

EVIDENCE FROM STRANDINGS FOR GEOMAGNETIC SENSITIVITY IN CETACEANS

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SUMMARY

We tested the hypothesis that cetaceans use weak anomalies in the geomagnetic field as cues for orientation, navigation and/or piloting. Using the positions of 212 stranding events of live animals in the Smithsonian compilation which fall within the boundaries of the USGS East-Coast Aeromagnetic Survey, we found that there are highly significant tendencies for cetaceans to beach themselves near coastal locations with local magnetic minima. Monte-Carlo simulations confirm the significance of these effects. These results suggest that cetaceans have a magnetic sensory system comparable to that in other migratory and homing animals, and predict that the magnetic topography and in particular the marine magnetic lineations may play an important role in guiding long-distance migration. The 'map' sense of migratory animals may therefore be largely based on a simple strategy of following paths of local magnetic minima and avoiding magnetic gradients.

INTRODUCTION

The problem of how migratory animals find their way has been a subject of curiosity and investigation for centuries. Although it is known that a variety of organisms from butterflies to birds regularly take highly accurate, long-distance journeys of extensive duration, how they navigate or pilot remains a mystery. Within the last 35 years a plethora of sensory modalities has been identified in homing and migratory birds which to date includes the use of a sun compass (Kramer, 1952), a star compass (Sauer, 1957), skylight polarization patterns (Kreithen & Keeton, 1974), odour (Papi, Fiore, Fiaschi & Benvenuti, 1972), infra-sound (Kreithen & Quine, 1979), ultra-violet light (Kreithen & Eisner, 1978) and magnetism (Keeton,

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1972; Walcott & Green, 1974). Many of these cues, however, are not available to aquatic animals and yet they also can make highly accurate journeys across apparently featureless seas.

The use of geomagnetic cues for orientation and navigation is perhaps the most surprising discovery to be made in this field so far, principally because it implies the presence of a previously unknown type of sensory receptor capable of transducing very weak features of the geomagnetic field to the nervous system (Kirschvink & Gould, 1981). However, geomagnetic sensitivity has been demonstrated in bacteria (Blakemore, 1975), bees (e.g. Gould, 1980; Walker & Bitterman, 1985), birds (e.g. Keeton, 1972; Walcott & Green, 1974; Walcott, 1978) and fish (Kalmijn, 1974; Walker, 1984) and the recent discovery of chains of biogenic magnetite crystals within many of them provides at least a theoretical basis for understanding how a magnetic sense might operate (e.g. Kirschvink & Gould, 1981; Kirschvink & Walker, 1985; Yorke, 1979, 1981; Blakemore & Frankel, 1981; Walker, Kirschvink, Chang & Dizon, 1984). One problem with the behavioural aspects of this work, however, is that most responses to geomagnetic stimuli are weak and difficult to observe in laboratory settings; this led Griffin (1982) to assert that perhaps organisms had no useful sensitivity to the geomagnetic field. Alternatively, a geomagnetic sense, which clearly should be very useful, might only be expressed under the influence of an unknown set of environmental conditions. Work on pigeons (Keeton, 1972; Wiltschko, 1983) indicates that several other sensory modalities supersede the magnetic sense when they are available.

For the biological reader, it is worth briefly comparing here the difference between the aeromagnetic (e.g. measured from low-flying aircraft) characteristics over the continents and those over most of the oceans; this distinction is highly relevant to the problem of oceanic navigation or piloting and leads to the suggestion that following or keeping track of local magnetic minima (rather than the maxima, for example) is not a bad strategy for long-distance pelagic navigation and could arise through natural selection. Continents are built up of complex assemblages of igneous, metamorphic and sedimentary rocks, which can possess large regional variations in their mineral and chemical contents. The most important variable which influences the surface magnetic field is the concentration of *coarse-grained* magnetite (Fe_3O_4). In magnetite crystals larger than about $20\ \mu\text{m}$, the magnetic moment will shift easily in the geomagnetic field and yield a strong magnetic moment aligned parallel to the local field. Rocks which contain large magnetite grains will, therefore, have higher than average magnetic susceptibilities. Particles of this size are common in most igneous and metamorphic rocks, and whenever a body of this sort intrudes into something with a lower magnetite concentration a strong positive magnetic anomaly flanked by more diffuse magnetic lows will typically result. Continents appear in general as magnetically 'flat' areas with superimposed 'hills' and a few 'holes'; the false-perspective maps of the iron-mine magnetic anomaly in Rhode Island shown by Gould (1980) and Kirschvink (1982) are good examples of this. In these places with a locally intense field the regional geomagnetic characteristics are unpredictable, and a migratory or homing animal is well advised to seek a magnetically 'flat' place before

using subtle features of the magnetic field as a reference. Pigeons seem to do this when released at magnetic anomalies (Walcott, 1978; Wagner, 1983).

This situation contrasts starkly with that seen over the world oceans, however. In the late 1950s and early 60s it was first realized that the oceanic crust has a totally different magnetic character, composed of long bands of magnetic highs and lows (Mason, 1958; Mason & Raff, 1961), aligned parallel to the axes of mid-oceanic ridges. Observations of this sort led directly to the Vine–Matthews–Morley hypothesis (Vine & Matthews, 1964; see also Glenn, 1982) which proposed that new ocean floor is continuously created at the mid-oceanic ridges through the process of sea-floor spreading (Hess, 1962) and that periodic reversals in the global geomagnetic field give rise to the marine magnetic stripes. As the new basaltic crust is injected and cools at the spreading ridge, *fine-grained* magnetite drops through its Curie temperature and permanently records the local geomagnetic field direction. The remanent magnetization produced in this fashion is stable over long intervals of geological time, and the alternating normal and reversely magnetized blocks produce anomalies at the ocean surface in most regions with amplitudes ranging from a few hundred to thousands of nanotesla (nT), compared with a geomagnetic total strength ranging from 29 000 nT at the equator to over 80 000 nT near the poles.

The Vine–Matthews–Morley hypothesis was dramatically confirmed in 1966 when it became apparent that the magnetic reversal sequence as worked out from dated volcanics on land (Cox, Dalrymple & Doell, 1967) and in deep-sea cores (Opdyke, Glass, Hayes & Foster, 1966) matched perfectly the symmetrical magnetic anomalies centred over oceanic ridges (Vine, 1966). Subsequent work has extended the geomagnetic reversal time scale back to about 160 million years and now permits the geological and tectonic history of almost all oceanic basins to be worked out in detail by simply towing or flying magnetometers over them. The Vine–Matthews–Morley hypothesis is therefore the cornerstone of modern plate tectonic theory, provides the mechanism for continental drift and is by far the single most important new concept in the earth sciences since the early 1800s (Glenn, 1982).

Of potentially great interest to the problem of animal migration and navigation is the fact that most of these marine magnetic lineations in the major ocean basins are aligned in a North–South fashion, a fortuitous result from the geometry of the spreading ridges which formed after the break-up of the continent Pangea during Mesozoic time. An animal could therefore use these lineations by counting or following minima to keep track of relative *longitude* during long migrations if it were sensitive enough to the magnetic field, while the smooth North–South variation of magnetic *inclination* would provide unambiguous *latitudinal* position. Depending on the age, depth and latitude of the sea floor, the magnitude of these anomalies can range from a few hundred to several thousand nanotesla – figures which are also well within the sensitivity range inferred for homing pigeons and honey bees and also well within the theoretical limits for magnetite-based magnetoreception (Kirschvink, 1979; Kirschvink & Gould 1981; Yorke 1981; Kirschvink & Walker, 1985).

The use of cetacean stranding positions in a test of a geomagnetic navigation or piloting hypothesis, as done by Klinowska (1983) and adopted here, may at first seem

to be a strange approach. Although something is obviously wrong with a living marine mammal that swims onto the shore, it *is* attempting to move somewhere, and it seems likely that cetaceans are more apt to strand in areas unfamiliar to them. For this reason stranding records probably contain more information about the sensory cues used during long-distance migration than any other set of positional data collected for them, with the exception of radio tracking studies (Mead, 1979). We wish to make it clear that our goal is *not* to test hypotheses about *why* cetaceans strand. Our goals are to test the hypotheses that: (1) cetaceans have a sensitivity to weak geomagnetic stimuli, and (2) that geomagnetic cues may influence their distributional patterns in a predictable manner. For this purpose, we use the stranding records merely as a subset of the positions of all living cetaceans.

Our approach for testing these geomagnetic sensory hypotheses therefore begins by noting that stranding positions within a magnetic 'valley' have an easily examined attribute: the coastline adjacent to a stranding should have higher intensity than does the stranding site. Our results indicate that, in most cetacean species, live strandings do indeed tend to happen at magnetically lower-than-average places along the coastline, confirming in a general way the hypothesis of Klinowska (1983). However, there are a few clear counter-examples which suggest that the situation in some species is more complex than this, and on occasion they may use other features of the geomagnetic field (e.g. magnetic highs, gradients, etc.) for guidance.

METHODS AND DATA

We used the extensive stranding data available for the eastern U.S. coast, which is one of the best areas for investigating the relationship between cetacean strandings and the geomagnetic field because of the availability of three large computerized data sets. First, the Smithsonian Institution in Washington, D.C., has maintained a catalogue of cetacean strandings in which the geographical locations of these events are either listed or can be determined using the given place names and detailed topographic maps. Second, the U.S. Geological Survey has conducted an aeromagnetic survey of the U.S. East-coast continental margin with dense coverage from Cape Canaveral in Florida to Cape Cod in Massachusetts. These data are available on magnetic tape in gridded digital format as discussed below and shown as a colour image on Fig. 1A,B: they constitute one of the most complete and extensive aeromagnetic data sets available for any portion of the globe. Finally, any test of stranding hypotheses necessarily depends on the geometry of the coastline itself; it must be known accurately to be of any use. For the analysis discussed in this paper we used the high-resolution digital world outline from the plotting package, SUPMAP, developed by the U.S. National Center for Atmospheric Research (NCAR).

Stranding data

The Marine Mammal Program of the Smithsonian Institution maintains a large data-base which contains records of stranding events occurring along the U.S.

coastline. This file contains information on strandings gleaned from records kept on specimens and data archived in museums, from reports in 'grey literature' and mass media, from published scientific literature, and from the SEAN monthly publications (Smithsonian Scientific Event Alert Network). Through the cooperation of the leader of the Marine Mammal Program, Dr James Mead, a sub-set of data was provided for us which included all strandings, from which we obtained records of live stranding events.

Geographical information provided in each record was of varying degrees of completeness. Some records contained geographical coordinates, others contained only beach or town names. We reviewed each record, and for those without coordinates we provided a best estimate of latitude and longitude (to the nearest minute) using National Ocean Survey marine charts whenever possible. This phase of the study was performed at the NMFS facility in La Jolla, and at this time no information on the magnetic intensity at the various coast locations was on hand. Although there was some degree of subjectivity associated with determining coordinates for stranding events, no systematic bias was possible without magnetic information. Besides geographical information, the species, number of animals involved, state of preservation (1 = live, 2 = freshly dead, 3 = slightly bloated, etc.), and a subjective measure of the degree of accuracy of a stranding location were included. Only locations known to within 1' were used in our analyses. Table 1 gives a list of species for which we were able to find live stranding events with highly reliable locations within the area of the aeromagnetic survey discussed next.

Magnetic data

The aeromagnetic survey of the U.S. Atlantic Continental Margin (Grim, Behrendt & Klitgord, 1982) is at the heart of this study; we obtained these data from the NOAA Geophysical Data Center on magnetic tape in high-density gridded digital format covering the areas shown on Fig. 1A,B. Each data point represents 0.036° spacing in latitude and longitude, or approximately a 4-km square. Flight tracks began between 5 and 20 km inland and continued out to the 2000-m isobath, and were generally spaced of the order of 2.5–5 km apart with altitudes between 300 and 450 m. The position accuracy was estimated to be better than ± 1 km using LORAN C, VLF and doppler-radar. Data from these flights were fitted by a method of least-squares to this gridded surface and corrected for diurnal variations. Grim *et al.* (1982) also subtracted the 1965 International Geomagnetic Reference Field (IGRF) and added a baseline of 52 000 nanotesla (nT). We removed 50 790 nT from this baseline to permit the residual field values to fit in 2 bytes of memory (Integer *2) on our VAX 11/780 computing system. (All of the analyses used here depend only on the relative field difference between pixels, so the subtraction of this constant has no effect on the overall analysis.)

We choose to represent this information as the colour images shown here in Fig. 1A,B. The gridded magnetic data have been mapped onto a 500×500 array of

pixels (picture elements), with the colour at each pixel representing the average field value for the 0.036° square (bright yellow areas indicate high magnetic field values and dark blue areas are low values with 256 shades of resolution covering the 2000 nT range of data values shown on the colour step wedge). Fig. 1A,B also shows the image of these data with a light background and the outline of North America and state boundaries superimposed. This method of representing the data avoids most of the visual confusion which results from attempting to plot geographical locations on a false-perspective, contoured surface as used previously (Gould, 1980; Kirschvink, 1982).

One problem with these data, however, is a long-distance shift in the average baseline value which increases by as much as 600 nT from South to North (W. Heinze, personal communication, 1984). The problem either lies in the 1965 IGRF correction to the raw data (it might not properly remove some of the non-dipole components of the main geomagnetic field) or there may be a thin zone containing native iron near the base of the crust in this portion of the Atlantic (D. Strangway, personal communication, 1985). As discussed later, this problem makes it difficult to conduct one of the more intuitive statistical tests.

Fig. 1. (A) and (B). Images of the aeromagnetic survey data for the Atlantic Continental Margin from Cape Canaveral, Florida, through Cape Cod, Massachusetts, with the coastline, political boundaries and live stranding events superimposed. The USGS aeromagnetic data are supplied in a gridded, digital format with each point or pixel (picture element) representing the residual magnetic field value after removal of the IGRF in a square 0.036 degrees in both latitude and longitude. In both A and B, the value of the residual magnetic field in each pixel is indicated by the shade of colour ranging smoothly (256 shades) from dark blue to bright yellow, with blue and yellow respectively indicating magnetic lows and highs. Each image has a 20-step colour wedge which shows the relative intensity calibration in 100 nanotesla (nT) steps across the entire 2000-nT variation in the magnetic data set. (This variation is about 2% of the total field strength before removal of the IGRF.) A one-degree latitude and longitude grid has been lightly superimposed on the magnetic data, and areas outside the boundaries of the aeromagnetic survey are shown in white. All live cetacean stranding locations referred to in this study are plotted in red, with the position of large mass stranding events (> 30 individuals) shown by the large red + marks, smaller mass strandings (between three and thirty individuals) by smaller + marks, and events of one or two individuals as single red pixels. Outside of the aeromagnetic survey area, the position of the coastline and state boundaries are plotted in green. Within the survey area, the position of the coastline can be followed both by the location of the stranding events and by a light reddish tint which has been added to the otherwise blue-yellow pixels. Abbreviations of state names and a few latitude and longitude coordinates are shown in black for reference. (A) Southern area from Cape Canaveral in Florida through Cape Hatteras in North Carolina. Several prominent magnetic minima which are branches of the East-coast magnetic anomaly cross the coast in the Florida-Georgia segment of this image, and are associated with mass-stranding events. These may be migration routes at sea, and sediments near their intersection points along the coast should have abundant whale-bone fossils as a result of numerous mass stranding events during periods of normal geomagnetic polarity. (B) Northern area from just north of Cape Hatteras in North Carolina through Massachusetts. The boomerang-shaped bright-yellow stripe running through the centre of the map is the East-coast magnetic anomaly, and south of this several faint marine magnetic lineations can be seen. The bright-yellow spot on the eastern margin of the image is the magnetic anomaly of a seamount.

1A

N.C.

S.C.

Ga.

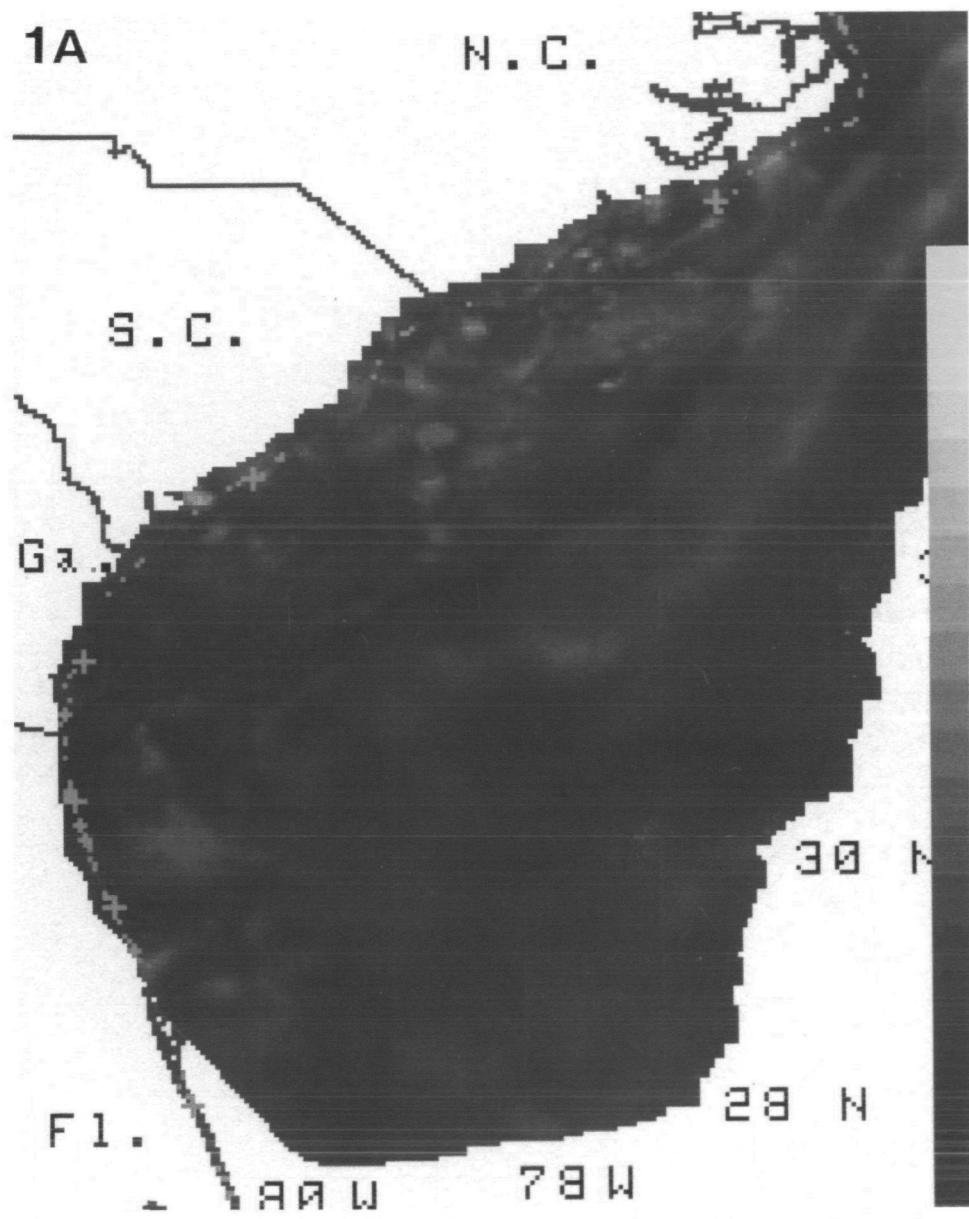
Fl.

30 N

28 N

78 W

78 W



1B

NY

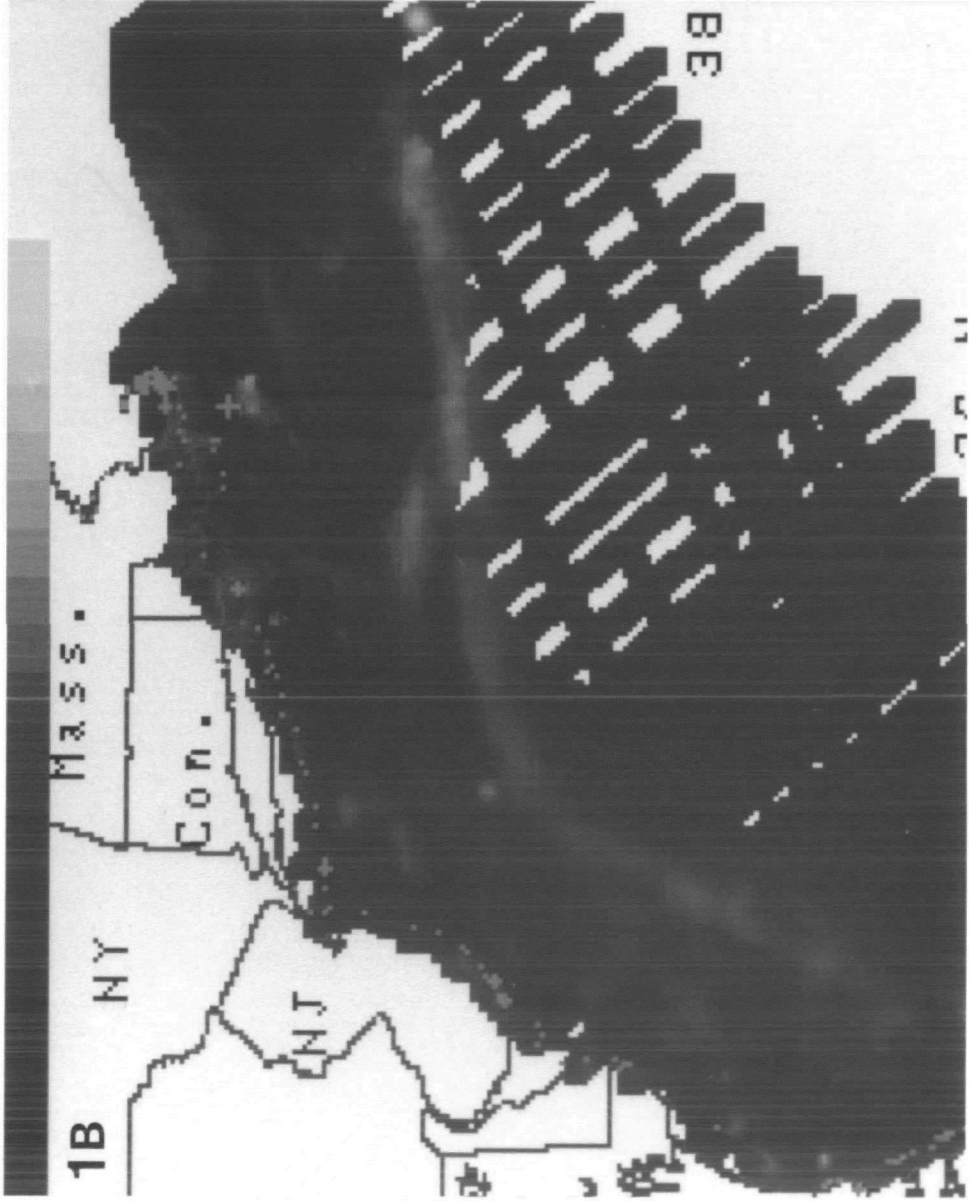
Mass.

Con.

NJ

3B

0 5 10



Coastline data

The third major data set, an accurate digital representation of the coastline within the aeromagnetic survey area, is needed in this study for two reasons. First, gross errors in the cetacean stranding file were easily found by checking their pixel assignments against those of the coastline. The position of any stranding event which 'happened' far out at sea or inland was suspect and was re-checked by consulting the geographical position of the stranding in the Smithsonian listing. Secondly, cetaceans live-strand along the *coast*, and by using the set of all coastal points we reduce the statistical problem to a one-dimensional analysis. The two-dimensional case is more complex, and inappropriate as it would incorporate off-shore and inland magnetic data where cetaceans do not strand.

We used the world digital outline data set obtained from the NCAR graphics program, SUPMAP, which contains high-resolution coastal outline positions accurate to 0.001° in both latitude and longitude. All pixels within the 500×500 map area which contain segments of the coastline were identified and numbered in consecutive order as they were encountered, beginning at Cape Canaveral in Florida and continuing to Cape Cod in Massachusetts. A total of 1364 distinct pixels was located in this search within the boundaries of the aeromagnetic data set, including offshore and barrier islands. Of these, 283 are included two or more times in the full set of 1692 due to meandering of the coastline. During this search, the total shoreline distance within each consecutive coastal pixel was also measured to provide the distance function needed for the statistical analysis discussed below.

Due to the presence of islands and rivers, the coastline is not one continuous stretch. In a few places it also wanders in and out of the area covered by the aeromagnetic survey and jumps onto and off islands. These discontinuities result in a total of 40 coastal segments within which the magnetic field is known continuously. The gaps between them imply that they must be treated as discrete entities in procedures discussed below; 23 of them contain one or more stranding events, and the 17 segments with no strandings are usually small islands or the inland side of brackish-water inlets. Segments without strandings were not used for any analysis discussed here.

Fig. 2 shows the plot of the residual total field values as a function of shoreline pixel number, and the histogram underneath it indicates the position and number of stranding events within each pixel. The locations of mass stranding events ($N \geq 3$) are shown by small arrows, and the approximate size of each event is indicated by the number next to the arrow. The size of these stranding events along with their approximate geographical location names can be used to locate their positions on the images of Fig. 1.

Statistical analysis

Any statistical approach used to test for a relationship among the data shown on Figs 1 and 2 should be conducted with an awareness of two potential problems with the analysis. First, and as noted earlier, a regional trend exists in the USGS

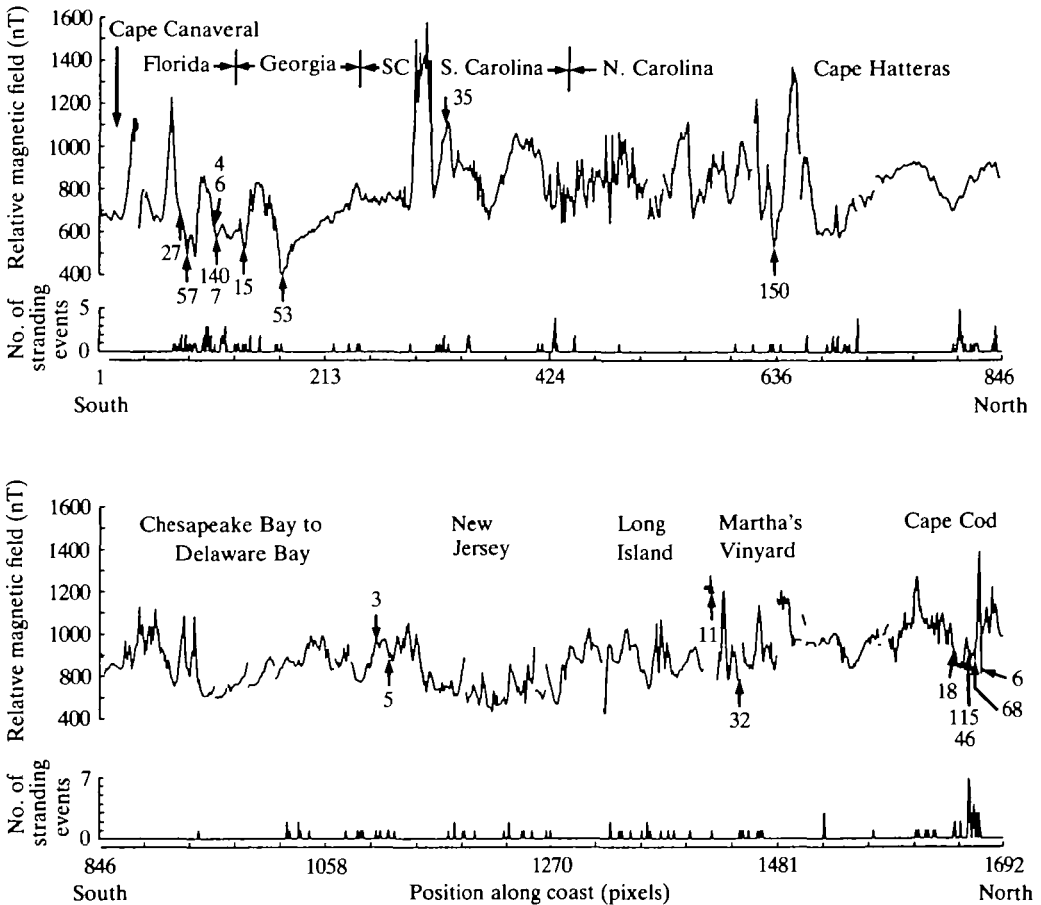


Fig. 2. Plot of the relative magnetic field in sequential segments along the coast from Cape Canaveral, Florida, through Cape Cod, Massachusetts, with a histogram showing the number of separate stranding events in each coast pixel. The data are shown in two halves, the upper and lower of which correspond approximately to the coastlines shown in Fig. 1A and B, respectively. Relative values for the magnetic data after subtraction of the IGRF are given in nanotesla (nT) as described in the text, and the total variation shown is about 2% of the total field strength before removal of the IGRF. Gaps in the magnetic curve show the boundaries between major adjacent coastal segments where the coastline has wandered out of the magnetic survey area or jumped to and from islands. (33 of the 40 coastal segments are large enough to be seen on this diagram, including all of those with stranding events. The other seven segments are only one or two pixels in length and not easily distinguished at this scale.) The average coastline length per pixel is 2.8 km. The location and size of mass stranding events are also indicated by the small arrows with the number of individuals in the stranded group. The location of southern state boundaries and other geographical reference points are shown along the top margin of each plot to aid in the location of each event on the images of Fig. 1.

aeromagnetic data as a result of incomplete removal of the IGRF. For this reason, any comparison of stranding locations with coastal field values should be restricted to those sub-regions without such obvious trends, or be made using only the relative field changes in the local coastal neighbourhood around each stranding site.

Similarly, care must be taken to compare each stranding event with its appropriate coastal segment. In all analyses conducted here, only those coastal segments which contain strandings of the cetacean group under consideration have been used as the basis for comparison.

The second, more subtle problem with this analysis arises from the gridded nature of the aeromagnetic data set. Although the north-south interval is a uniform 0.036° in latitude (or 4 km), the longitude width decreases as the cosine of the latitude. Southerly coastal pixels therefore represent a greater area than those in the North, and for this reason statistical tests should not be based directly on the distribution of magnetic field values at each coastal pixel. We avoided this problem by using the relative distance up or down the coastline from each stranding event as the basic measure for comparison.

At this point there are several statistical approaches which one might use to test for a relationship between stranding sites and the geomagnetic field. Perhaps the simplest (and most flawed) would be to ask whether the average field value at the strandings is significantly different from that of the coastal segment in question. Strandings near the bottom of local geomagnetic 'valleys' would produce a mean less than the coastal average, and the opposite for strandings near magnetic highs. Unfortunately, we have found that this general approach is easily biased by the presence of residual trends in the IGRF, and even by restricting the analysis to small segments of the coastline it is difficult to be confident of the results.

A better statistical approach is to examine the local coastal neighbourhood around each stranding event. A line of magnetic minima ('valley') where it intersects the coastline is at a position where the total field should increase away from the axis as followed from it up and down the coastline. The null hypothesis of no magnetic relationship to strandings implies that, on the average, the magnetic field along the coast should neither be higher nor lower than the magnetic field at the stranding sites. Therefore, the difference between the field value at a stranding and those from that of neighbouring coastline should on average be zero. Systematic departures from zero could either be due to strandings at extrema or adjacent to sharp magnetic highs or lows. Because this approach only compares the local field differences around a stranding event, the absolute field intensity is subtracted out and the problem of the regional bias in the IGRF discussed earlier is avoided. We have found that a suitable measure to test for stranding differences is to determine how close the field value at a stranding site is to the minimum and maximum values in its local vicinity. Let

$$x_{i,r} = \left(\frac{B_{i,\max} + B_{i,\min}}{2} \right) - B_{i^{\text{th}} \text{ stranding}}, \quad (1)$$

where $B_{i,\max}$ and $B_{i,\min}$ are respectively the minimum and maximum field values within a distance of 'r' km from the i^{th} stranding site, and $B_{i^{\text{th}} \text{ stranding}}$ is the field value at the i^{th} stranding. A suitable test of the null hypothesis is therefore to decide whether the average value of this group of magnetic field deviation parameters is distinct from zero; a significantly positive mean implies that strandings tend to happen close to local minima, and a negative mean implies that they strand near a

local magnetic high. If \bar{x}_r is the average of these values from equation 1 at a radius, r , based on $i = N$ stranding events with variance, s^2 , then the statistic

$$t = \frac{\bar{x}_r \sqrt{N}}{s} \quad (2)$$

will have the Student's t -distribution with $(N-1)$ degrees of freedom (Sokal & Rohlf, 1981). Large magnitudes of t imply rejection of the null hypothesis, with the sign of t indicating strandings near either magnetically low or high places, respectively.

We conducted this analysis as a function of increasing radius (r) around the stranding sites in 5-km increments up to a maximum of 100 km (100 km is roughly the maximum distance a migrating whale could travel in 1 day). This procedure allows an estimate of the scale of magnetic features which might be influencing the choice of the cetacean's stranding sites. For each radius, only those strandings which were at least a distance r from the boundaries of its coastal segment were included. This constraint was imposed because the field is not continuous between adjacent coastal segments, and it is necessary to restrict this analysis to the particular stretch of coastline where the stranding happened. It is also improper to include a stranding event on a short coastal segment (or near an edge) if the current radius exceeds the continuous coastline on either side of it. In this analysis, therefore, the number of strandings included will monotonically decrease as the radius increases and strandings near the edges of coastal segments drop out. This is not a great problem, however, as the Student's t -statistic given in equation 2 allows for such variation in sample size.

The statistical approach outlined above lends itself to a direct check of significance through Monte-Carlo simulations, which, in addition, also provide a check of whether or not the Student's t -tests are applicable to the distributions at hand. A disagreement between the t -tests and the Monte-Carlo results would imply that the population of potential $x_{i,r}$ values drawn from the neighbourhoods around each stranding event is significantly non-normal. This might happen, for example, if there were a few large positive anomalies superimposed upon an otherwise randomly fluctuating background. As will be discussed later, this particular situation is common with geomagnetic data as a result of susceptibility anomalies. Note that significant deviations in mean field value (either high or low) from these tests imply that the cetaceans were following some cue related to the geomagnetic field. For this, two-tailed tests are clearly appropriate because we are interested in either high or low departures. Using two-tailed rather than one-tailed tests is also the conservative approach as it minimizes the risk of erroneously rejecting the null hypothesis (type I error).

The Monte-Carlo method as we apply it to this problem involves first programming the computer to make a batch of 'random' whale positions equal in number to that present in each group of live strandings. We then calculate the set of $x_{i,r}$ values for this group using equation 1 in the same fashion as was done for the real batch. The mean value of this simulation for each radius is compared with that found for the real group and a record is kept concerning which is the largest or smallest. We then

repeat this procedure 1000 or more times, and count the number of simulations with mean values greater than and less than that of the real group at each radius. This gives a direct measure of the significance of the real stranding set compared to random chance (e.g. if, at any particular radius, 5 Monte-Carlo simulations out of 1000 yield mean values less than that of the real cetacean group, one would reject the null hypothesis of no geomagnetic influence at the $P < 0.005$ level on a one-tailed test, or at the $P < 0.01$ level on the two-tailed tests used here).

From the discussion of Mead (1979) it is clear that there are regional biases in the reporting of cetacean stranding events in the Smithsonian database. These biases and the regional bias in the IGRF must be considered in the actual process of selecting random positions to match the strandings in the Monte-Carlo simulations. It is therefore very important that each random sighting 'observation' be created in such a fashion so as to be within a reasonable distance of its corresponding stranding event from the Smithsonian data set. For this purpose we defined an interval along the coast around each real stranding event within which one random stranding position was chosen per simulation. Points within this interval could not be more than 100 km from the real stranding site because we felt that this was a reasonable distance for a whale to travel in 1 day (swimming at about 4 km h^{-1}), and was small enough to prevent the observing and IGRF biases from becoming serious. In addition, points within this interval could not be closer to either edge of coastal segment than was the real event. This constraint was necessary to prevent the Monte-Carlo whales from being thrown out of the analysis at a radius less than that of the whale it was supposed to simulate. Finally, a random whale was thrown out of the analysis at radii above the maximum for the real event in order to match the number of random whales with real whales at each radius.

The Monte-Carlo simulations also permit another type of check on the distribution of stranding sites relative to the magnetic field. It is conceivable that cetaceans might choose to strand at coastal locations with abnormal variations in the field (e.g. places where not only the \bar{x} values are distinct relative to the geomagnetic field, but that the variance, s^2 , may also be significantly non-random). This situation could arise, for example, if at different times during the year the preference within a species shifts from magnetic lows to highs, or if they are responding to field gradients in some fashion. Therefore in each of our 1000 Monte-Carlo simulations, we also calculated the s -values and compared them with those observed in the actual stranding data set.

RESULTS

Results from the analyses described above are shown in Fig. 3 for each species or subgroup within the stranding data set. In these diagrams, the average value of the magnetic field deviation parameter (\bar{x}_r from equation 1) is plotted at intervals of 5 km from the stranding sites out to a distance of 100 km. Results from the Monte-Carlo simulations are also shown at each radius value by a series of circle, square and diamond symbols in three sizes (small, medium and large; small symbols imply significance at $P < 0.05$, medium at $P < 0.01$, and large at the $P < 0.001$ level on two-

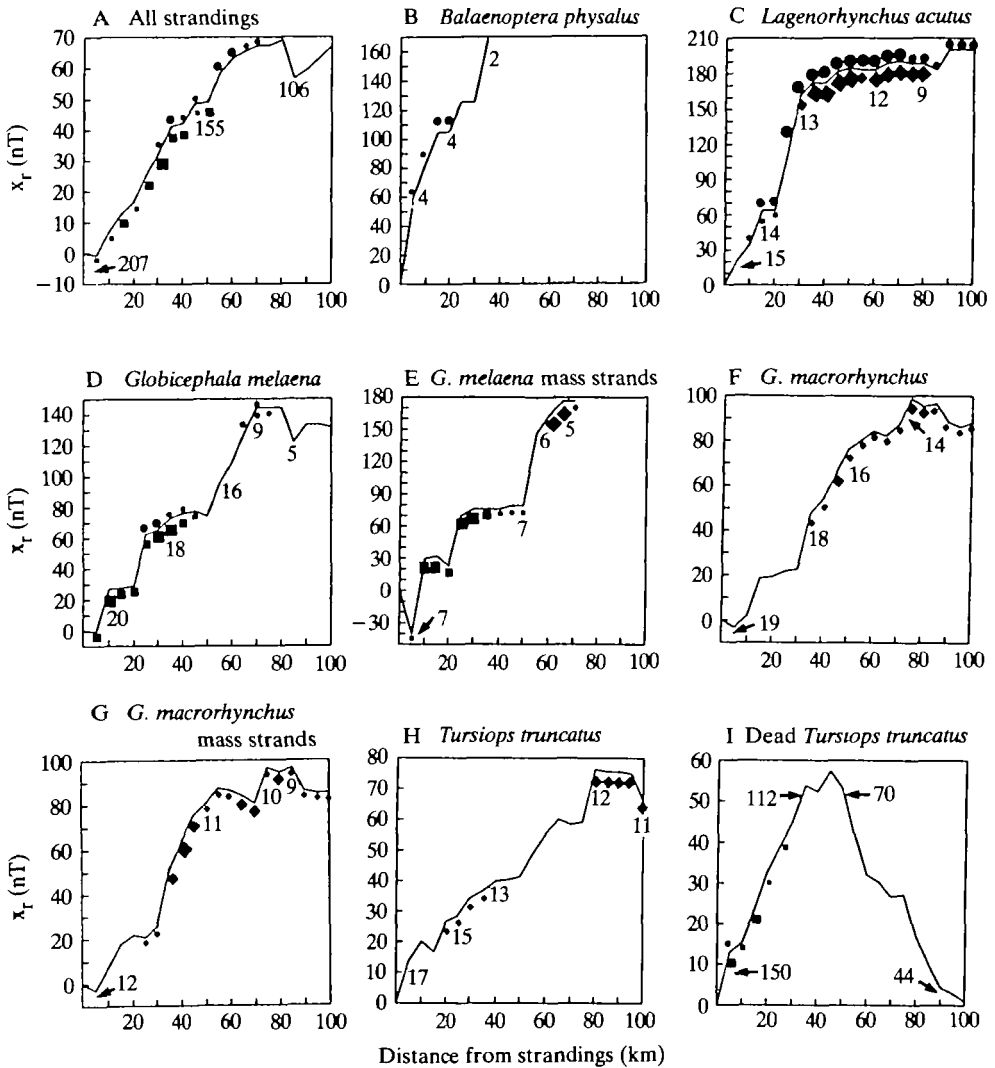
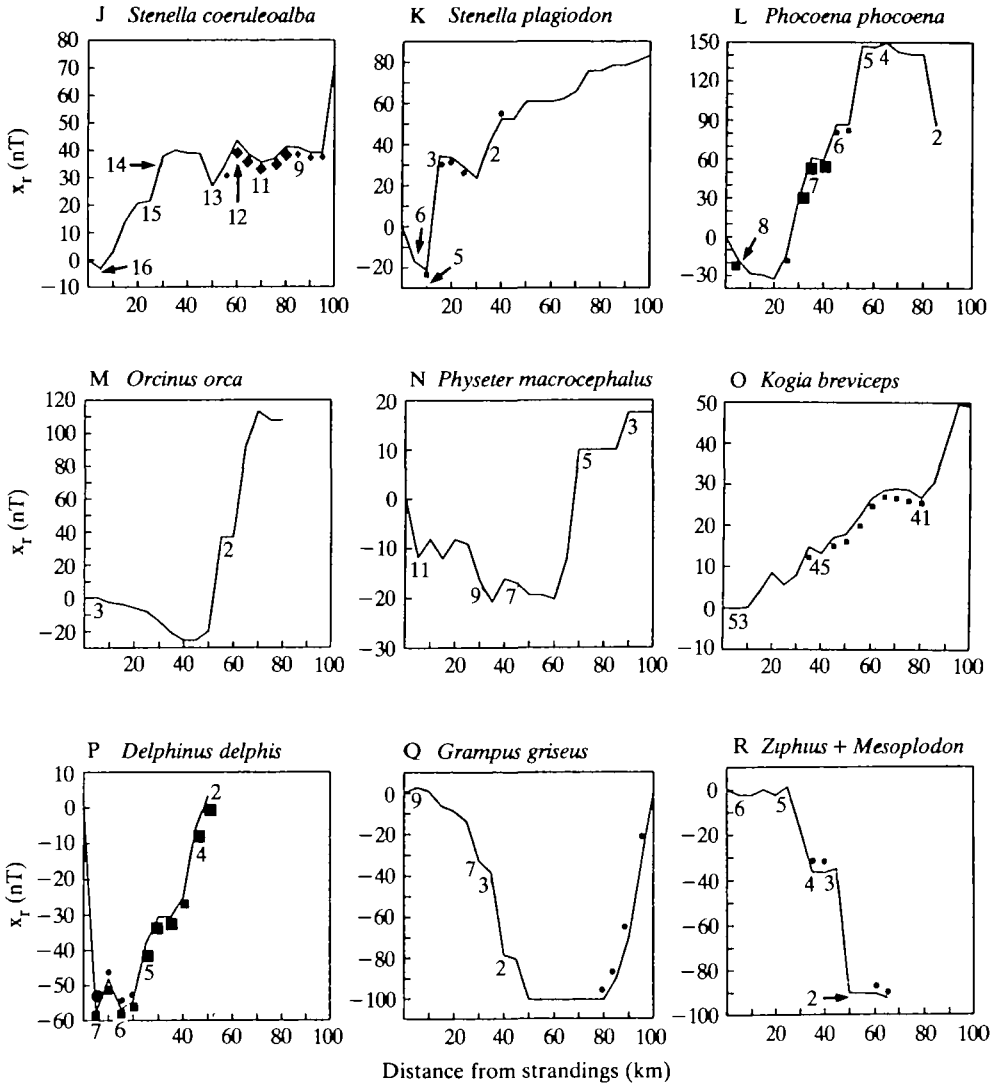


Fig. 3. Average magnetic field deviation parameters (in nT) (from equation 1) as a function of distance from stranding events. Values of this parameter were calculated in 5-km increments up to 100 km for each of the species groups indicated. Positive values imply that the strandings preferentially happen near local magnetic minima, while negative values imply strandings near local magnetic highs. These figures therefore give a clue as to the shape of the average magnetic 'valley' or 'hill' around which the strandings occur. At each radius value, significant deviations of either the mean or variance of the deviation parameters (measured through the Monte-Carlo simulations) are indicated by the size of the circle, square or diamond symbols as follows: small implies $P < 0.05$, medium implies $P < 0.01$, and large implies $P < 0.001$ on two-tailed tests. The circles show results from the comparison of mean values, while diamond and squares show results from the variance comparison with diamonds and squares respectively indicating low and high. Numbers written below the curves give the number of stranding events left in the analysis at that radius.



tailed tests). Circles indicate departures of the mean value of \bar{x}_r with its sign indicating whether it was towards high or low fields. Similarly, the diamond symbols indicate that the variance of the $x_{i,r}$ values was significantly low while the squares indicate abnormally high variance.

Table 1 lists typical results from these analyses for the 14 separate species in which we have three or more stranding events within the magnetic data area. For species which strand more rarely we have grouped them into the nearest taxonomic categories (e.g. all family Ziphiidae, the miscellaneous Delphinidae, and all Balaenopteridae). Two species (*Globicephala melaena* and *G. macrorhynchus*) account for most of the live mass stranding events which happen within the magnetic data area (8 and 11 respectively), and for these we have also run separate analyses giving unit weight to all events in which three or more individuals were stranded. In addition, we ran the analyses on the entire live stranding data set of 212 events and 158 records

Table 1. Results of the neighbourhood analyses as shown on Fig. 3 at representative radii for various species and groups of cetaceans examined in this study

SUB-ORDER	Neighbourhood extremes										
	Family	Species and common name	Number of strandings survey area	Radius (km)	Number with this radius	Average local field deviation (nT)	Standard deviation (s,nT)	t (n-1 d.f.)	P	Monte-Carlo P	
										Mean	Variance
		All species combined	212	35	168	41.4	114.4	4.69	<0.001***	0.006**	0.002** _H
		<i>Globicephala melaena</i> (long-finned pilot whale)	22	70	9	144.4	56.1	7.73	<0.001***	0.046*	0.016 _L **
		Only mass strandings	8	60	6	164.6	10.9	36.83	<0.001***	0.09	<0.001 _L **
		<i>Globicephala macrorhynchus</i> (short-finned pilot whale)	19	75	14	99.0	116.9	3.17	<0.01**	0.57	0.008**
		Only mass strandings	11	45	12	75.3	75.5	3.46	<0.01**	0.28	0.004 _L **
		<i>Stenella coeruleoalba</i> (striped dolphin)	17	60	12	43.6	37.3	4.05	<0.01**	0.63	0.01 _L **
		<i>Stenella plagiodon</i> (spotted dolphin)	6	15	3	34.7	3.5	17.09	<0.01**	0.08	0.014 _L *
		<i>Lagenorhynchus acutus</i> (Atlantic white-sided dolphin)	16	30	13	161.9	29.2	20.02	<0.001***	<0.001***	0.002 _L **
		<i>Tursiops truncatus</i> (bottlenose dolphin)	17	80	12	76.3	73.9	3.57	<0.01**	0.35	0.005 _L **
		Dead <i>Tursiops truncatus</i>	158	5	150	12.9	58.7	2.70	<0.01**	0.012*	0.008 _H **
		<i>Grampus griseus</i> (Risso's dolphin)	9	30	7	-32.6	68.1	-1.27	>0.20	0.09	0.998
		<i>Delphinus delphis</i> (common dolphin)	7	15	6	-56.8	127.3	-1.09	>0.20	0.012*	0.006 _H **
		<i>Orcinus orca</i> (killer whale)	3	55	2	36.8	3.2	16.3	<0.05*	0.66	0.11 _L
		Miscellaneous Delphinidae	5	60	3	170.3	68.5	4.3	<0.05*	0.24	0.34 _L

ODONTOCETI
(toothed whales)

Table 1. Continued

SUB-ORDER	Neighbourhood extremes										
	Family	Species and common name	Number of strandings survey area	Radius (km)	Number with this radius	Average local field deviation (nT)	Standard deviation (s,nT)	t (n-1 d.f.)	P	Monte-Carlo Mean	Variance
ODONTOCETI (toothed whales)	Physeteridae	<i>Physeter macrocephalus</i> (sperm whale)	11	45	7	-16.9	70.4	-0.64	>0.50	0.15	0.68 _L
		<i>Kogia breviceps</i> (pigmy sperm whale)	53	50	45	18.1	149.6	0.83	>0.20	0.60	0.018 _H
		<i>Kogia simus</i> (dwarf sperm whale)	6	70	6	32.7	187.3	0.43	>0.50	0.78	0.36 _H
ODONTOCETI		<i>Phocoenidae Phocoena phocoena</i> (harbour porpoise)	8	35	7	61.1	160.0	1.01	>0.20	0.22	<0.001 _H
		All family Ziphiidae	6	35	4	-36.1	70.0	-1.03	>0.20	0.046*	0.44 _H
MYSTICETI (baleen whales)	Balaenopteridae	<i>Balaenoptera physalus</i> (fin whale)	4	20	4	105.1	74.7	2.82	>0.05	0.006**	0.702 _H
		All Balaenoptera	7	15	7	59.2	71.2	2.2	>0.05	0.014*	0.19 _H

In this table, the number of strandings in the survey area refers to those stranding events which were accurately located and occurred within the boundaries of the U.S.G.S. aeromagnetic data set. The radius value given in the table is the distance for which the local field deviation parameter of equation 1 in the text has been calculated, and for which the results are included in this table. As can be seen on Fig. 3, these values have been chosen as typical for those intervals where the departures from the null hypothesis are most pronounced. Also given in the table are the number of stranding events which remain in the analysis at that radius (these correspond to the small numbers on the diagrams of Fig. 3), the average value of the parameter (x) from equation 1, the standard deviation(s) around the mean value of this parameter, the value of Student's t-statistic and P-value for two-tailed tests, and the significance of both the mean and variance of the distribution as measured through Monte-Carlo simulations. For all of the probability levels, * indicates P < 0.05, ** indicates P < 0.01, and *** indicates P < 0.001 on two-tailed tests. The subscripts L and H on the variance Monte-Carlo results indicate whether the actual stranding value was on the low or high side (respectively) in comparison to the 1000 or more Monte-Carlo simulations.

of dead *Tursiops truncatus* which were highly decomposed when found (decay types 4 and 5 from the Smithsonian listing).

The tendency for most cetaceans to strand near magnetically low spots is apparent in their combined results (Fig. 3A; Table 1). Significantly positive values of the magnetic field deviation parameters are achieved within a 15-km radius of the stranding sites (with the t -statistic), and this becomes and remains very highly significant ($P < 0.001$) above 20 km. This result does not depend upon our use of the deviation parameter of equation 1, as we have obtained similar results using several other measures of where strandings occur relative to local magnetic field variations (including a weighted average of the field deviations up and down the coastline).

The Monte-Carlo simulations, however, present an interesting but somewhat more conservative picture as shown on Fig. 3A. Positive values of the mean deviation parameters are significant in the 30- to 70-km interval, with the highly significant ($P < 0.01$) levels being reached three times. This difference between the Student's t -test and the Monte-Carlo simulations is probably due to the presence of more magnetic highs than lows along the coast as can be seen on Fig. 2 and was mentioned earlier. This asymmetry will tend to add a small positive slope to the diagrams in Fig. 3 which, in turn, will tend to bias the t -tests towards more significant results. For this reason we follow the conservative approach and base our conclusions on the Monte-Carlo results rather than solely on the t -tests.

In addition, the Monte-Carlo simulations reveal that the variance of the deviation parameters for the combined stranding group is abnormally high at radii ranging from 5 to 55 km ($P < 0.05$ to $P < 0.001$). It therefore seems that either the overall set is inhomogeneous (e.g. some small fraction of the cetaceans may be seeking the magnetic highs rather than the lows in which to strand), or that sections of coastline with unusually high magnetic variability tend to attract strandings. To explore further the source of this variance, we subdivided the total stranding data set into the various species and ran the same Monte-Carlo analyses on them.

Highly significant tendencies ($P < 0.01$ or $P < 0.001$) for strandings to happen at magnetic minima were observed in *Lagenorhynchus* (Fig. 3C), *Balaenoptera* (Fig. 3B) and *Globicephala* (Fig. 3D) despite the smaller sample size when compared to the whole group, and significant ($P < 0.05$) tendencies in the same direction were observed in *Tursiops* (Fig. 3I) and *Stenella* (Fig. 3K).

This tendency for cetaceans to strand at magnetically low spots is clearly seen in Fig. 4A,B. In both of these diagrams the profiles of the magnetic field around the stranding events have been superimposed on top of each other with both the relative coastal distance and magnetic fields set to the point (0, 0) in the centre as indicated by the thick horizontal and vertical lines on each diagram. These graphs resemble 'spiders' with long thin legs all radiating out from a central point. If all strandings for a species were to happen exclusively at local magnetic minima, all of the spiders' 'legs' would point forward (up) into the top quadrants on both sides of its centre. Similarly, stranding points at magnetic highs will send the 'legs' downwards into the bottom quadrants, and a magnetically random set of strandings will yield a pattern of legs radiating out in all directions. Both of the spider plots shown in Fig. 4

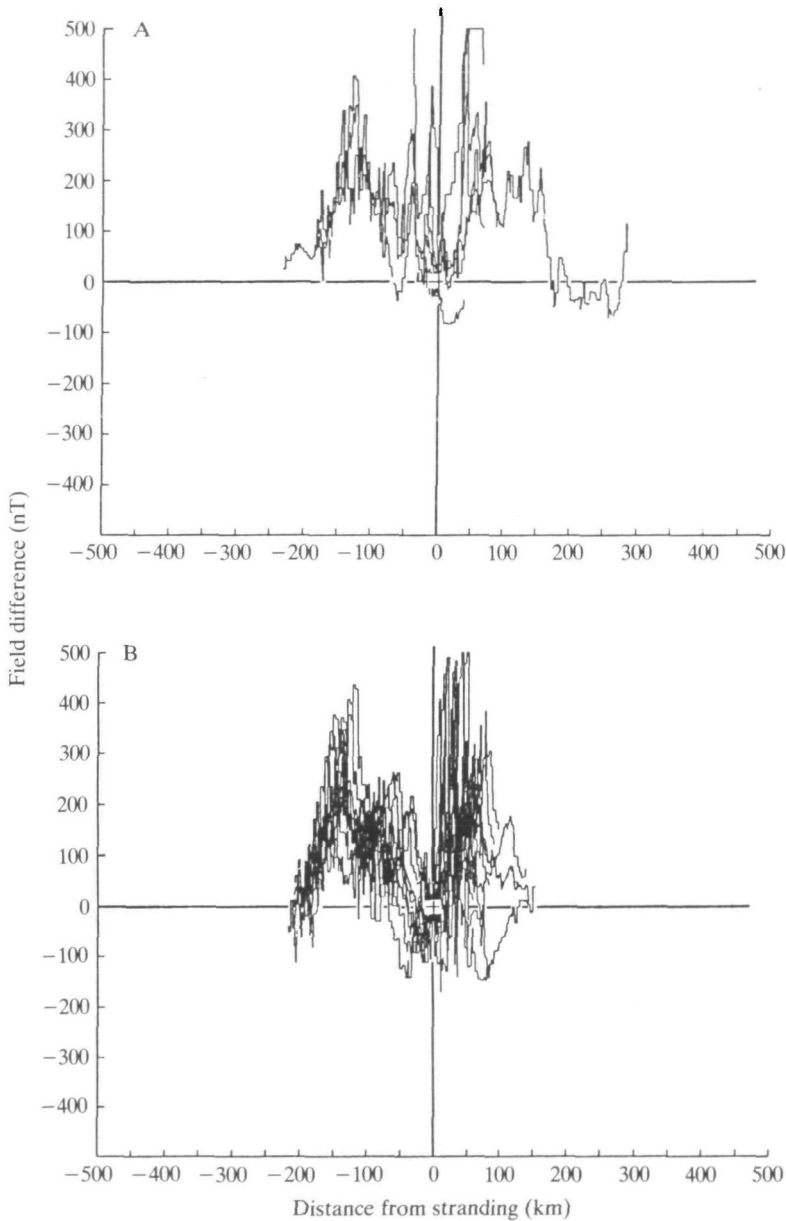


Fig. 4. Spider diagrams of the magnetic field around stranding positions. For both species shown, all of the stranding events have been stacked so that their geographical and magnetic positions coincide at the centre of the diagram. Away from this central point, the magnetic field changes are plotted as a function of total coastline distance within each pixel (north to the right), and each line on the plot is terminated at the end of its respective coastal segment. These diagrams therefore show all of the data which are used in making the diagrams of Fig. 3. The lines (or 'spider legs') will all point upwards away from the centre if strandings are happening at local magnetic minima, and will point downwards if they are at local maxima. Thus, the null hypothesis of no relationship of strandings to the geomagnetic field predicts that there should be roughly equal numbers of 'legs' in each of the four quadrants around the centre of the diagram, which is clearly not the case. (A) *Balaenoptera physalus* (fin whale); (B) *Lagenorhynchus acutus* (Atlantic white-sided dolphin).

are from species (*Balaenoptera physalus* and *Lagenorhynchus acutus*) which give strong results for the analyses of Table 1 and Fig. 3; the average tendency for the arms to point upwards is clear.

On the other hand, three of the groups including *Delphinus* (Fig. 3P), *Grampus* (Fig. 3Q), and the family Ziphiidae (Fig. 3R) display the opposite tendency ($P < 0.05$) of stranding at magnetic highs, with *Delphinus* reaching a very highly significant deviation ($P < 0.001$) at only 5 km. These 22 stranding events, however, are only 10% of the total number of records and by themselves would probably not be enough to cause the large variance noted above in the total stranding group.

Several of the species groups also have surprisingly high variance measurements (indicated by the square symbols on Fig. 3) irrespective of whether or not they have significant tendencies to strand at either minima or maxima. These include *G. melaena* (Fig. 3D,E), the dead *Tursiops* (Fig. 3I), *Phocoena* (Fig. 3L), *Kogia breviceps* (Fig. 3O) and *Delphinus* (Fig. 3P). These high variances are associated with tendencies to strand both at maxima (e.g. *Delphinus*, Fig. 3P) and minima (e.g. *G. melaena*, Fig. 3D). As one might expect, several groups which have this high variance show no significant tendency to strand at minima or maxima, and could be composed of inhomogeneous groups doing both (e.g. *G. melaena*, *Phocoena phocoena*, *Kogia breviceps*) as discussed below.

None of the analyses presented so far give clues as to whether or not any of the cetaceans were following continuous paths of local magnetic minima when they intercepted the coastline. The most continuous such path in our data set, however, is the prominent part of the East-coast magnetic anomaly which runs ashore in the middle of the Georgia coast (seen as a deep blue streak on Fig. 1A). Two of the mass stranding events happen where branches of this East-coast magnetic minimum run ashore. These are the only mass stranding events in Georgia and can be seen in the top diagram of Fig. 2 labelled by the arrows indicating groups of 15 and 53. Both are precisely at the minima of the valleys. Visually at least, our data are compatible with the hypotheses that some of the cetaceans were following these magnetic minima prior to beaching themselves. Although this observation is suggestive, it should be checked with similar data from the prominent marine magnetic lineations over true oceanic crust.

Klinowska (1983) reports using the locations of beached cetacean carcasses as a control for comparison with live stranding events. A major assumption in this approach is that the animals died at sea and were then washed ashore; from the Smithsonian listings used in our study it is often difficult to distinguish this from true live stranding events which were not discovered until long after the animals died and decayed (Mead, 1979). For this reason one might expect some similarity in the magnetic parameters of both live and dead strandings. We ran these analyses on 158 positions for badly decomposed (types 4 and 5) *Tursiops truncatus* given in the Smithsonian listing because this is predominantly a coastal animal (Mead, 1979). We again found a weak but significant correlation with low magnetic fields and a high variance (Table 1; Fig. 3I, radius 5 km), suggesting that this may indeed be the case.

DISCUSSION

It seems clear from the analyses presented above that there is a statistically robust relationship between cetacean live stranding positions and the residual geomagnetic field along the U.S. Atlantic continental margin. Significant tendencies to strand at locations with low magnetic intensity were found in species from both suborders of Cetacea. The question then is whether or not cetaceans possess a geomagnetic sensory system capable of guiding their way, or whether other environmental parameters such as bathymetry or currents could be responsible for the observed effect.

Klinowska (1983 and written communication) found no relationship with the geomagnetic field and the locations of dead whales which washed ashore, indicating that there is no apparent relationship between oceanic water currents, tides and geomagnetic anomalies. (Unlike the American stranding records, it is apparently possible to separate true live stranding events from dead carcasses washing ashore in the British records.) Oceanic currents also tend to intersect the coastline on a much larger scale (thousands of km) than the typical variations in the geomagnetic field (10–100 km scale). Live strandings also seem to happen with roughly equal probability on both rocky and sandy beaches (Geraci & St. Aubin, 1979).

A bathymetric effect is perhaps a more viable alternative hypothesis to account for the observed relationships with the magnetic field. In areas of high latitudes with steep magnetic inclination, a submarine canyon or valley which has cut through geological strata of uniform susceptibility will locally weaken the geomagnetic field at the ocean surface. If cetaceans were attempting to follow such bathymetric features (with echolocation, for example) when they beached themselves, a correlation between stranding location and geomagnetic intensity might result. Of course, this hypothesis predicts the existence of bathymetric relief along the Atlantic continental shelf which mirrors the magnetic variations and requires that the basement has enough magnetic susceptibility to produce measurable anomalies at the surface. To test this hypothesis we examined the large-scale (1:1 000 000) map series compiled by Belding & Holland (1970) and published by the American Association for Petroleum Geologists (AAPG). Most of the offshore topography along the Atlantic continental margin is basically flat, due to the bevelling effect of numerous glacio-genic sea-level transgressions and regressions during the Pleistocene. In general, the topography along this coast is subdued and characterized by barrier islands, with average regional slopes on the shelf of less than 1° (McGregor, 1984). None of the major magnetic lineaments seen in Fig. 1 has any visible relationship with nearshore bathymetry, and even the well-developed submarine canyons off the New Jersey and New York coasts (e.g. Hudson & Baltimore Canyons) fail to show up on the magnetic map of Fig. 1.

The apparent lack of correlation between the bathymetric and aeromagnetic data for the Atlantic margin is a fairly straightforward result of its geological history. The North American plate broke away from the supercontinent of Pangea roughly 160 million years ago during a rifting event which led to the formation of the Atlantic Ocean. As these plates moved apart, the highly magnetic volcanic rocks associated

with the rifting event were gradually buried under a blanket of weakly magnetized sediments which in some areas reach a thickness of 14 km (McGregor, 1984). Thus, with the exception of more recent volcanism associated with seamounts, the magnetic characteristics of the continental shelf are still dominated by deeply buried volcanic rocks. For example, the large magnetic high which marks the transition from the continental shelf to the slope (this is called the 'Blake Spur' magnetic anomaly and can be seen as a NE-SW trending yellow streak on Fig. 1A) is related to the rift-related faulting and volcanism which formed during the break-up event, and can be seen in the seismic profiles of Alsop & Talwani (1984). In contrast, the overlying sediments generally have such a low magnetic susceptibility that even a large valley near the surface will yield little, if any, aeromagnetic expression. Therefore, it seems unlikely that the geomagnetic stranding correlations noted earlier could be an artifact of bathymetry in this region.

The simplest remaining hypothesis is that cetaceans possess a highly developed sensitivity to the geomagnetic field which enables them to use local variations in it for guidance, and that this is reflected in their stranding locations. In turn, this implies the presence of specialized receptors capable of transducing weak geomagnetic stimuli to the nervous system. Note that many of the stranding positions seen on Fig. 2 suggest that total intensity variations of less than 50 nT (0.1% of the total field) are enough to influence stranding location. (Similar K-index correlations imply the same order of sensitivity in birds, a topic which is discussed by Gould, 1982; Kirschvink, 1982, 1983 and Kirschvink & Walker, 1985.)

Klinowska (1983) has also suggested that live cetacean strandings tend to happen where local minima ('valleys') in the geomagnetic total intensity field cross the British coastline, and that they actively avoid entering areas of locally higher intensity. (Note this does not address the question of why they strand.) This effect is similar to the observation of Walcott (1978) that pigeons released at magnetic anomalies are confused. Further analysis of Walcott's data (Gould, 1980, 1982; Kirschvink, 1982) also shows a tendency for the birds to avoid local magnetic highs during the initial phase of flight, a strategy which probably aids in their initial assessment of their position relative to the home loft. The weak strength of the magnetic variations which produce these effects and their occurrence on sunny days (when sun-compass orientation is possible) implies that the response is more than a simple compass one. Rather, it probably depends on an ability to sense small fluctuations or changes in the total intensity field (Kirschvink & Gould, 1981; Kirschvink, 1982).

These variations are so small that the overall effect is probably not the result of a simple directional compass, and the extreme sensitivity is difficult to achieve with a magnetic sensory system based on electrical induction (Jungerman & Rosenblum, 1980; Rosenblum, Jungerman & Longfellow, 1985). Ferromagnetic material (probably magnetite) has been reported in the head region of cetaceans by Zoeger, Dunn & Fuller (1981) and more recently by Bauer *et al.* (1985), but the authors found so much magnetic material in the tissues that they could not focus on any specific site as the focus of a possible sensory organ as has been done for yellowfin tuna, *Thunnus albacares* (Walker *et al.* 1984). Large numbers of magnetite-based magnetoreceptors

could in theory yield the required geomagnetic sensitivities if arranged in a signal-averaging network (Kirschvink, 1979; Kirschvink & Gould, 1981; Yorke, 1981; Kirschvink & Walker, 1985). The recent extraction of chains of magnetite crystals from the dermethmoid tissue of salmon (Kirschvink *et al.* 1985) also suggests that the general vertebrate magnetoreceptor may be something like a modified hair-cell mechanoreceptor; it certainly seems worth conducting similar investigations in cetaceans.

Why is there a general tendency for the strandings to happen at geomagnetic minima rather than maxima? A migrating animal on the oceans would be equally able to follow the magnetic highs, lows, or perhaps the maximum gradients during a long journey, as all of these would help maintain track of relative longitude using the marine magnetic lineations. However, the simplest approach is to follow the local minima, because both the highs and gradients are more prone to a positive susceptibility bias from seamounts and oceanic fracture zones. In addition, many migratory animals regularly cross the boundary between the continental shelf and the oceanic crust in their travels, and a strategy of avoiding high fields and gradients could be used over both continental and oceanic terrains. For this reason, marine magnetic lineations are reasonable features in the magnetosphere for animals to follow, and their relationship with migration routes (if any) warrants further investigation, particularly at sea. Despite this, cetaceans might have other uses for geomagnetic cues even while they are not migrating. Some seamounts (or Guyots), for example, are characterized by higher levels of productivity than the surrounding waters, and cetaceans may exploit this. Seamounts generally produce a large, symmetrical magnetic 'hill' superimposed on the undulating magnetic topography of the oceans, one of which is the only bright yellow spot on the eastern margin Fig. 1B.

A few of the mass stranding events do happen near clear magnetic maxima, an example of which is the group of 35 short-finned pilot whales (*G. macrorhynchus*) which went ashore on Kiawah Island near Charleston, South Carolina, on 2 November 1973 (visible on Figs 1A and 2 as the only mass-stranding event in South Carolina). Coupled with the apparent tendency for three of the groups in the analysis (*Delphinus*, Fig. 3P; *Grampus*, Fig. 3Q; and Family Ziphiidae, Fig. 3R) to strand near magnetic maxima, this would suggest that the cetacean's choice of whether to follow magnetic lows or highs may depend upon a variety of unknown behavioural conditions. The stranding data set may in general be biased towards the lows, as strandings are thought to occur more often in animals which are migrating or otherwise outside their familiar territory (Mead, 1979). However, a smaller fraction of strandings may occur at other times. This line of reasoning predicts that a similar analysis of the position of cetaceans at sea may find seasonal and/or regional shifts from one magnetic state to another depending upon behaviour (e.g. lows may be sought during migration, and the highs might be used during feeding or while trying to remain in one place). A situation of this sort could lead to the high variance values found in several of the species groups mentioned earlier. This is clearly the case of the *G. melaena* mass strandings; as seen in Fig. 3E the variance abruptly changes

from high to low (square to diamond symbols) when the Kiawah Island event is thrown out of the neighbourhood analysis after the 55 km radius.

Results from this study lead to an interesting and testable prediction concerning the abundance of whale bone fossils in tertiary nearshore sediments along the Atlantic continental margin. Locations where such long, continuous magnetic minima cross the coastline (like those in Georgia, Fig. 1A) should generate a substantially higher flux of whale bones to surrounding sediments, and there should be measurable variations in their local abundance associated with the magnetic topography. Similarly, when the Earth's magnetic field reverses itself many of the local minima will turn into local maxima (and *vice versa*), and the stranding flux should shift to other points along the coastline. This predicts that in places where magnetic lows currently cross the coastline, whale bone fossils should be more numerous in sediments deposited during normal polarity intervals than during times of reversed polarity. In a continuous section spanning long intervals of time, it should be possible to predict the magnetic polarity pattern based on the abundance of whale fossils. Numerous sedimentary deposits are known along the Atlantic coastline where this prediction could be tested (e.g. Ray, 1984).

In summary, the cetacean live-stranding records from the U.S. Atlantic continental margin strongly support the hypothesis that they are using some features of the geomagnetic field while finding their way. This study and that of Klinowska (1983) reach similar conclusions, and both predict that cetaceans located and/or tracked at sea should show similar relationships with respect to the marine magnetic lineations. If this proves to be true, it would have major implications for commercial fisheries which exploit magnetically-sensitive fish like tuna (Walker, 1984) and salmon (Quinn, Merrill & Brannon, 1982), as well as perhaps lead to better techniques for resource estimation and management. We are at present testing this hypothesis with sighting records of 25 000 marine animals from the Cetacean and Turtle Assessment Program (U.S. Bureau of Land Management) along the Atlantic Margin.

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