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Geographic and temporal variations in strandings of beaked whales (Ziphiidae) on the coasts of the UK and the Republic of Ireland from 1800-2002

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ABSTRACT

This study analyses published records of beaked whale strandings from the coasts of the UK and the Republic of Ireland between 1800 and 2002. Strandings of northern bottlenose whales (*Hyperoodon ampullatus*) were lowest in April and highest in September. The number of strandings between months differed significantly from an even spread over all months of the year, with more strandings between July and October. Most strandings in late summer and autumn occurred on North Sea coasts and their stomach contents included the squid *Gonatus fabricii*, which is found only in more northern waters. This suggests that these whales may be migrating southward at this time of year. Most strandings of Sowerby's beaked whales (*Mesoplodon bidens*) also occurred in late summer and autumn, although this was not significant. Strandings of Cuvier's beaked whales (*Ziphius cavirostris*) occurred almost exclusively on the Atlantic coasts of the UK and in Ireland. There were significantly more Cuvier's beaked whale strandings than expected in January and February and in June and July. A Cuvier's beaked whale which stranded in northern Scotland in February contained similar prey to two whales stranded in north-western Spain at the same time of year, suggesting this animal could have been feeding in more southern waters prior to stranding. Seasonal patterns of strandings of northern bottlenose and Cuvier's beaked whales were significantly different with more of the former stranding in August to October and more of the latter from November to July. This is consistent with a hypothesis of temporal segregation between the two species to reduce potential competition for prey.

KEYWORDS: DISTRIBUTION; MIGRATION; NORTHERN HEMISPHERE; MOVEMENTS; NORTHERN BOTTLENOSE WHALE; SOWERBY'S BEAKED WHALE; CUVIER'S BEAKED WHALE; STRANDINGS; NORTH ATLANTIC; NORTH SEA

INTRODUCTION

The beaked whales (Ziphiidae) are one of the most enigmatic families of marine mammals and much of their biology remains unknown. This is due, in part, to their oceanic distribution and preference for deep waters beyond the shelf edge. As a result, much of what is currently known about beaked whales comes from the study of stranded animals. Oceanic cetaceans may strand for two basic reasons, they may die or become incapacitated and be carried by currents to where they strand, or they may make 'navigational errors' and travel into shallow waters, where they become disoriented or suffer from a lack of suitable food, and subsequently strand (e.g. Klinowska, 1985). Around the coasts of Britain and Ireland, the main surface currents are dominated by the North Atlantic Drift (North Atlantic current) and travel north along the western coasts with branches of currents heading into coastal regions, such as the English Channel, Bristol Channel, Irish Sea and the Sea of the Hebrides. Strandings in these areas may represent passively transported individuals. In terms of potential 'navigational errors', there are a number of locations which could act as 'traps' for oceanic cetaceans around the coasts of the UK and Ireland, such as the North Sea (considered by Smeenk (1997) to be a sperm whale trap).

Records of stranded cetaceans can be used to infer information on a variety of aspects of their biology, such as distribution, diet, timing and routes of migrations, contaminant burdens, reproduction and genetic composition of populations (e.g. Katona *et al.*, 1988; Law *et al.*, 1996; Smeenk, 1997; MacLeod, 2000; Santos *et al.*, 2001a; b). However, data obtained from strandings have a number of inherent biases and weaknesses which must be taken into account when interpreting such data (Klinowska, 1985). Using information from a large number of stranding events collected over a long time period in any analysis will counteract some of the limitations, in particular reducing the importance of a small number of 'atypical' strandings events, and may allow the separation of regular patterns from random variation. However, with oceanic species, such as beaked whales, strandings are relatively rare events and long time series of data are required to obtain sufficient numbers of strandings to investigate any aspect of their biology.

One of the longest continuous time series of strandings records comes from the coasts of the UK and the Republic of Ireland (Klinowska, 1985). Systematic records have been kept continuously since 1913 and have been published on a regular basis (Harmer, 1914; 1915; 1916; 1917; 1918; 1919; 1921; 1923; 1924; 1927; Fraser, 1934; 1946; 1974; Sheldrick, 1989; Sheldrick *et al.*, 1994). In addition, non-systematic records of beaked whale strandings are available at least as far back as 1800 (e.g. Sowerby, 1804). To date, six species of beaked whales have been recorded stranded on the coasts of the UK and Ireland (e.g. Harmer, 1927; Herman *et al.*, 1994; Berrow and Rogan, 1997).

Beaked whale strandings around the UK and Ireland have previously been investigated on a number of occasions (e.g. Fraser, 1974; Evans, 1980; Sheldrick, 1989; Sheldrick *et al.*, 1994; Berrow and Rogan, 1997). Some of these studies have provided summaries of strandings over relatively short time periods (Fraser, 1974; Sheldrick, 1989; Sheldrick *et al.*, 1994). Berrow and Rogan (1997) discussed the seasonal pattern of strandings of beaked whales, amongst other cetacean species, in Ireland while Evans (1980) mentions beaked whales as part of general discussions of cetacean distribution in the northeast Atlantic. None of these previous investigations have covered the whole area (UK and Ireland) and/or time-frame (1800-2002) encompassed by this study, nor included any statistical analysis of beaked whale strandings patterns. For three of these species (the northern

bottlenose whale *Hyperoodon ampullatus*, Sowerby's beaked whale *Mesoplodon bidens*, and Cuvier's beaked whale *Ziphius cavirostris*), the number of individuals recorded is now sufficient to allow a detailed investigation of geographic and temporal variations in the number of strandings.

In UK and Irish waters, northern bottlenose whales have been sighted in the deep water beyond the shelf edge both to the west of Ireland and Scotland and to the north in the Faroe-Shetland channel (Pollock *et al.*, 2000; O Cadhla *et al.*, 2001). In addition, this species has been sighted as far north as the Norwegian Sea, and in the past was hunted in this area and around Iceland (Sigurjónsson and Vikingsson, 1998; Bjorke, 2001). Similarly, Sowerby's beaked whale has been sighted in deep water to the west of Ireland, to the north and west of Scotland and as far north as 71°30'N in the Norwegian Sea (Carlström *et al.*, 1997; Pollock *et al.*, 2000; O Cadhla *et al.*, 2001). In addition, both species have been recorded in winter months (November to February) in the Bay of Biscay to the south of the UK and Ireland (Brereton and Williams, 2001). The nearest location where Cuvier's beaked whales have commonly been sighted is in the southern Bay of Biscay, around 600-700km to the south of the UK coast (Williams *et al.*, 1999). However, Cuvier's beaked whales are also known to occur in the deep waters to the west of Ireland (Pollock *et al.*, 2000; O Cadhla *et al.*, 2001) and there is one sighting as far north as northern Scotland (Evans, 1992). Nevertheless, there are no confirmed records of Cuvier's beaked whales further north than this in the northeastern Atlantic.

In other parts of the world, beaked whale occurrence is known to vary throughout the year. For example, along the Pacific coast of Japan, Baird's beaked whales (*Berardius bairdii*) appear in May, densities increase during the summer and this species disappears from these waters by December (Kasuya and Miyashita, 1997). Similarly, Cuvier's beaked whales were caught throughout the year in southern Japan, but were caught in more northern areas only from July to December (Nishiwaki and Oguro, 1972). In the northeast Atlantic, an annual southward movement of northern bottlenose whales has been inferred from variations in catches in a number of fisheries which took this species. In the Norwegian Sea, a southward migration apparently begins in July, with most northern bottlenose whales having left this area by August, although some remain behind until November (Mitchell and Kozicki, 1975). Around Iceland, catches of northern bottlenose whales occurred from the end of March until the start of November, with the greatest numbers being caught at the start of July (Sigurjónsson and Vikingsson, 1998). Similarly in the Faroes, although whales may be caught all year round in the local drive fishery, the majority of northern bottlenose whales have been caught from August to October, and this is presumed to coincide with an autumn migration past the east of the Faroes (Bloch *et al.*, 1996). Previous studies have suggested that there are also seasonal movements of beaked whales around the UK and Ireland. For example, Mitchell and Kozicki (1975) suggested that strandings of northern bottlenose whales reflect a north-south seasonal movement in UK and Irish waters. However, other authors, such as Hooker (1999), have suggested this evidence is not clear-cut and that other explanations for the observed strandings patterns are possible, such as offshore-nearshore movements.

In the present study, records from the UK and Ireland were analysed to identify geographical and seasonal patterns in strandings of three species of beaked whales, which may relate to variations in patterns of distribution of living animals in the area. Published information on stomach contents of stranded beaked whales from the northeast Atlantic were used to infer the direction and extent of movements of beaked whales prior to stranding.

In addition, MacLeod *et al.* (2003) hypothesised that *Ziphius* and *Hyperoodon* species occupy a similar dietary niche with a high potential for competition between species from these two genera. If this is true, there must be some mechanism to limit competition. They proposed spatio-temporal segregation, with each species either occurring in different areas or occupying the same areas at different times. Within the northeast Atlantic, northern bottlenose whales and Cuvier's beaked whales occupy a similar dietary niche, feeding on similar-sized individuals of the same species (e.g. Santos *et al.*, 2001a; b), so conforming with the hypothesis of dietary niche overlap with high potential competition between these species. Therefore, the strandings data were investigated to see if there was any support for the proposed spatio-temporal segregation.

METHODS

Data on beaked whale strandings between 1800 and 2003 were collated from published records (Harmer, 1914; 1915; 1916; 1917; 1918; 1919; 1921; 1923; 1924; 1927; Fraser, 1934; 1946; 1974; Sheldrick, 1989; Herman *et al.*, 1994; Sheldrick *et al.*, 1994; Berrow and Rogan, 1997; Smiddy, 1997; MacKay *et al.*, 1998; 2002; Berrow and Storer, 2001; Berrow and Dalebout, 2002; Berrow *et al.*, 2002; Quigley and Flannery, 2002), on-line databases (Irish Whale And Dolphin Group Strandings Database: *www.iwdg.ie/strandings*) and recent unpublished data (SAC Veterinary Science Division, unpublished data; Natural History Museum, unpublished data). For each record, information on the location, date and species was entered into a database. For almost all records, published locations were listed only by place names or map references which were converted into latitude and longitude.

Strandings were not sub-divided by cause of stranding. Accurately identifying the true cause of a stranding is often not possible. For example, animals which make navigational errors may then suffer from a lack of available food which can affect their health and subsequently lead to death from starvation or infection. In such a case, the original navigational error cannot be picked up from an examination of the carcass except possibly through the location of the animal. Conversely, illness or poor health may lead to navigational errors and subsequent stranding.

Similarly, there was no separation of records into live or dead strandings. Within the area covered by this study, there are regions with relatively remote coastlines, such as parts of Ireland or northwest Scotland, where strandings may not be detected for several days, or more, after they occur. Therefore, although the condition of an animal when it was found is known, it is not always certain whether it was alive or dead when it came ashore. This is particularly true of older records when communications were not as fast as today.

Finally, unless individuals were specifically known to have stranded together at the same place and time, they were considered separate data points. This avoided any possible problems in trying to ascertain whether individuals which stranded in close proximity in space and/or time were in reality linked in any way and if so how. Although this may lead to some stranding events being counted twice, the number of such possible double counts was low (under 2% of all cases).

The area under consideration was separated into seven separate regions (Fig. 1): northern Atlantic coasts (Cape Wrath to John O'Groats, including the Northern Isles); mid-Atlantic Coasts (from a line approximating the Islay Front between Ireland and southern Scotland to Cape Wrath, including the Western Isles); southern Atlantic coasts (from Cork in Ireland along south-west and west Irish coasts to the Islay Front area); Irish Sea Coasts (from Cornwall on the west coast of the UK and Cork in Ireland north through the Irish Sea to the Islay Front); the northern North Sea coasts (John O'Groats to just south of Sunderland and consisting of the northern half of the UK North Sea coastline); southern North Sea (the southern half of the UK North Sea coasts) and English Channel coasts (from Dover to Lands End, including the Channel Islands). The number of individuals of each species of beaked whale stranded in each region was recorded by month and the data were examined for geographic and temporal variations. Chi-squared tests were used to test the null hypothesis that strandings for each species did not differ significantly from an even spread between each month of the year, while Kolmogorov-Smirnov tests were used to test the null hypothesis that there were no differences in the distributions of strandings in each month between pairs of regions. This last analysis was only conducted for regions with 10 or more stranding events.

To test whether strandings patterns are consistent with the hypothesis of spatio-temporal segregation between northern bottlenose whales and Cuvier's beaked whales, the numbers of individual whales stranding in four time periods during the year (November to January, February to April, May to July and August to October) were compared using a Chi-Squared test. This analysis was undertaken only for strandings in western regions (northern, mid and southern Atlantic and Irish Sea coasts), the area where spatio-temporal segregation has been hypothesised to occur and for the period of systematic recording of strandings (1913-2002).

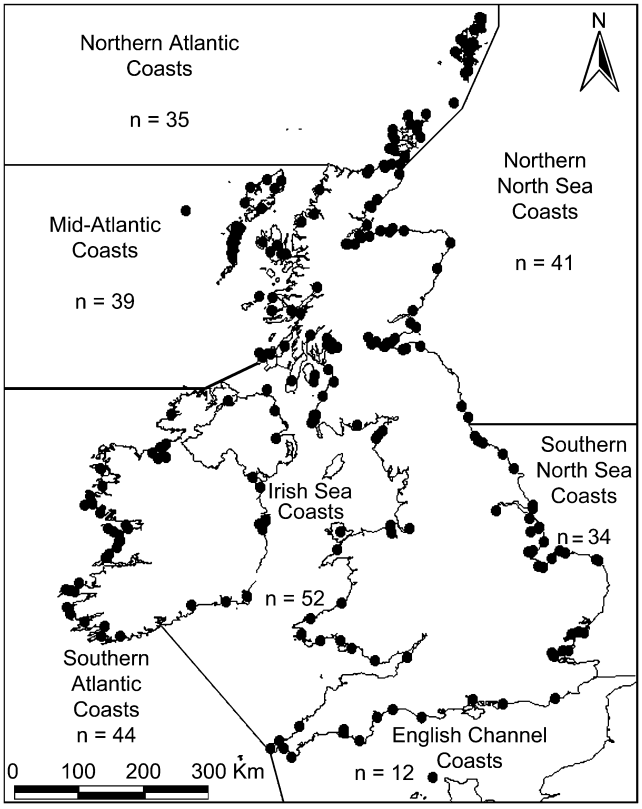

Fig. 1. Regions of the United Kingdom and the Republic of Ireland used in analysis of beaked whale strandings. Black dots represent strandings records for beaked whales between 1800 and 2002.

RESULTS

Records of 257 beaked whale strandings which occurred between 1800 and 2002 were located. Of these, 251 were listed as identified to species level. These were 109 northern bottlenose whales, 70 Sowerby's beaked whales, 63 Cuvier's beaked whales, 7 True's beaked whales (*Mesoplodon mirus*), 1 Gervais' beaked whale (*Mesoplodon europeaus*) and 1 Blainville's beaked whale (*Mesoplodon densirostris*). For all regions, with the exception of the English Channel which only had 12 stranding records, the numbers of strandings were of the same order of magnitude (between 34 to 52 —Fig. 1). The locations of strandings of northern bottlenose whales, Sowerby's beaked whales and Cuvier's beaked whales are plotted in Fig. 2.

Northern bottlenose whales

Strandings of northern bottlenose whales were highest in September ($n = 33$) and lowest in April ($n = 0$) and the intra-annual pattern of strandings differed significantly from an even spread across all months ($\chi^2 = 114.1$, d.f. = 11, $p < 0.001$ —Fig. 3a). Fewer strandings occurred than expected between November and June (significantly fewer in December and April: $\chi^2 = 5.3$, d.f. = 1, $p = 0.022$ and $\chi^2 = 8.8$, d.f. = 1, $p = 0.030$ respectively) while there were more strandings than expected between July and October (significantly more in August, September and October: $\chi^2 = 5.8$, d.f. = 1, $p = 0.016$; $\chi^2 = 66.1$, d.f. = 1, $p < 0.001$; $\chi^2 = 14.1$, d.f. = 1, $p = 0.0002$ respectively).

The number of northern bottlenose whales stranded in each region varied from four strandings on English Channel coasts to 36 on Irish Sea coasts (Fig. 2). Between the different regions, there were differences in the month of peak strandings (Fig. 3a). On northern Atlantic coasts, the peak number of strandings occurred in June, on the mid-Atlantic coasts the peak was in October, September on Irish Sea coasts and August and September on south Atlantic coasts. On North Sea coasts, strandings of northern bottlenose whales peaked in September in the northern region and July and August in the southern region. On English Channel coasts, the total number of strandings (4 events) was too low to consider seasonality. Five regions had a sufficient number of strandings to allow comparisons of the distribution of strandings with month. The distribution of strandings by month differed significantly between the northern Atlantic region and all regions which were compared to it (mid-Atlantic coasts: D = 0.627, $n_1 = 11$, $n_2 = 10$, $p < 0.05$; Irish Sea coasts: D = 0.652, $n_1 = 11$, $n_2 = 36$, $p < 0.05$; northern North Sea coasts: D = 0.527, $n_1 = 11$, $n_2 = 20$, $p < 0.05$; southern North Sea coasts: D = 0.616, $n_1 = 11$, $n_2 = 8$, $p < 0.05$). Therefore, it was concluded that there was a difference in the distribution of strandings by month between northern Atlantic coasts and the other regions and that the peak of strandings in this region occurs earlier in the year (June) than in other regions (July to October depending on region). However, there were no significant differences between mid-Atlantic coasts and Irish Sea coasts (D = 0.144, $n_1 = 10$, $n_2 = 36$, $p > 0.05$) or between the two North Sea regions (D = 0.489, $n_1 = 20$, $n_2 = 18$, $p > 0.05$).

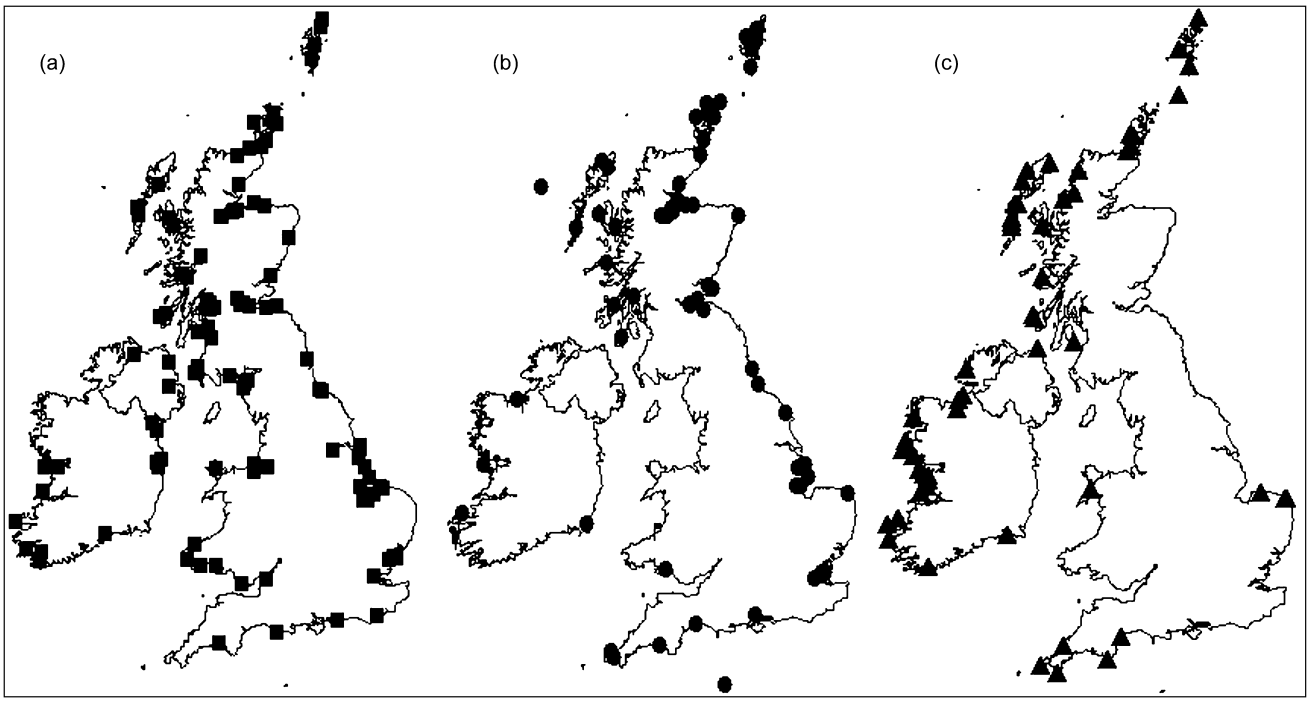

Fig. 2. Locations of strandings of: (a) northern bottlenose whales; (b) Sowerby's beaked whales; and (c) Cuvier's beaked whales on the coasts of the United Kingdom and the Republic of Ireland between 1800 and 2002.

Sowerby's beaked whales

While the number of strandings of Sowerby's beaked whales varied between months (Fig. 3b), with the highest numbers occurring between July and October, this did not differ significantly from an even spread across all months ($\chi^2 = 12.6$, d.f. = 11, $p = 0.323$). The number of strandings varied from four on south Atlantic coasts to 20 on northern North Sea coasts. Between the different regions, there were differences in the timing of the majority of strandings. On northern Atlantic coasts, most strandings occurred between March and August (11 out of 14) and on the mid-Atlantic coasts between July and September (6/8). Both the Irish Sea coasts and the southern Atlantic coasts had no obvious periods with higher numbers of strandings. On North Sea coasts, most strandings occurred between August and October (11/20) in the north and between July and October (10/13) in the south. Again, on English Channel coasts the total number of strandings (5 events) was too low to identify any definite peaks in occurrence. Three regions had a sufficient number of strandings to allow comparisons of the distribution of strandings with month. The distribution of strandings by month did not differ significantly between the northern Atlantic coasts and northern North Sea coasts ($D = 0.386$, $n_1 = 14$, $n_2 = 20$, $p > 0.05$) or southern North Sea coasts ($D = 0.489$, $n_1 = 14$, $n_2 = 13$, $p > 0.05$) or between the two North Sea regions ($D = 0.196$, $n_1 = 20$, $n_2 = 13$, $p > 0.05$). Therefore, the null hypothesis that there was no difference in the distribution of strandings in each month between these regions was accepted.

Cuvier's beaked whales

Strandings of Cuvier's beaked whales were highest in July and January ($n = 11$ in both) and lowest in October and November ($n = 1$ in both) and the pattern of strandings differed significantly from an even spread across all months ($\chi^2 = 30.6$, d.f. = 11, $p = 0.001$). Fewer strandings than expected occurred in April and May and between August and December and there were more strandings than expected in January and February and in June and July (significantly more in January and July: $\chi^2 = 8.59$, d.f. = 1, $p = 0.003$; $\chi^2 = 8.60$, d.f. = 1, $p = 0.003$ respectively). The number of Cuvier's beaked whale strandings varied from zero on the northern North Sea coasts to 21 on mid-Atlantic coasts. Only the three Atlantic regions and the Irish Sea coasts had more than three strandings per region. In all of these four regions, most strandings occurred between January and July (Fig. 3c). Only two regions, the mid and southern Atlantic coasts, had sufficient numbers of strandings to allow the frequency of strandings in each month to be compared. The difference between these regions was not significant ($D = 0.336$, $n_1 = 21$, $n_2 = 16$, $p > 0.05$) and therefore, the null hypothesis that there were no differences in the frequency of strandings in different months between the two regions was accepted.

In terms of the frequency of strandings in different months, northern bottlenose whales (NBW), Sowerby's beaked whales (SBW) and Cuvier's beaked whales (CBW) all differed significantly from each other (NBW vs SBW: $D = 0.224$, $n_1 = 106$, $n_2 = 69$, $p < 0.05$; NBW vs CBW: $D = 0.556$, $n_1 = 106$, $n_2 = 56$, $p < 0.05$ and SBW vs CBW: $D = 0.224$, $n_1 = 69$, $n_2 = 56$, $p < 0.05$). Therefore, in each case the null hypothesis was rejected and it was concluded that there were significant differences in the frequency of strandings in each month between each species. Northern bottlenose whales have a strong peak in strandings between July and October, while strandings of Sowerby's beaked whales are more evenly spread throughout the year. Cuvier's beaked whales differ from both of these species as most strandings occurred between January and July.

Other species

Of the remaining three beaked whale species recorded from the UK and Ireland, True's beaked whale has the most strandings records (7), all from southern Atlantic coasts and spread throughout the year. Gervais' beaked whale and Blainville's beaked whale were both recorded only once, Gervais' beaked whale from the southern Atlantic region in January and Blainville's beaked whale from the Irish Sea in July.

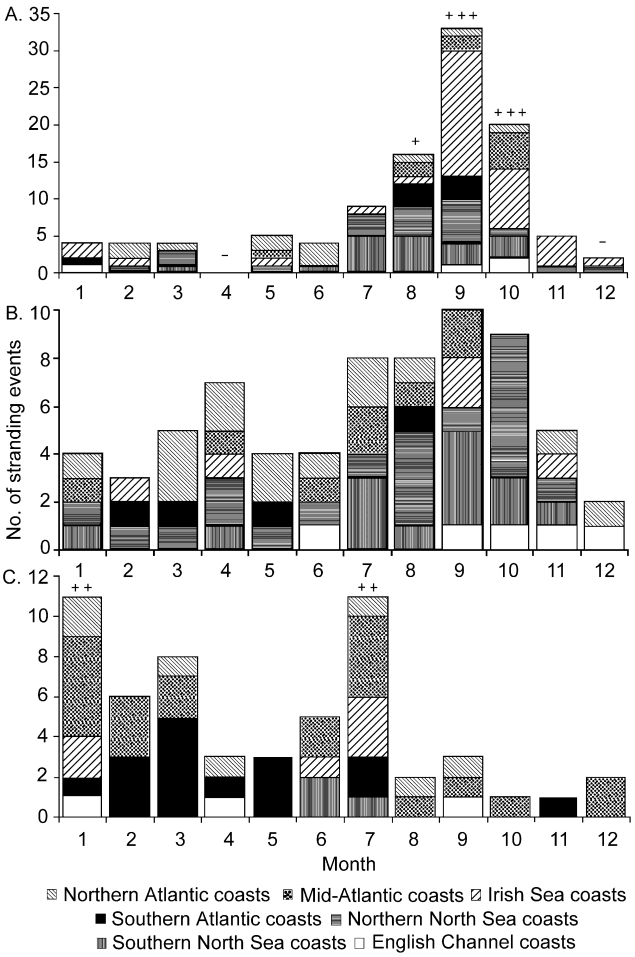

Fig. 3. Number of strandings for different beaked whale species in each month and region of the United Kingdom and the Republic of Ireland (1800-2002). Minus (-) signs indicate values which are significantly lower than expected if strandings were evenly spread throughout all months and plus (+) signs indicate significantly higher than expected (+ or —: $0.05 > p \geq 0.01$; ++ or – $0.01 > p \geq 0.001$; +++ or --- $p < 0.001$). A = Northern bottlenose whales; B = Sowerby's beaked whales; C = Cuvier's beaked whales.

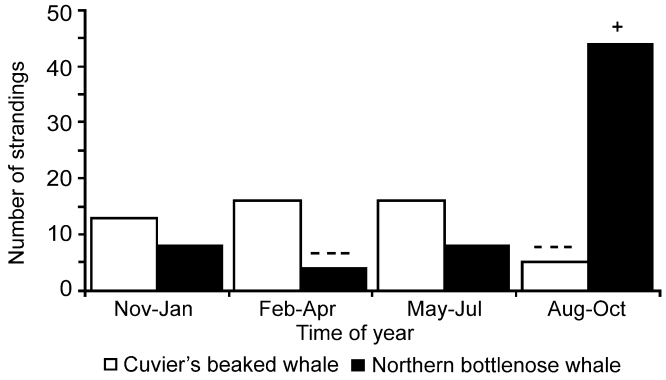

Fig. 4. Number of strandings in western regions of the United Kingdom and the Republic of Ireland (northern, mid and southern Atlantic and Irish Sea coasts) of northern bottlenose whales and Cuvier's beaked whales in three month periods between 1913 and 2002 (the period where systematic recording of strandings has occurred). Minus (-) signs indicate values which are significantly lower than expected if both species had the same seasonal pattern of strandings and plus (+) signs indicate significantly higher than expected. (+ or —: $0.05 > p \geq 0.01$; +++ or ---: $p < 0.001$).

Comparison of northern bottlenose and Cuvier's beaked

The number of northern bottlenose whale and Cuvier's beaked whale strandings in western regions (the three Atlantic regions and Irish Sea coasts) between 1913 and 2002 in four periods of the year (November to January, February to April, May to July and August to October) differed significantly from the expected values ($\chi^2 = 85.4$, d.f. = 3, $p < 0.001$ —Fig. 4). In this comparison, more Cuvier's beaked whale strandings occurred from November to July and significantly fewer than expected from August to October ($\chi^2 = 54.4$, d.f. = 1, $p < 0.001$). Northern bottlenose whales showed a reverse trend with fewer strandings than expected from November to July (significantly less in February to April: $\chi^2 = 13.1$, d.f. = 1, $p = 0.0003$) and significantly more than expected from August to October ($\chi^2 = 6.2$, d.f. = 1, $p = 0.013$).

DISCUSSION

Interpreting the distribution of living animals from strandings records is problematic, particularly when trying to infer seasonal variations in their distribution. This is particularly true of oceanic species, which are not usually found in coastal waters. An animal which dies far from shore may be carried long distances on surface currents or by prevailing winds. When stranding rates vary with season, this may reflect changes in species distribution, but it could also reflect changes in the likelihood of dead animals reaching the shore. In particular, seasonal changes in current speed, strength or direction, changes in wind strength and direction and changes in the frequency of storms could all affect the rate of stranding of oceanic species on the nearest coasts. Therefore, care must be taken that any seasonal changes in the distribution of a species inferred from seasonal changes in stranding patterns are both biologically plausible and are consistent with findings from other avenues of investigation.

Northern bottlenose whales

The variations in the numbers of individual beaked whales stranding in the different regions might reflect patterns of movements of beaked whales. For northern bottlenose whales, the variation in number of individuals stranding in different months suggests a period of movement around the coasts of the UK and Ireland between July and October, with a peak in September when most strandings occurred. Such movements may represent north-south migrations or offshore-nearshore movements, or a combination of the two. The significant difference in the frequency of strandings in each month between the northern Atlantic region and other regions to which it was compared, with the peak in strandings occurring earlier in the summer than more southern regions, suggests there may be a southerly component in the direction of movement of northern bottlenose whales at this time of year.

Stomach contents of stranded northern bottlenose whales in the North Sea in later summer and early winter contained mainly the hard remains (the chitinous mandibles) of the oceanic squid *Gonatus fabricii* (Clarke and Kristensen, 1980; Lick and Piatkowski, 1998; Santos *et al.*, 2001b). The prevalence of this cephalopod species in the diet, for which the southern limit of distribution is believed to be the southern Norwegian Sea (Bjorke, 1995), suggests that the whales had previously been feeding in the northern North Atlantic. Smeenk (1997) suggested that sperm whales (*Physeter macrocephalus*) which strand in the North Sea in winter are animals which have mistakenly entered this area during southward migrations in late autumn and that the

North Sea effectively functions as a trap for such oceanic species during southward movements. This hypothesis is consistent with the strandings of northern bottlenose whales in the North Sea reported here; the large number of strandings of northern bottlenose whales at this time of year may represent animals which have moved south from the northern North Atlantic and inadvertently entered the North Sea. While in the North Sea whales may try to continue their usual movement in a south-westerly direction (which would normally take them through the deep water to the west of the UK and Ireland) and as a result strand in areas which appear to offer 'outlets' to the south-west. This would explain why northern bottlenose whale strandings in the western North Sea are clustered in estuaries, such as the Moray Firth, the Firth of Forth, the Humber Estuary and the Thames estuary, which run inland in a westerly direction from the coast. This has also been suggested for sperm whales stranding in the North Sea (Santos *et al.*, 1999). The peak in strandings of northern bottlenose whales reported here for September occurs two months after reported movements of animals from the Norwegian Sea and peak catches around Iceland, and one month after the start of increased catches in the Faeroes, suggesting that the movements may be part of a larger-scale movement throughout the northern northeast Atlantic (Mitchell and Kozicki, 1975; Bloch *et al.*, 1996; Sigurjónsson and Vikingsson, 1998). This suggests that the peak in numbers of northern bottlenose whale strandings in late summer and autumn most likely reflects a southward movement of whales rather than a simple offshore-nearshore movement.

Northern bottlenose whales are generally sighted in deep waters beyond the shelf edge to the north and west of the British Isles. The southward movement in late summer and autumn suggested by the stranding pattern presumably takes place primarily in such waters. If this is the case, deep water areas, such as the Faroe-Shetland Channel, may form 'corridors' for movements of northern bottlenose whales. However, some animals may also move into shallower shelf waters during the southward movements. For example, whales are occasionally seen in the coastal waters between the Western Isles and mainland Scotland, particularly in August and September (Evans, 1992). The high numbers of strandings in the Irish Sea at this time of year suggests animals may also pass through this area as they travel south. There are at least three possible reasons for animals entering such coastal waters as they move south. These are: (1) navigational errors similar to those which take animals into the North Sea 'trap'; (2) animals following movements of prey which enter coastal waters at the time northern bottlenose whales move south; and (3) that such areas are used as 'short cuts' between deep water areas such as the Faroe-Shetland Channel and the Rockall Trough or the Bay of Biscay. Currently, there are insufficient data to test which, if any, of these possibilities is correct.

If the grouping of strandings in July to October for northern bottlenose whales represent animals which are moving south, there may be an opposite movement of animals at other times of the year. Strandings of northern bottlenose whales between January and March (Fig. 3a), may be representative of a second period of movement heading in a northward direction. This is supported by the fact that a male northern bottlenose whale which stranded in Denmark in February contained a mandible from the octopod *Vampiroteuthis infernalis* which has not been recorded further north than Spain (Santos *et al.*, 2001b) and had a more varied diet than those whales stranded later in the year. The smaller number of strandings early in the year may indicate either that animals move northward further offshore than their southward movements, as suggested by Evans (1980), or that animals are less prone to fall into navigational 'traps', such as the North Sea, when moving north and so strand in lower numbers.

Sowerby's beaked whales

Little is known about the distribution of Sowerby's beaked whales around the UK and Ireland. Only a small number of definite sightings have been recorded, all in deep waters beyond the shelf edge (e.g. Pollock *et al.*, 2000). Most strandings occur along North Sea coasts and this led some people to suggest that the North Sea area was the centre of distribution for this species (e.g. Moore, 1966). However, despite high levels of survey effort (e.g. Hammond *et al.*, 1995; 2002), there are no published definite sightings of Sowerby's beaked whales in the North Sea. In addition, most sightings of Sowerby's beaked whales which have been recorded have occurred in waters deeper than 500m (e.g. Hooker and Baird, 1999; Pollock *et al.*, 2000), compared with water depths of less than 200m available in the North Sea. Therefore, it is unlikely that the North Sea is a normal part of the range of this species (MacLeod, 2000). Although month-to-month variation in numbers of strandings was not statistically significant, most recorded strandings occurred between July and November with a possible secondary peak in April (Fig. 3b). In addition, as in northern bottlenose whales, strandings of this species on North Sea coasts in late summer and autumn were concentrated in estuaries. The similarities in the geographic distribution of strandings between this species and northern bottlenose whales suggests that the two species may have similar seasonal movements, and that Sowerby's beaked whales also move southward in late summer and autumn, with some animals getting caught in the North Sea trap, and northward in late winter and spring. However, the comparison of strandings frequency in each month suggests that although the geographic pattern may be similar between northern bottlenose whales and Sowerby's beaked whales, the extent and/or timing of these movements may differ. There is little available stomach contents information on Sowerby's beaked whales in the northeast Atlantic that could be used to infer where these animals had been feeding prior to stranding, and more data are needed.

Cuvier's beaked whales

In contrast to northern bottlenose whales and Sowerby's beaked whales, most Cuvier's beaked whale strandings occur in the first half of the year, between January and July. Within this time there are two apparent peaks, one between January and March and one in June and July (Fig. 3). In addition, there are very few strandings of Cuvier's beaked whales from North Sea coasts, where high numbers of strandings of the other two species occur. Furthermore, all the Cuvier's beaked whale strandings in the North Atlantic region have occurred between March and September. This strongly suggests that Cuvier's beaked whales have a different pattern of seasonal distribution than either northern bottlenose whales or Sowerby's beaked whales.

Firstly, these data suggest Cuvier's beaked whales do not routinely go far enough north to enter the North Sea 'trap' at any time, as indicated by the lack of strandings on North Sea coasts. Therefore, we propose that the normal northern limit of Cuvier's beaked whale in the northeast Atlantic is located somewhere around the latitude of the Shetland Islands (around 60°30'N) and that this species does not regularly occur in more northern areas of the northeast Atlantic, such

as the Faroe-Shetland Channel or the Norwegian Sea. However, Cuvier's beaked whales may occur at more northern latitudes in the central North Atlantic as there have been a small number of strandings in Iceland (Petersen, pers. comm.). This difference in distributional limits between the northeast and central North Atlantic may reflect a similarity in sea surface temperatures in southern Iceland and Shetland. Secondly, the proposed northern limit in the northeast Atlantic may only be reached in spring and summer months, the only time when strandings occur on northern Atlantic coasts. This, combined with the bimodal peak in strandings suggests that Cuvier's beaked whales may move northward between January and March to the most northern waters of their range in the northeast Atlantic in spring and summer, before moving southward again from June onwards. The stomach of a Cuvier's beaked whale stranded in North Uist in the mid-Atlantic region in February contained no fresh remains of cephalopods and most of the species identified in the diet were similar to those found in the stomachs of two Cuvier's beaked whales stranded in northwestern Spain in February (Santos *et al.*, 2001a). This suggests that the Scottish individual had been feeding further south and may have recently moved into more northern waters before stranding.

Other species

The lack of strandings in any regions other than Ireland and the small total number of strandings suggests that True's beaked whales occur only in more southern waters to the south of Ireland, and possibly as far north as Irish waters on occasions. However, all the animals could have been transported from further south by the prevailing surface currents. Similarly, the strandings of Gervais' beaked whale and Blainville's beaked whale are consistent with a more southern distribution, either with a very occasional occurrence in southern UK and Irish waters or with these animals being transported by prevailing surface currents from further south.

Comparison of northern bottlenose and Cuvier's beaked

The strandings data suggest that there are differences between northern bottlenose whales and Cuvier's beaked whales in their patterns of occurrence around the UK and Ireland. Northern bottlenose whales occur further north than Cuvier's beaked whales, which do not routinely appear to occur north of Shetland in the northeast Atlantic, while northern bottlenose whales regularly enter the North Sea, presumably from waters north of Shetland (a possibility supported by stomach contents data). This is indicative of spatial segregation between the two species in the more northern regions of the northeast Atlantic. The seasonal distribution of strandings also suggests that there is some temporal segregation in the Atlantic waters to the west of the UK and Ireland. Cuvier's beaked whales appear to move northward into these waters in late winter and spring (again supported by stomach contents data) and southward out of the most northern waters in this area in summer. In contrast, the peak in strandings of northern bottlenose whales does not occur until late summer and early autumn, when animals may be moving southward into this area. These differences in spatial and temporal distribution of strandings between these two species are consistent with the hypothesis of spatio-temporal segregation between *Ziphius* and *Hyperoodon* to reduce potential competition for the same prey resources proposed by MacLeod *et al.* (2003).

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