Distribution and relative abundance of striped dolphins, and distribution of sperm whales in the Ligurian Sea cetacean sanctuary: results from a collaboration using acoustic monitoring techniques

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ABSTRACT

The distribution and relative abundance of groups of striped dolphins (*Stenella coeruleoalba*) in the Ligurian Sea cetacean sanctuary, based on acoustic surveys carried out in the summers of 1994-1996, is presented. Abundance indices based on acoustic detections were adjusted for covariates likely to influence the detectability of dolphin vocalisations, such as wind speed, background noise and sea state. Dolphin vocalisation rates were shown to vary diurnally, being higher at night, and this effect was also modelled and removed. Results showed that dolphin groups were fairly evenly distributed throughout the sanctuary, but they were more abundant in offshore waters, peaking at water depths between 2,000-2,500m. Preliminary sightings results also indicated larger-sized groups in offshore regions. Relative abundance does not appear to vary significantly over the summer months. Sperm whales (*Physeter macrocephalus*) were detected at 4% of monitoring stations, representing at least 61 different group encounters. Although not common, they appeared to be widely distributed in deep water throughout the study area.

KEYWORDS: MEDITERRANEAN; SANCTUARIES; INDEX OF ABUNDANCE; MONITORING; SURVEY-ACOUSTIC; OCEANOGRAPHY; ACOUSTICS

INTRODUCTION

On 22 March 1993, 96,000km^2 of the northwestern Mediterranean Sea, extending between the French and Italian Riviera, Corsica and Northern Sardinia, and centred on the Ligurian Sea, was declared a sanctuary for the protection of whales and dolphins by Ministers from Italy, Monaco and France. The sanctuary finally came into existence on 25 November 1999, when the formal Agreement was signed by those countries. In undertaking this action, these Governments recognised that this was a particularly important area of distribution for cetaceans, which are under threat in many parts of the Mediterranean. Article 9 of the Declaration states that the signatories should encourage and stimulate research programmes aimed at monitoring the effect of the measures implemented in the framework of the Declaration.

In response to this, scientific teams from the International Fund for Animal Welfare (IFAW), the Tethys Research Institute (TRI) and Group de Recherche sur les Cétacés (GREC) established a collaborative programme to investigate ways of monitoring cetacean populations in the new sanctuary that are compatible with their existing cetacean research in the area. This paper presents information on the relative abundance of striped dolphins (*Stenella coeruleoalba*) in the Ligurian Sea, and the effect of certain environmental variables on their distribution, based on a cooperative acoustic survey. The intention of this work was to provide information on distribution and population trends that will be useful in managing the sanctuary, and results that would be complementary to line transect surveys. Some less detailed results of sperm whale (*Physeter macrocephalus*) detections are also presented.

Striped dolphins are by far the most commonly encountered cetacean in the Ligurian Sea. They face a number of threats in the Mediterranean, including entanglement in driftnets, overfishing and pollution (Aguilar, 2000). The striped dolphin is the cetacean species that suffers the largest mortality in driftnets within the Mediterranean (Di Natale and Notarbartolo di Sciara, 1994). Although the exact size of the striped dolphin bycatch is not known, the level of mortality exceeds ‘the safe take limit’ of 2% for the western Mediterranean population, and is unsustainable (IWC, 1994).

Between 1990 and 1992 a massive die-off of striped dolphins occurred in the Mediterranean Sea, spreading eastward from the Catalonian coasts to the Aegean Sea. This was due to an outbreak of a morbillivirus infection (Aguilar and Raga, 1993). It has been suggested that high PCB concentrations found in Mediterranean striped dolphins and other Mediterranean cetaceans may have depressed the dolphin’s immune system, contributing to the morbillivirus outbreak (Kannan *et al.*, 1993).

Previous line transect studies conducted during the summer months have indicated population sizes of 117,880 for the entire western Mediterranean (Forcada *et al.*, 1994), with an estimate of 25,614 individuals for the Corsican-Ligurian Basin in 1992 (Forcada *et al.*, 1995). Gannier (1998b) obtained a similar estimate for the sanctuary area based on a smaller scale summer survey in

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1996. On the basis of both genetic and morphometric data, Archer (1996) concluded that populations of striped dolphins in the Mediterranean are isolated from those in the North Atlantic.

The teams involved in this research decided to experiment with passive acoustic techniques for this study because, provided that standardised techniques and equipment are used, these should allow several independent research groups, operating from different vessels of similar type, to collect consistent data. In addition, acoustic methods would allow data to be collected during periods when the teams' primary cetacean research activities were not possible (for example, at night, during passage and when weather conditions were poor).

The range at which cetacean vocalisations can be detected will be affected by a variety of factors including the levels of background noise in masking frequency bands, and the propagation properties of the medium. In addition, some behavioural variation may be expected in the vocalisation rates of the animals. During a survey, variations in these conditions arise with or without a random survey design, leading to imprecision and possible bias. The methods used here attempt to make adjustments for some of the varying conditions that influence detectability during surveys (Robel *et al.*, 1969) using generalised linear models (e.g. Nicholls, 1989). After this adjustment, the effects of other factors on dolphin distribution, such as bathymetric variables, can be better examined.

METHODS

Survey methods

Surveys were conducted over three summers in 1994-1996, from motor sailing vessels, ranging in size from 12-20m, towing identical hydrophone arrays on 100m of cable. Each array consisted of two *Benthos* AQ4 hydrophones, each with a *Magrec* preamplifier, mounted 3m apart in the centre of a 10m long, 25mm diameter, oil-filled polythene tube. The preamplifiers were designed with high-pass filters, which suppressed noise below 200Hz by 6dB per octave. This reduced the levels of lower frequency background noise, while still allowing effective monitoring of odontocete vocalisations.

Survey tracks were chosen to provide a more-or-less even coverage of the area, although sometimes tracks were dictated by logistical considerations, e.g. for the survey vessel to make a passage to a port. Knowledge of, or assumptions about, cetacean distributions were not allowed to influence the designation of survey tracks. Survey effort was suspended if the vessel diverted to close with cetaceans encountered during the day.

While vessels were conducting acoustic surveys, hydrophones were monitored and one-minute recordings were made at regular intervals. If the boat was sailing fast it would be slowed down at monitoring stations, and if it was motoring, the engine would be put out of gear to facilitate efficient acoustic detection. On the IFAW research vessel, *Song of the Whale*, hydrophones were monitored every 15 minutes. Such frequent monitoring was not compatible with the work routine on other vessels. On the Tethys vessel, *Gemini Lab*, hydrophones were monitored every 20 minutes, while on the GREC vessel a 20-25 minute schedule was adopted.

Monitoring personnel were required to score the strength, on a scale between 0 (not heard) and 5 (very loud), of dolphin clicks or whistles, and sperm whale clicks. They also scored the strength of background water noise, background ship noise, noise generated by their own vessel as well as recording their own vessel's speed and whether or not its engine was on. All monitoring personnel listened to a training tape that gave examples of different types and strengths of vocalisations and background noises. Field workers were also encouraged to compare how they scored particular sessions throughout the season to improve consistency.

The location of each monitoring station was recorded and environmental conditions were noted each hour. Where possible, data were entered directly into the *LOGGER* data collection program, in other cases records were made on pre-prepared sheets and transcribed to computer files later.

On one occasion, an experiment was undertaken to assess the range over which dolphins could be heard with the hydrophone equipment used during these surveys. A field worker was dropped off in a dinghy with a tape recorder and hydrophone equipment similar to that used during this study. The main research vessel then followed a group of dolphins as they swam away, while the fieldworker in the dinghy listened and made a continuous tape recording. The range between the main research vessel, which was close to the dolphins and the dinghy, was determined by using the vessel's radar.

Data used

The analysis described here uses only the data recorded in the field; no analysis of the tape recordings made at listening stations has been carried out.

The response data used for analysis of dolphin distribution were binary outcomes denoting presence or absence of dolphin groups at listening stations, where independent groups were determined *post hoc* as explained below. Typically, dolphins would be heard at several consecutive stations, and it seemed likely that the boat was within acoustic range of the same dolphin group during such periods. To obtain data on independent encounters with groups, consecutive positive detections were considered to be part of the same group encounter until no dolphins had been detected for at least 40 minutes. The time, location and associated covariates of each group encounter were taken at the midpoint of these strings of detections. Forty minutes was chosen as the critical time interval because, with a survey speed of 5 knots, a vessel would have travelled over 1.5 miles in that time, which was greater than the acoustic range observed for dolphins in this area during this work.

As with dolphin detections, strings of positive stations were considered to be encounters with a single sperm whale group. Detections were considered to be from a new group when no sperm whales had been detected for at least one hour. An hour was chosen as the time interval for determining a new encounter based on knowledge of sperm whale acoustic behaviour. Feeding sperm whales usually show a predictable pattern of behaviour. They make long dives that can extend for 30-50 minutes or more, interspersed by periods of 8-12 minutes at the surface (Gordon and Steiner, 1992; Watkins *et al.*, 1999). During dives, sperm whales click almost continuously, with only short pauses of less than a minute. Clicking usually starts within a few minutes of leaving the surface and ceases several minutes before whales reach the surface. While at the surface they are usually silent (Gordon *et al.*, 1992). Thus, typical silent periods for diving whales are of the order of 20 minutes or less, and if sperm whales are heard during a survey after an hour or more with no detections, it is likely that a new group has been encountered.

Audibility covariates
At each listening station a set of 'audibility' covariates relating to detectability were collected. These are shown in Table 1.

Table 1

Covariates recorded at listening stations, their type (number of levels given in parentheses for discrete variables) and their means of assessment.

Variable	Variable type	Method of assessment
wind speed	continuous	anemometer
boat speed	continuous	speedometer
engine state (on/off)	discrete (0-1)	switch
sea-state	discrete (0-10)	visual
time-of-day	continuous	GPS
self-noise	discrete (0-5)	aural
water-noise	discrete (0-5)	aural
ship-noise	discrete (0-5)	aural

Those variables not assessed aurally were considered important *a priori* because they were unambiguous and could be reliably measured. Sea state and wind speed are well known to affect ambient noise conditions in the ocean (Urick, 1983). If the research boat's engine was on it would contribute to background masking noise, and would also be likely to be the primary means by which dolphins would be alerted to the presence of the boat. It was expected that dolphin vocalisation rates would vary diurnally, based on previous experience (e.g. Gordon, 1987).

The variables assessed aurally are more subjective (more inter- and intra-observer variation) than other data and the masking effect of these noises will depend on a number of factors, including their spectra, which were not measured.

Environmental covariates
Two 'environmental' variables expected to relate to the distribution of dolphins were acquired post-survey for each listening station: water depth and angle of bottom slope, calculated by interpolation between the closest contours. These calculations were performed using routines in Atlas GIS and specially written MATLAB programs. Data on coastlines and depth contours were exported from the GEBCO 97 Digital Atlas (BODC, Proudman Laboratory, Birkenhead, Merseyside, L43 7RA, UK).

Modelling methods
The relationship between presence/absence of dolphin groups and other predictive variables was determined using generalised linear models (GLMs). These are appropriate for data with a combination of categorical and continuous predictor variables. The link function was a logit, suitable for binomial responses. This type of model is asymptotic so that fitted values cannot fall outside the interval [0,1], and uses maximum likelihood estimators appropriate for binomially distributed variables (McCullagh and Nelder, 1983).

The GLMs in the present study were of the form:

$$\text{logit}\,(p_i) = \text{intercept} + \alpha_1 x_{i1} + \ldots + \alpha_n x_{in} + ß_1 y_{i1} + \ldots + ß_m y_{im} + \gamma_1 \sin(\omega.t_i) + \gamma_2 \cos(\omega.t_i)$$

where, for listening station i:

p_i is the regression estimate of the detection rate;
α_j is the coefficient of discrete term x_{ij} (e.g. sea state) with $j = 1,\ldots,n$;
$ß_k$ is the coefficient of continuous term y_{ik} (e.g. wind speed or depth) with $k = 1,\ldots,m$;
γ_1 and γ_2 are the coefficients of the two temporal terms, and t_i the time-of-day.

$\gamma_1\sin(\omega t) + \gamma_2\cos(\omega t)$ represents the temporal variation as a phased sinusoid, using the relationship:

$$\gamma_1.\sin(\omega t) + \gamma_2.\cos(\omega t) = \gamma_3.\sin(\omega t + \phi)$$

where ϕ is the phase constant, ω the angular frequency, and t_1, t_2 and t_3 are amplitude terms.

Models examined included hierarchical subsets of the above terms. Two models were compared by their change in 'deviance' (twice the log likelihood ratio). The degree of improvement from the introduction of new parameters was assessed, and a superior model selected. Specifically, the reductions in deviance brought about firstly by the audibility variables, and secondly by other environmental variables after adjustment for these audibility variables, were examined. This analysis used the 'logistic regression' procedure in SPSS 7.0 (Norušis, 1990).

In the model selection of the audibility variables, those covariates recorded by non-aural means (Table 1) were included by default. The aurally-assessed covariates were considered less reliable, and for this reason, these covariates were included in the model by forward stepwise selection. Some of the audibility predictor variables are highly correlated, for example, wind-speed and sea state. One potential effect of this collinearity is to give misleading significance values; however, optimum model-selection was not a prime concern. The parameter values of the selected model were examined and found to be of sensible magnitude and sign.

In some cases, the teams collected and measured covariates differently and the scoring of the more subjective factors is also likely to be more consistent within a single group's data (because observers compared their rating systems) than between them. For these reasons, the effects of covariates on detection probability were modelled separately for each organisation's dataset.

Relative abundance of striped dolphins
For each listening station *i*, we have:

d_i a binary response indicating presence/absence of a dolphin group.
p_i an estimate, provided by the GLM, for the expected probability of detecting dolphin groups given the audibility conditions and time-of-day at the survey station.

To examine geographical distributions, data were assigned to cells in a grid comprised of 25 n.mile squares. For each sub-area *j*, there is a set of listening stations $\mathbf{i}_j$ with associated response data $\mathbf{d}_j$ and predictor data $\mathbf{p}_j$. Our estimate of relative abundance for area *j* is $\bar{\mathbf{r}}_j = \bar{\mathbf{d}}_j/\bar{\mathbf{p}}_j$.

If we assume that the audibility covariates affect detectability independently of the environmental covariates (only the latter being causally related to the underlying distribution of the animals), then adjusting for audibility conditions should give reduced bias and improved precision for relative abundance.

Group sizes from sightings were compared between two bathymetric regions: the area of water of depth greater than 2,000m was designated 'offshore', and the area of shallower water 'onshore'. The 2,000m contour was chosen as a convenient but arbitrary boundary because approximately half the stations were in each of the two areas.

Relative abundance of sperm whales

The total number of sperm whale detections was too small to allow a GLM approach to investigate factors affecting sperm whale audibility and distribution (but see Gordon *et al.*, 1998, for an example of this method applied to sperm whales for a dataset with more acoustic detections). Here, only general data on sperm whale detections are presented to provide a qualitative impression of distribution and abundance.

RESULTS

During the period of this study, virtually all of the visual encounters of dolphin groups by all three research teams were of striped dolphins. For example, during its 1994 season *Song of the Whale* logged 100 encounters with striped dolphins and only single encounters with bottlenose dolphins (*Tursiops truncatus*), Risso's dolphins (*Grampus griseus*) and pilot whales (*Globicephala melas*). The vocalisations of Risso's dolphins and pilot whales are rather dissimilar to those of striped dolphins. Examples of both species were provided on the training tape and it is likely that they would have been distinguished by monitoring personnel in the field. However, even if they were not, the sightings records suggest that they would have made an insignificant contribution to the overall dataset and it seems reasonable to consider that the vast majority of acoustic encounters were with striped dolphins.

A total of 5,428 acoustic monitoring stations were completed. Table 2 shows how this effort was distributed between different research teams and over time, while Figs 1a and 1b show the geographic distributions of survey effort within the sanctuary area. Most of the area of the sanctuary was well covered by the survey. Some areas, such as the corridor between San Remo in Italy and Calvi in northern Corsica, received particularly high coverage.

Table 2

Distribution of monitoring effort: number of monitoring stations by year and by organisation.

Year	IFAW	TETHYS	GREC	Total
1994	2,696	739	-	3,435
1995	-	-	422	422
1996	-	696	875	1,571
Total	2,696	1,435	1,297	5,428

Effects of audibility covariates

The effects of the audibility covariates were generally as expected. For example, detection rate fell with increasing wind speed, sea state and levels of background noise. Fig. 2 shows examples for the IFAW *Song of the Whale* data. The model chi-square statistics for the audibility covariates without time-of-day are shown in Table 3. In this table, the chi-square value approximates the reduction in deviance of a model with the predictor variable(s) included compared to a model without. The change in deviance is highly significant for both IFAW and TETHYS data (indicating rejection of the

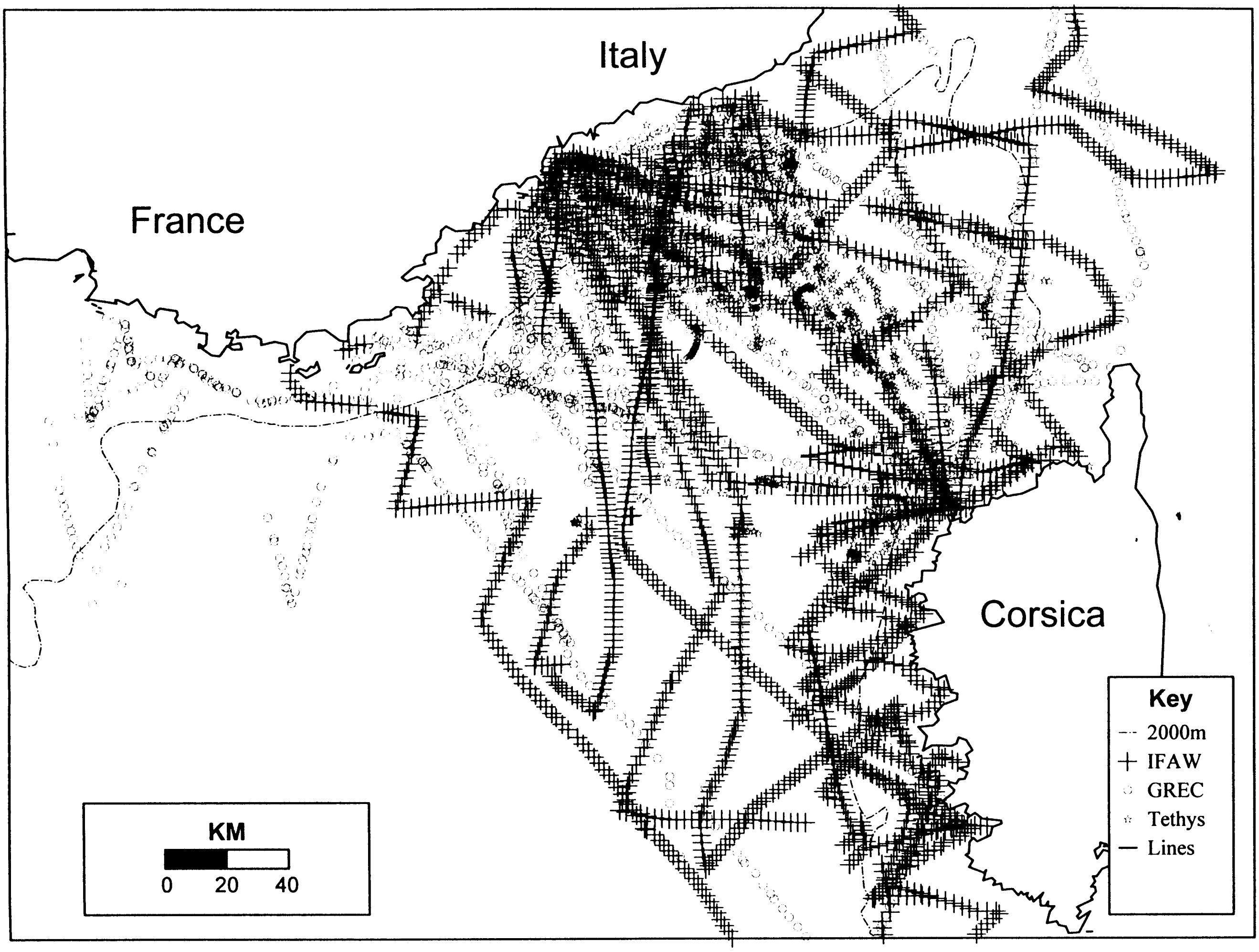

Fig. 1a. Distribution of acoustic stations monitored by each organisation.

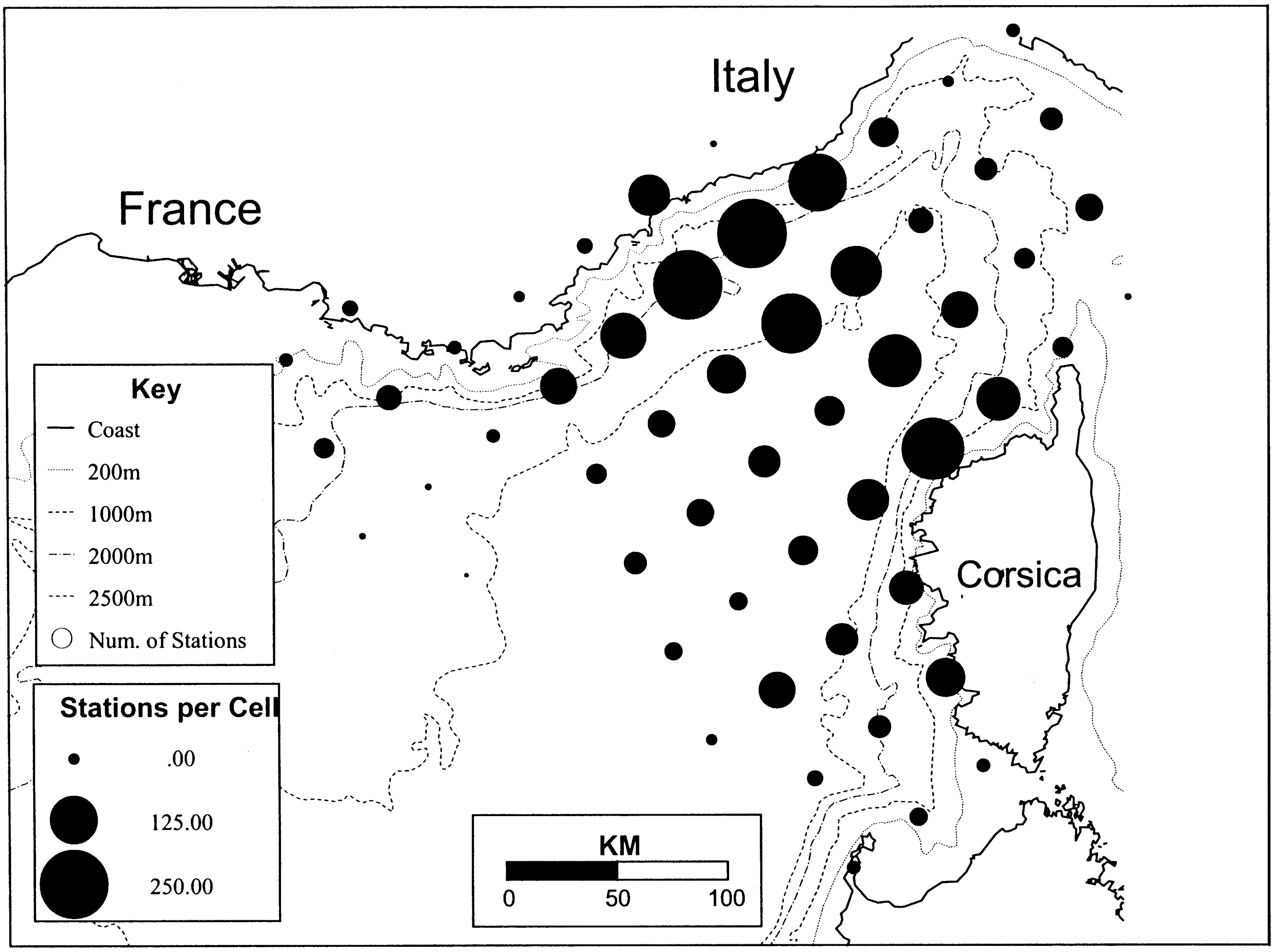

Fig. 1b. Distribution of acoustic monitoring effort in a 25 n.mile square grid.

null hypothesis that all model coefficients are zero); GREC did not record this information using the standard procedure.

Initially, the audibility covariates were incorporated into models without time-of-day. A marked diurnal variation in detection rate, which seems to represent a diurnal change in dolphin vocal behaviour, was evident (Fig. 3). The introduction of temporal terms to the model was significant for all three organisations' data (Table 3).

Distribution and relative abundance of striped dolphins

Seasonal and spatial variation was investigated, after adjustment for audibility covariates. Geographical distribution of adjusted detection rates is indicated in Fig. 4. Adjustments have been made for all audibility and temporal covariates. (These maps were plotted and compared for unadjusted detection rates, and showed a somewhat similar picture.) Dolphins are distributed throughout the sanctuary, but seem to be more abundant in offshore regions and in the northern part of the Ligurian Sea.

The relationship between detection rate and certain geographic variables (range to coast, depth and bathymetric slope) were investigated more thoroughly for the IFAW data, which was the largest of the three datasets. Fig. 5 shows detection rate against depth. A marked increase in detection rates, peaking in the 2,000 and 2,500m depth zone, is evident. Table 4 shows statistical results for models with linear and quadratic terms. Of these three, the depth model is the best predictor of detection rate. As discussed above, sequential acoustic detections are considered as encounters with single dolphin schools. Dolphin density will be a product of group density and group size. Although group size could not be assessed acoustically with the techniques used in these surveys, some visual data on group size were collected. The visually estimated sizes of 161 groups of striped dolphins (96 encountered by IFAW and 65 by GREC) were compared for groups encountered in 'offshore' and 'inshore' waters. Table 5 summarises these data. Group size was significantly higher in offshore waters (Mann-Whitney U test, $P = 0.042$). However, we do not feel that group sizes were estimated sufficiently accurately during encounters for these data to be used to estimate the relative density of individuals. Despite this, it should be noted that if group sizes are larger offshore, as these data indicate, this will enhance the observed pattern of higher detection rates of groups in offshore waters.

Distribution of sperm whales

Sperm whales were detected at 220 of 5,428 stations (4%) and these represented at least 61 separate group encounters. The number of whales heard at each station ranged from 1-3 with an overall mean of 1.5. The distribution of monitoring stations at which whales were and were not detected is shown in Fig. 6. Although not abundant, sperm whales were widely distributed throughout the area. The observed frequencies of sperm whale group encounters in different depth zones ($<$1,000m; 1,000-2,000m; 2,000-2,500m; $>$2,500m) were compared with expected values (based on number of monitoring stations in each depth zone) using a chi-squared test. Encounters were less frequent than

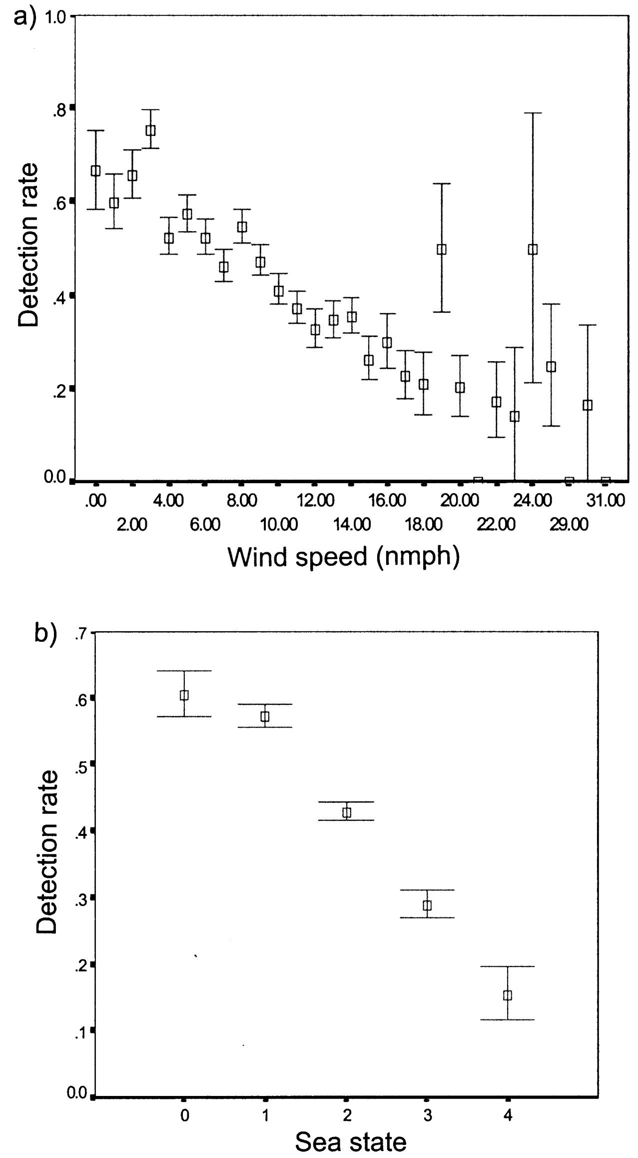

Fig. 2. Detection rate versus (a) wind speed and (b) sea state (IFAW data). Bars are standard errors assuming binomial distributions.

expected in waters < 1,000m than in waters > 1,000m (χ^2 = 5.27, *df* = 1, *P* = 0.02). However, the frequency of encounters was not significantly different from expected between all depth zones (χ^2 = 5.917, *df* = 3, *P* = 0.116) or between the bands greater than 1,000m depth (χ^2 = 0.562, *df* = 2, *P* = 0.755).

DISCUSSION

Distribution and relative abundance of striped dolphins

The deep water and offshore distribution of striped dolphins indicated by this work is consistent with this species' generally oceanic habit (Jefferson *et al.*, 1993), although it is notable that in this area, dolphin density seems to fall beyond the 2,500m contour. These observations broadly agree with those of Gannier (1998a) who found that a very low relative abundance of dolphins in waters less than 500m increased continuously through the 2,000-2,500m depth stratum.

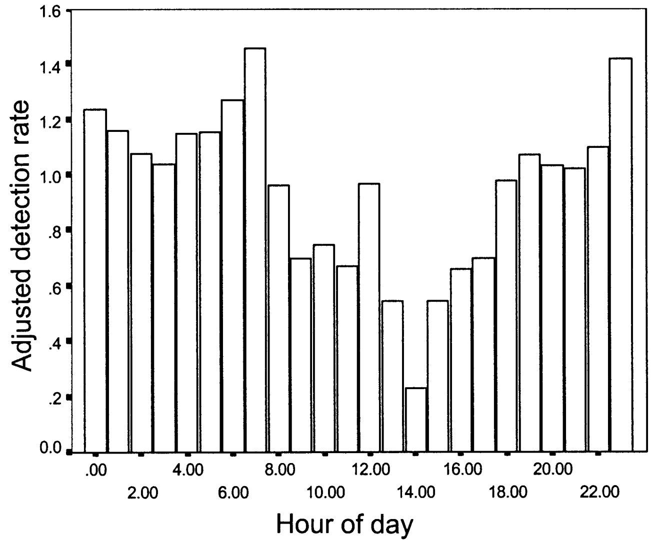

Fig. 3. Detection rates by time of day (IFAW data) after adjustment for 'audibility' covariates.

A prominent oceanographic feature in the Ligurian Sea is the Ligurian Sea Front. This lies between a peripheral, less saline coastal zone, and a more saline central zone of mainly Levantine water. Off Cape Ferrat (France), the front is found approximately 12 miles from the coast (Boucher *et al.*, 1987; Fig. 7). Coastal currents flow within the peripheral zone: a north-bound current flows along the west coast of Corsica and joins the Ligurian current to the north of the island; together these move across the northern end of the Ligurian Sea and turn to flow in a south-westerly direction along the French-Italian Riviera coast (Millot, 1987). Nutrients are brought to the surface in the frontal zone making it an area of increased biological activity, with maximum concentrations of both chlorophyll biomass and zooplankton being found here. Boucher *et al.* (1987) found that, for many species, the frontal zone was an area where they were localised during their growing and spawning phases. Downwelling transport of organic matter from the euphotic zone to deep levels also occurs here, supporting populations of midwater plankton (Baussant *et al.*, 1992).

Fig. 7 shows that, for much of its length, the Ligurian Sea Front occurs in water depths between 2,000 and 2,500m. It is possible, therefore, that the peak in dolphin abundance at these depths indicated here could reflect an association with the more productive frontal zone. A front is a dynamic structure and its position is likely to vary with time. It would thus be interesting to compare dolphin distribution and behaviour with direct, up-to-date observations of the front's location, e.g. provided by satellite imagery.

Table 3

Model statistics for audibility covariates

		IFAW			TETHYS			GREC		
Added variables	Given variables	df	χ^2	P	df	χ^2	P	df	χ^2	P
Audibility (not time of day)	-	18	260.6	0.0000	34	271	0.0000	n/a	n/a	n/a
Time of day	Audibility (not time of day)	2	183.3	0.0000	2	81.2	0.0000	2	25.7	0.0000

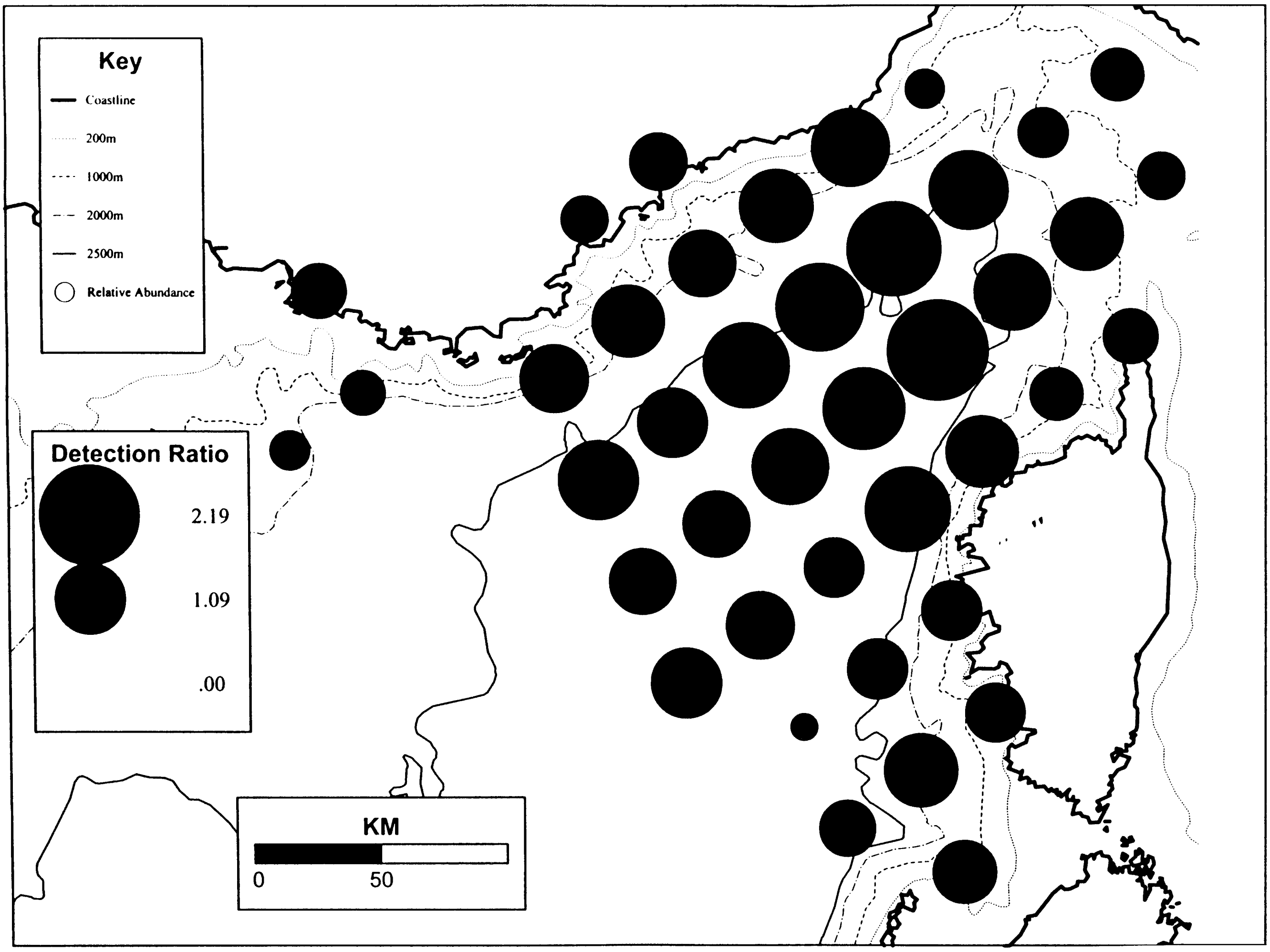

Fig. 4. Rates of detection of dolphins in different 25 n.mile grid cells. Detection ratio is the observed detection rate/predicted detection rate (based on modelled covariates).

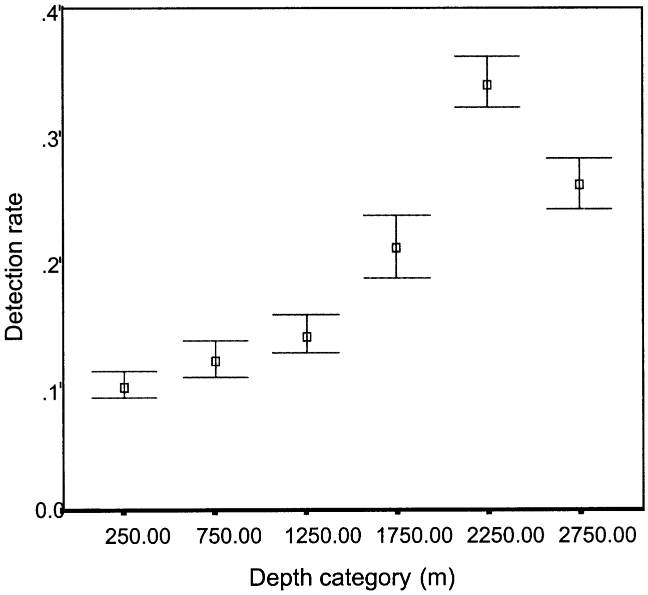

Fig. 5. Mean detection rate for dolphin groups against water depth (IFAW data).

Striped dolphin densities within the sanctuary appeared to remain fairly constant throughout the summer months (June-September) when this work was carried out. To date, most cetacean survey work has been confined to the summer. Gannier and Gannier (1997) showed a marked reduction in relative abundance of dolphins in the winter months, though sightings conditions were also poor at this time of year. Acoustic methods, which are less affected by bad weather than visual techniques, could be used to improve knowledge of seasonal abundance.

The marked diurnal variation in vocalisation rates, shown here, suggests that striped dolphins may be more active at night. It is possible that, like other oceanic dolphins (e.g. spinner dolphins, Norris and Dohl, 1980; and dusky dolphins, Würsig *et al.*, 1991), they feed mainly on fish and cephalopods that migrate towards the surface at night. This suggestion is supported by Gannier (1999) who showed that, off the French Ligurian coast, dolphins move inshore and produce echolocation signals at higher rates, suggestive of foraging activity, at night.

Acoustic detection rates, which are assumed here to be a proxy for dolphin density, will be affected by propagation conditions. Through the summer months (*ca* May to September), a stable thermocline develops in the Ligurian Sea at a depth of ~30-60m with a sound velocity minimum at around 60-80m (Mediterranean Ocean Database *http://modb.oce.ulg.ac.be/*). In these conditions, sound will tend to be refracted away from the surface, reducing the potential for long range propagation of dolphin vocalisations produced near the surface. The thermocline is stable day and night so it is unlikely that diurnal variation in propagation conditions could explain the diurnal changes in acoustic detection rates demonstrated during this study. In the frontal region, upwelling of cold water results in a less pronounced thermocline at a shallower depth, and in some cases this

Table 4

Model statistics for environmental variables (IFAW data).

Added variables	Given variables	df	χ^2	*P*	exp(B)
Day of year	Audibility	1	0.88	0.347	0.9972
depth d (m)	Audibility	2	46.43	0.0000	d 1.0009 d^2 1.0000
Distance to coast r (nm)	Audibility	2	29.08	0.0000	r 1.0841 r^2 0.9988
Slope s	Audibility	2	16.98	0.0000	s 0.8383 s^2 1.0063

Table 5

Comparison of sizes of striped dolphin groups observed in offshore and onshore waters.

Depth	No.	Mean	Median
<2000m (onshore)	37	13.1	6
>2000m (offshore)	124	21.5	12
Overall	161	19.6	10

could result in different propagation patterns, theoretically resulting in better sound propagation. The relatively high frequency sound of dolphin whistles will be heavily attenuated by absorption effects however, so that even here there is limited scope for long range propagation of these signals. We feel that it is unlikely that the potential for improved acoustic propagation in the frontal zone explains the more general distribution of detection rates revealed here. Nevertheless, during future acoustic surveys' attempts to measure propagation conditions and effective range throughout the survey area should be made.

Some shortcomings of the work described here should be noted. For example, it would have been useful to measure the accuracy with which different workers from different teams scored recordings of a series of standard monitoring sessions on different occasions. The analysis was weaker, and made more complicated, by a lack of consistency in the data collection protocols followed by the different partners. In particular, certain predictors found to be significant in the data from one organisation were not recorded by other organisations. Clearly, in the future, it is essential that all collaborators should collect the same data on the same schedule in exactly the same way.

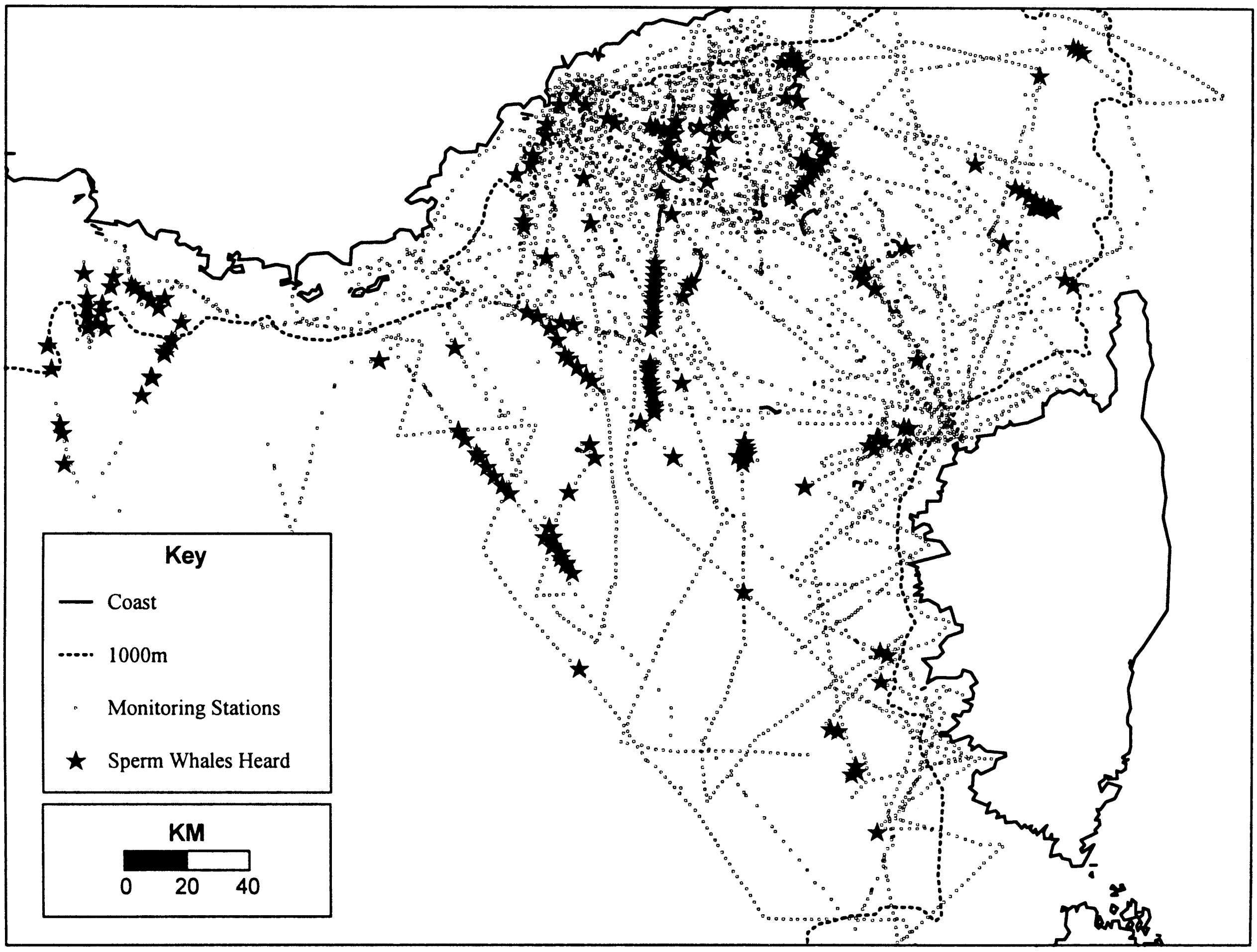

Fig. 6. Distribution of stations at which sperm whales were heard during the survey.

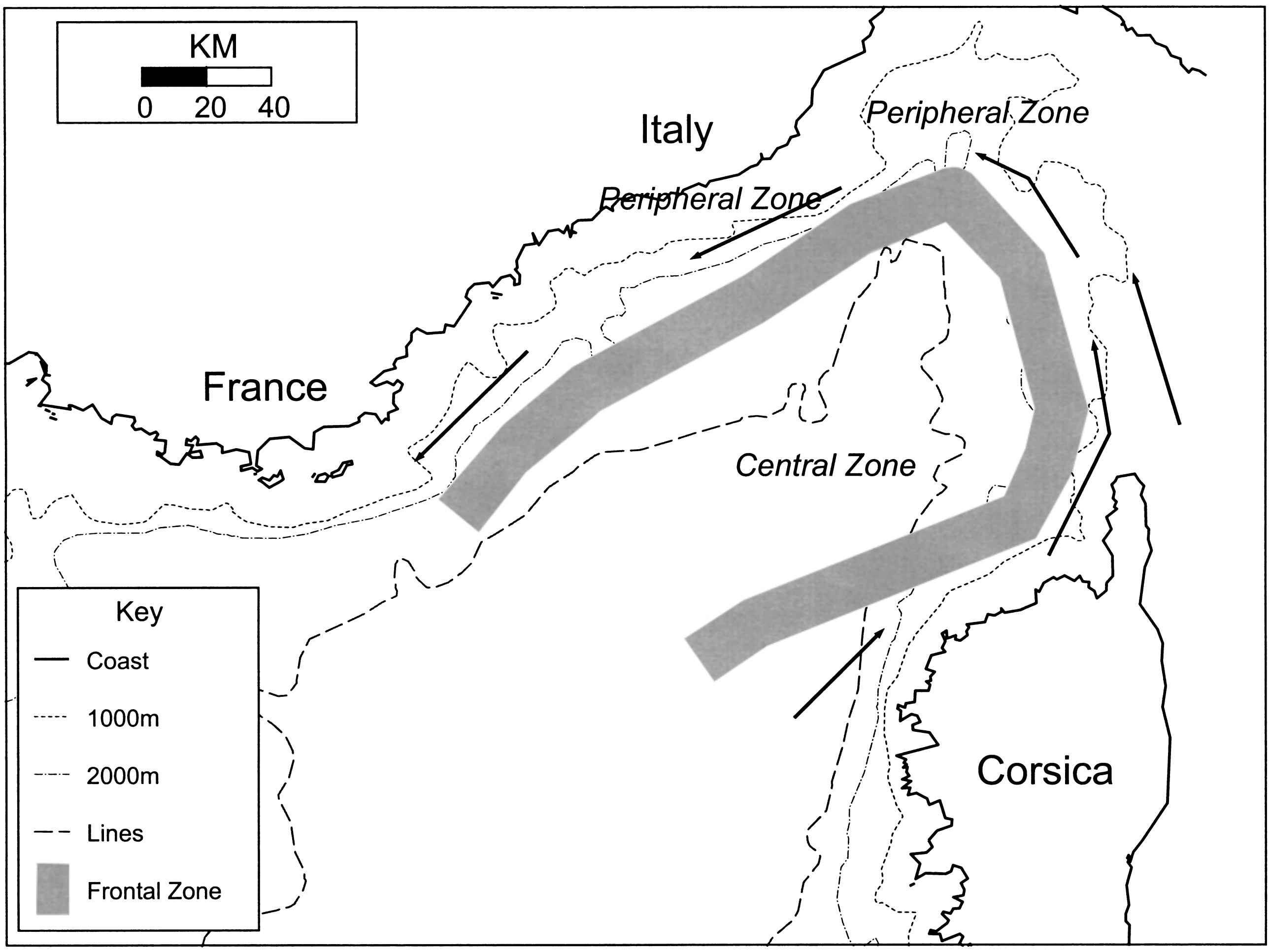

Fig. 7. Typical location of Ligurian Sea Front and coastal currents (indicated by arrows) after Boucher *et al.*, (1987).

Future development

By using identical acoustic equipment, three different research groups were able to collaborate to collect a substantial amount of data on the distribution and vocal behaviour of striped dolphins in the Ligurian Sea sanctuary. These data provide a robust measure of relative abundance that has been useful in indicating geographical distribution, and may, if extended into the future, reveal trends in population abundance. The data provided by this technique are best used in conjunction with other visually-collected data for such variables as group size. One of the ways in which data on seasonal and geographical distributions provided by acoustic techniques would be useful is in planning the geographical allocation of effort in large-scale dedicated sightings surveys and identifying areas of higher abundance and greater sensitivity.

Two refinements to the analysis techniques used are given below.

(1) Logistic regression efficiently models relationships of a sigmoid form, but is not well-suited to the complex and often patchy distributions of animals. Methods based on Generalised Additive Models (Hastie and Tibshirani, 1990) provide flexibility in this respect, by incorporating non-parametric, smoothed functions with forms suggested by the data itself.

(2) The collapsing of detection series to single group detections, as was done here, is simple to understand and easy to apply. However, an alternative approach, more consistent with a modelling framework and providing interpretable quantitative information, would be to incorporate an autoregressive component in the model. This would allow adjustment to be made for the serial correlation in detections before testing other explanatory variables.

So far, only the data on vocalisations and noise levels noted in the field have been investigated. Analysis of the tape recordings made at the monitoring stations might yield improved results, especially if spectra of both signals and noise were to be measured. In the case of very characteristic signals, such as whistles, there are good prospects for using computer algorithms to detect and measure the signals (see e.g. Sturtivant and Datta, 1995). Although such machine methods are unlikely to be as sensitive as the human ear at detecting quiet signals, they do offer the very significant advantage of removing the element of human variability.

ACKNOWLEDGEMENTS

The authors would like to thank the field teams and the crews of the research vessels, without whose dedication this work would have been impossible. An early version of this paper was much improved by the input of two anonymous reviewers.

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