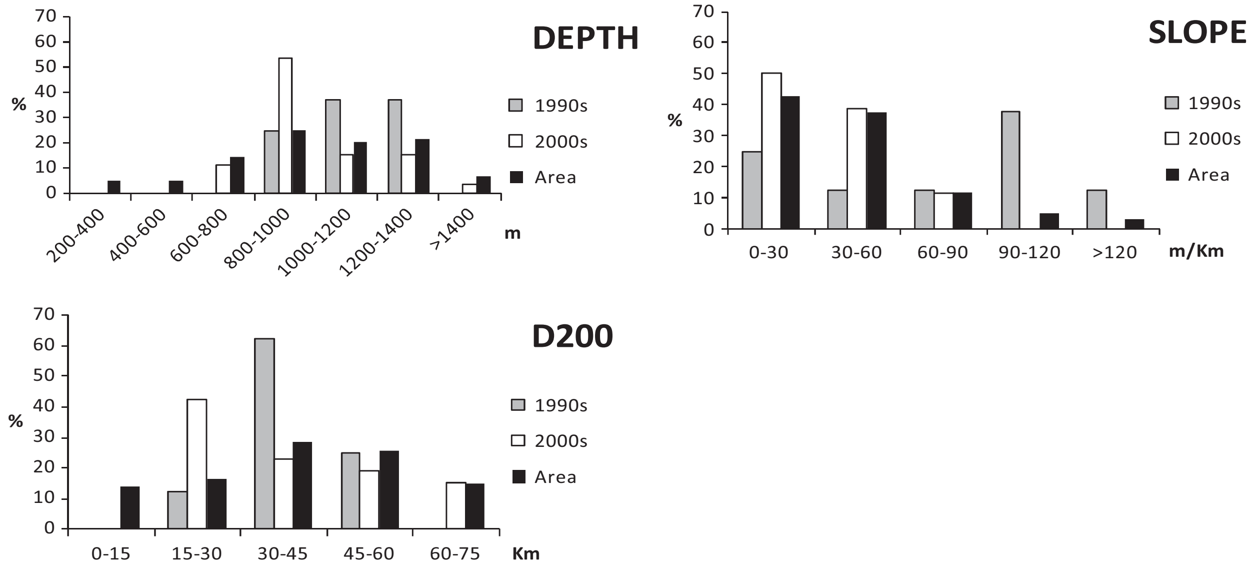

Fig. 5. Percentage distribution of CBW sighting locations in the two study periods and monitored points along the transect for Depth, Slope, Distance from the 200 m isobath.

than in the 2000s (30.04 ± 3.5 $m \cdot km^{-1}$) and, whereas in the latter period the animals' distribution appeared consistent with the frequency of values in the study area, in the 1990s Cuvier's beaked whale sightings concentrated with more than 40% of cases in the highest classes (90–120 $m \cdot km^{-1}$ class), much higher than the expected frequency (Chi-squared test, $P < 0.05$; Fig. 5).

Cuvier's beaked whale observations occurred at different ranges of distances from the 200-m isobath: in the 1990s a higher percentage of observations than expected was recorded in the 30–45 km class, whereas in the 2000s a more variable frequency distribution was observed, with a higher percentage than expected for the class 15–30 km. The absolute minimum and maximum distances were both recorded in the 2000s (15 and 70 km), which is consistent with the greater distribution of sightings found in the kernel analysis (Figs 4 and 5).

Pooling the effects of all variables together, the results of the GAM analyses performed on the 1990s and 2000s data sets separately (Table 2) indicated that in the 1990s, only slope had a slight influence on beaked whale presence ($P < 0.1$), whereas in the 2000s, both D200 and Aspect E strongly influenced habitat selection ($P < 0.001$ and <0.05, respectively).

Based on the percentage of deviance explained ($\text{Dev.Expl.}_{1990s} = 49.7\%$; $\text{Dev.Expl.}_{2000s} = 29.7\%$), AIC and the results check, both models account for a suitable predictive ability.

Plots of EGVs illustrated the non-linear relationship between species distribution and habitat features (*e.g.* distance from the 200-m isobath) and the differences in this relationship between the two investigated periods (Fig. 6). The revised prediction models based on the 1990s and 2000s data showed that changes occurred in the predicted most suitable habitat between the two investigated periods (Fig. 7).

A positive relationship was found between the probability of occurrence of Cuvier's beaked whale predicted from the model and the presence or absence of the species in the independent data set used for validation (Fig. 8a and b). The relationship was statistically significant only for the prediction based on the 2000s data ($P = 0.0064$). By contrast, no relationship was found between the probability of occurrence of Cuvier's beaked

Table 2. Generalized additive modelling results.

study period	intercept	D200	slope	depth	aspectN	aspectE	dev. expl. (%)	AIC
1990s (n = 38)	•		•				49.7	34.4336
2000s (n = 126)	***	**				*	29.7	108.8567

AIC, Akaike information criterion; aspectN, aspect North; aspectE, aspect East; D200, distance from 200-m contour; dev.expl., explained deviation; n, number of sightings.

Significance codes: P = 0 '***' P = 0.001 '**' P = 0.01 '*' P = 0.05 '•' P = 0.1 ' ' P = 1.

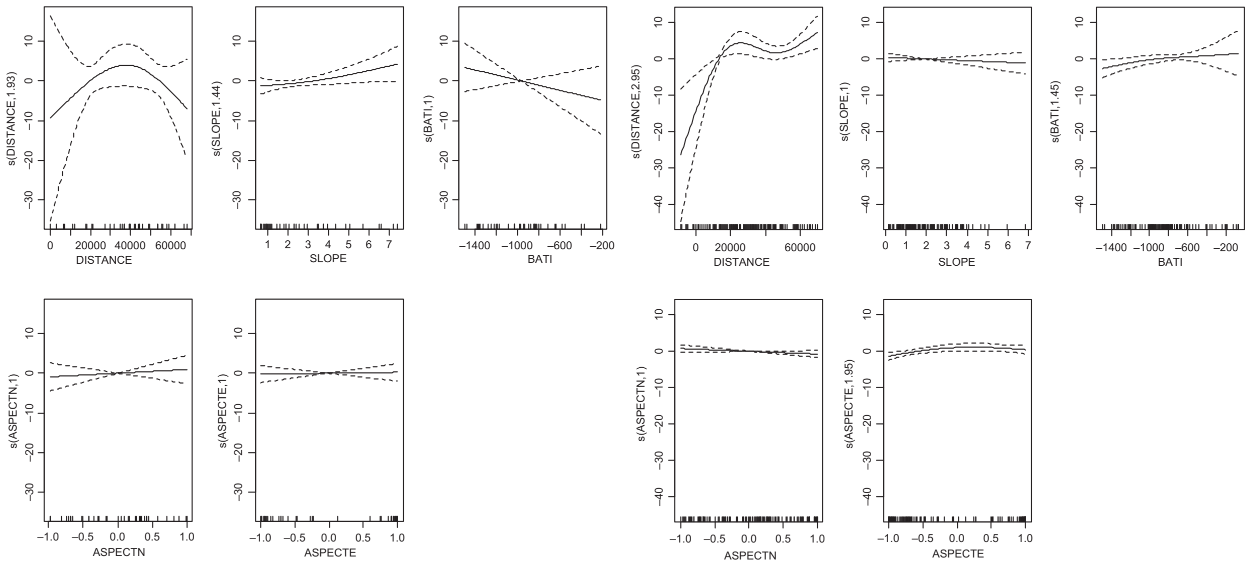

Fig. 6. Plots of EGVs for the species distribution model based on 1990s data (left) and 2000s data (right).

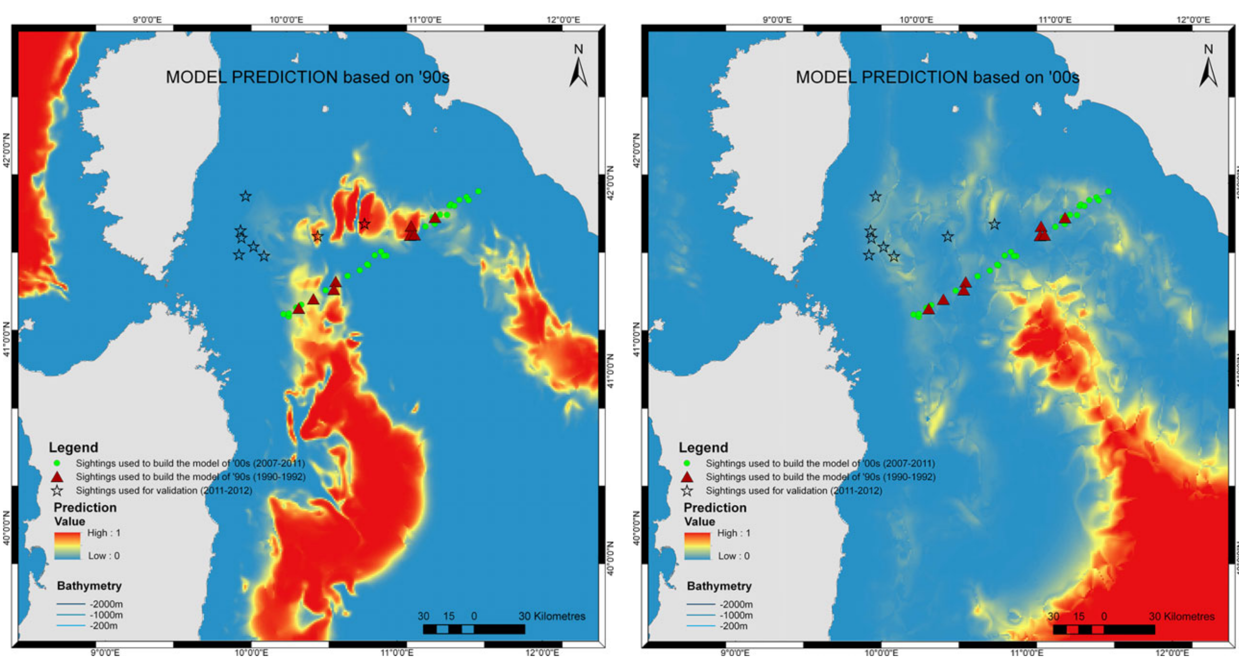

Fig. 7. Model predictions based on the 1990s data (left) and on the 2000s data (right). Scale bar from low predictive values (blue) to high predictive values (red). CBW sighting positions are indicated as red triangles (1990s), green dots (2000s) and stars (sightings used for the validation).

whale predicted from the model based on the 2000s data and the presence or absence of Cuvier's beaked whale in the 1990s and *vice versa* (Fig. 8c and d; $P > 0.05$).

Based on the high percentage of deviance explained (49.7%), the model built on the 1990s data seemed to work well, despite the small number of Cuvier's beaked whale sightings and although no independent data set was available for that period. The 2000s data performed a suitable model, which was also validated against an independent data set. The results also showed that the 2000s

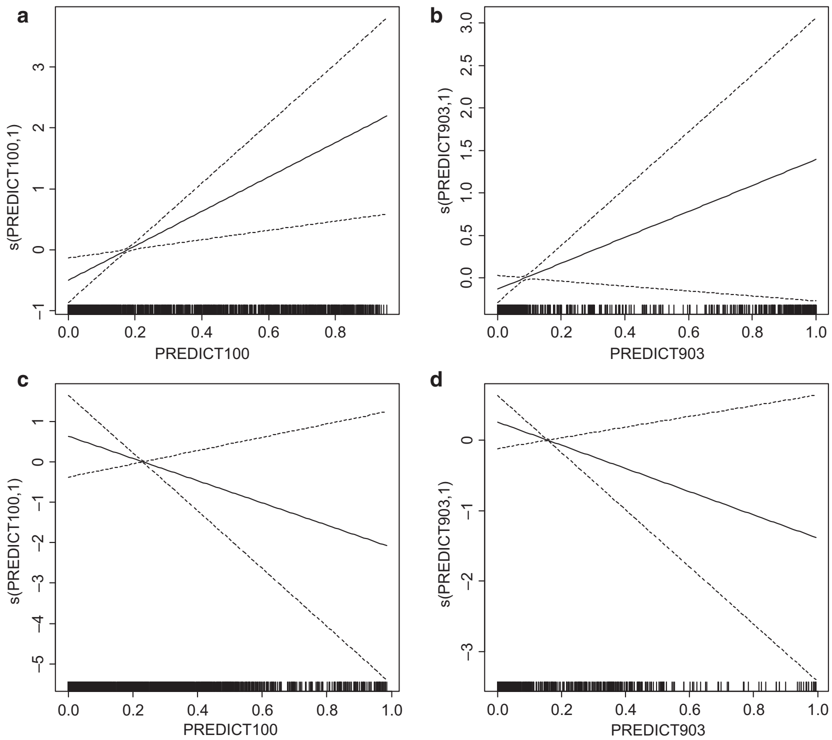

Fig. 8. Validation plots. Prediction based on 2000s data *versus* independent dataset (P-value = 0.0064) (a), prediction based on 1990s data *versus* independent dataset (P-value = 0.095) (b), prediction based on 2000s data *versus* 1990s data (P-value = 0.17) (c), prediction based on 1990s data *versus* 2000s data (P-value = 0.12) (d).

data did not fit the predicted habitat based on the 1990s data and, similarly, the predicted habitat based on the 2000s data did not fit the 1990s data.

Discussion

This study confirms the presence, amongst other cetaceans, of Cuvier's beaked whales in the Central Tyrrhenian Sea. The species was recorded over a 20-year time span and the constant presence during the investigated periods (1990–1992, 2007–2011) gives an indication of the long-term site fidelity of the species in the area, as reported for other regions (cf. Allen *et al.* 2012).

The percentage of Cuvier's beaked whale sightings with respect to the total sightings of all cetacean species was higher during the latter study period (2000s) and, although not statistically significant, the sighting rate (SPUE) was almost twice than that of the 1990s. Comparing our results with those obtained for CBW in other research studies in the Tyrrhenian Sea, Gannier & Epinat (2008) obtained a SPUE similar to the one of our last period (0.081 for the Southern Tyrrhenian; 0.102 for Northern Tyrrhenian), pooling data from 1996 and 2007 in different seasons. Marini *et al.* (1996), within the same research of the present study in the 1990s, but combining data from all seasons, reported a lower SPUE of 0.02. In the Ligurian Sea, Gannier & Epinat (2008) reported a much lower SPUE (0.013) whereas Moulins *et al.* (2007) reported higher sighting rates, in the range of 0.1–0.6 sightings/100 km, for optimal slopes, surveying Cuvier's beaked whale's most favourable habitat with a sampling design optimized for the species.

Looking at the effect of weather conditions on the detectability of the species, Marini *et al.* (1992) reported that all sightings in the 1990s period were recorded in conditions with a Beaufort scale of <2. In the 2000s all sightings were also recorded in conditions with a Beaufort scale of <2 and no sightings ever occurred in a higher sea state, confirming how the detectability of this species changes with weather conditions (Barlow *et al.* 2006).

Mean group sizes in the 1990s and in the 2000s were consistent with the one observed for the whole Mediterranean basin (1.80 $\pm$ 1.18, Gannier & Epinat 2008).

The distribution of sightings illustrated that a change occurred during the two investigated periods, with wider range of habitat and different hot-spots occupied by Cuvier's beaked whales during the latter period compared with the 1990s. According to the literature, beaked whales are distributed in medium–deep waters and steep slopes, albeit within a large range of habitats, all over the world (MacLeod *et al.* 2006). The geographical complexity of the Tyrrhenian Sea offers a variety of suitable areas for the species; the fine scale of the present study allowed us to identify habitat use over a long time span and analyse preferences in relation to different physiographical features. Mean depth was constant during the two research periods (around -1000 m): both studies considered for comparison (Moulins *et al.* 2007; Gannier & Epinat 2008) reported greater values of depth (-1369 ± 498 m and −1544 ± 489 m, respectively). In the GAM analyses, depth was not a significant variable, confirming that other features defined habitat suitability for Cuvier's beaked whale in this complex area. Slope classes were used differently during the two periods, much steep during the 1990s than in the 2000s. Habitat selection seemed to be determined by the highest classes of slope exclusively in the 1990s, resulting the only significant variable in the GAM analysis. This feature was also found to discriminate the habitat suitability in other models for Cuvier's beaked whale (Ferguson *et al.* 2006; Praca *et al.* 2009; Smith 2010) although the presence of the species in different slope classes was recently revealed in the Ligurian Sea, from where Tepsich *et al.* (2014) reported the existence of a second type of habitat not closely related to steep canyon axes. Distance from the 200-m isobath was instead the most significant variable in the 2000s in the present study, along with the aspect easting. During this period, a variable distribution of distance was observed, within 15–70 km from the continental shelf, in line with the broader spatial range of sightings.

Both suitability models for the 1990s and 2000s data appeared to work for each individual time period; the best predictive power obtained for the model of the 1990s was probably because of the lower number of sightings distributed in relatively restricted areas. Differences were evident in the areas of greatest habitat suitability predicted by the two models. Therefore, both the raw data and predicted distributions showed marked differences in the presence of Cuvier's beaked whale in relation to habitat features between the 1990s and the 2000s. Given the consistency of the sampling design of this study, this difference cannot be the result of different spatial or seasonal coverage or by low temporal resolution of the surveys, which could have made the results influenced by causality, especially for a rare and elusive species such as Cuvier's beaked whale. Therefore, from a methodological point of view, the results indicate that great care must be taken when pooling together data over a long period of time or when transferring the predictions of models from one time period to another.

Fluctuations in Cuvier's beaked whale distribution were also identified in the Bay of Biscay by Smith (2010) although in this area the species always selected the same habitat characteristics. By contrast, in our study we found evidence for changes in Cuvier's beaked whale habitat selection over time.

Many factors could have induced these changes. The results highlighted the higher percentage of Cuvier's beaked whale in species composition, the higher sighting rate and a wider distribution of Cuvier's beaked whale during the latest period compared with the 1990s. These features point out a possible increase in the Cuvier's beaked whale population size in the study area between the two research periods. The presence of more animals in the area would lead to extend the distribution of the species towards new available habitats and, in fact, we noticed a broader range of environmental features in the 2000s, identifying wider suitable habitats in the model.

The driving forces behind these changes remain unclear. However, two possibilities exist that would be worthy of further investigation. First, climate-induced variations in prey distribution and marine circulation could have affected Cuvier's beaked whale distribution (cf. MacLeod 2009). In this respect, increasing temperatures and salinities have been registered in the Central Tyrrhenian Sea since the late 1980s (Gasparini *et al.* 2005; Schröder *et al.* 2006) and were indicated as possible signs of ecological modifications that could have driven the summer increase and the changes in habitat use of fin whales in the area in recent years (Arcangeli *et al.* 2014). Secondly, anthropogenic activities that mostly affect deep-diving species (nautical traffic, geological investigation or military exercise) could also have influenced Cuvier's beaked whale presence in the study area. The development of the maritime transport network in the area in the last 20 years has been documented (Bultrini *et al.* 2009), as the growth of the main port of the Central Tyrrhenian Sea (Civitavecchia), making it plausible that the marine traffic in the area has increased.

Regardless of the possible mechanisms for the observed changes in spatial distribution, the long-term site fidelity and the relatively high, increasing, presence (as well as the year-round presence, Marini *et al.* 1996) of Cuvier's beaked whale in the Central Tyrrhenian Sea highlight the importance of this marine region for the species; in the meantime, these results ask for further in-depth investigation to understand if the recorded changes in habitat use can be linked to a population increase or to a negative response to pressures that could force the species to move towards different habitats.

Conservation implications

In terms of conservation of the Cuvier's beaked whale, our results appear to expand the definition of what is considered to be suitable habitat for this species and indicate that the temporal scale of the analysis can considerably affect the interpretation of results from beaked whale habitat studies. Thus, great care must be taken when working with historical Cuvier's beaked whale data sets, especially those collected over relatively short time periods and when using them as the basis for current or future management decisions based on spatial distributions. Any management plan for this species needs to be assessed at a small scale (Allen *et al.* 2012) and be ready to be adapted over time.

This study confirms the importance of long-term and continuous monitoring, which can not only increase the ecological understanding of cetacean species but may also be able to identify shifts in patterns of habitat use and therefore in spatial distributions. The sampling design utilized in this study appears to be able in delivering information at fine scale, suitable to be extended also outside the surveyed transect and to be a reliable survey programme to improve knowledge about distribution, relative abundance, trend and habitat use of the species over time. Indeed, the ability to detect and keep track of any changes occurring in these factors is important to predicting the responses of cetaceans to future environmental changes and to figure out how the ranges of species might change. This is a fundamental step for progressing dynamic conservation management approaches in changing environment scenarios.

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