Seasonal distribution of white-beaked dolphins (*Lagenorhynchus albirostris*) in UK waters with new information on diet and habitat use

SARAH J. CANNING[1,4], M. BEGOÑA SANTOS[1,2], ROBERT J. REID[3], PETER G.H. EVANS[4], RICHARD C. SABIN[5], NICK BAILEY[6] AND GRAHAM J. PIERCE[1]

[1]School of Biological Sciences (Zoology), University of Aberdeen, Tillydrone Avenue, Aberdeen, Scotland, AB24 2TZ, UK, [2]Centro Oceanográfico de Vigo, Instituto Español de Oceanografía, PO Box 1552, 36200 Vigo, Spain, [3]Wildlife Unit, Scottish Agricultural College Veterinary Services, Drummond Hill, Stratherrick Road, Inverness, Scotland, IV2 4JZ, UK, [4]The Sea Watch Foundation, 11 Jersey Road, Oxford, OX4 4RT, UK, [5]Department of Zoology, Natural History Museum, Cromwell Road, London, SW7 5BD, UK, [6]Fisheries Research Services Marine Laboratory, 375 Victoria Road, Aberdeen, Scotland, AB11 9DB, UK

The white-beaked dolphin, Lagenorhynchus albirostris*, is commonly found throughout the North Sea and shelf waters of the North Atlantic. Little is known about the behaviour and ecology of this species, especially in British coastal waters. In this paper we present details of the seasonal and geographical distribution of white-beaked dolphins around the UK, along with new information on their diet and habitat use. Analysis of historical stranding records show a segregation of the sexes, with a significant difference between when males and females strand in UK waters. There has been a steady decline in reported strandings since the 1970s and seasonal differences in the distribution of strandings suggest that sea temperature may limit white-beaked dolphin distribution around the British coast. Stomach contents' analysis, from dolphins stranded mainly on the Scottish east coast, identified haddock and whiting as the predominant fish species being taken. Boat surveys were performed along the north-east Scottish coast to examine relationships between topography, environmental conditions, dolphin presence and group size. Dolphin presence was related to seabed slope and aspect while variation in temperature explained almost 45% of variation in observed group size, with smaller groups associated with higher sea temperatures.*

INTRODUCTION

The white-beaked dolphin (*Lagenorhynchus albirostris*) inhabits cold temperate and sub-Arctic waters and is commonly found throughout the North Sea and the shelf waters of the North Atlantic (Northridge *et al.*, 1997; Kinze *et al.*, 1997; Reeves *et al.*, 1999). It is the second most frequently reported cetacean around the UK (Evans, 1992) and the predominant dolphin species recorded in the North Sea (Hammond *et al.*, 2002). In the UK, most sightings are from around Scotland and the east coast of England (Evans, 1990; Northridge *et al.*, 1995; Reid *et al.*, 2003), although a change in distribution has been reported on the west coast of Scotland in recent years (Evans *et al.*, 2003; MacLeod *et al.*, 2005). White-beaked dolphins have been sighted around Britain throughout the year, although with a dramatic increase in frequency during the summer months when the animals move inshore (Evans, 1992; Northridge *et al.*, 1995; Weir *et al.*, 2007).

Although group sizes of up to 1500 have been reported (Tomlin, 1967; Fraser, 1974; Katona *et al.*, 1983), most reports refer to groups of ten animals or less (Evans, 1992; Kinze *et al.*, 1997; Reid *et al.*, 2003). Stomach contents' analysis has shown that white-beaked dolphins are feeding on a wide range of fish and squid species including cod, whiting and hake (Kinze *et al.*, 1997; Reeves *et al.*, 1999). In the field, they have been observed to be associated with herring (Harmer, 1927; Fraser, 1946; Evans, 1980) and mackerel shoals (Evans, 1987) on the west coast of Scotland and anecdotal evidence from east coast fishermen suggests inshore sightings may coincide with mackerel appearing in coastal waters.

While much is known about the general distribution of this species, little is known about their behaviour, particularly in the coastal waters around Britain and Ireland. The main purpose of this paper is to bring together, for the first time, different sources of information regarding the distribution and behaviour of white-beaked dolphins in UK waters. Stranding data were analysed with reference to inter-annual, seasonal and geographical trends in distribution around the British Isles and stomach content analysis provides new information on diet in Scottish waters. In addition, sightings data gathered from boat surveys performed off north-east

Corresponding author:
S.J. Canning
Email: s.j.canning@abdn.ac.uk

Scotland were analysed to examine the habitat use of this species in coastal waters.

MATERIALS AND METHODS

Data collection

HISTORICAL STRANDING RECORDS

Stranding records for white-beaked dolphins in Great Britain and Ireland collected between 1907 and 2003 were assembled for analysis of yearly, seasonal and geographical trends. Prior to 1992, British strandings were collected and published by the Natural History Museum in London (Harmer, 1927; Fraser, 1934, 1946, 1953, 1974; Sheldrick, 1989; Sheldrick *et al.*, 1994). A more systematic recording programme began in 1992, with the Museum continuing to collect information for England and Wales and the Scottish Agricultural College (SAC) Veterinary Services collecting the Scottish data. All UK strandings data are collated and stored in a central database held by the Natural History Museum. The Irish data are collected, verified and published by the Irish Whale and Dolphin Group (www.iwdg.ie).

STOMACH CONTENTS´ ANALYSIS

When the condition of a stranded animal permits, a full post-mortem is carried out to try to establish cause of death, as well as to collect the samples needed to gather information on the age, diet and reproductive status of the animal. Hard remains of fish and cephalopods were removed from the stomachs of white-beaked dolphins stranded around Scotland between 1992 and 2003 by SAC Veterinary Services in Inverness (Figure 1) and identified using reference material and published guides (Clarke, 1986; Härkönen, 1986; Watt *et al.*, 1997). Original prey size was estimated from measurements on otoliths and beaks using published regression relationships. For stomachs in which one fish species was represented by >30 otoliths, a random sample of 30–50 otoliths was measured: see Santos *et al.* (2004) for a full description of the methods. Note that no corrections were made for possible loss or reduction of size of prey remains due to digestion. Cephalopod beaks are relatively robust, but otoliths are subject to some digestive erosion (Tollit *et al.*, 1997).

BOAT SURVEYS

Boat surveys were carried out along the south-east Grampian coastline, Scotland to explore relationships between white-beaked dolphin presence, group size and habitat type. Using a 10 m long fishing vessel, surveys were conducted in all months of the year except January, normally at least once per month, on days when wind speed was less than 15 mph. The primary survey route travelled was between Stonehaven and Aberdeen (39 km round trip, Figure 1). Additional surveys were carried out between Stonehaven and St Cyrus (45 km), and evening surveys were performed during the summer between Catterline and Newtonhill (20 km round trip). Surveys were generally within 7 km of shore and a Global Positioning System was used to record the position, speed and direction of travel of the boat at 15-min intervals. The sea state, swell height and visibility were recorded at the same time. The position of the boat was then noted at the start of every cetacean sighting and at 15-min intervals for the duration of the sighting. Species, group size, composition and behaviour of the animals were also recorded. Additional sightings recorded by the boat skipper when out on other business were also used for some of the analysis.

Data analysis

GEOGRAPHICAL AND TEMPORAL PATTERNS IN STRANDINGS

The strandings data (N = 349) were grouped according to body length, sex, geographical location, year, month and season of stranding. Geographical location was assigned by dividing the coastline into six regions (Figure 1) and seasons were defined as winter (January–March), spring (April–June), summer (July–September) and autumn (October–December).

Frequencies of strandings were calculated and compared for individual regions around the British Isles and for each coast (east = region 1–3, west = region 4–6, Figure 1) using chi squared tests. In order to factor in a value for effort, the numbers of white-beaked dolphins reported stranded during each decade between 1910 and 2003 were expressed as a proportion of all reported stranded cetaceans (for that decade) and examined for temporal and geographical variation in occurrence using regression analysis and Friedman's Tests.

Generalized additive models (GAM) were fitted to quantify relationships between the presence of stranded white-beaked dolphins and the explanatory variables year, region, length and sex. Region and sex were entered as nominal values. Zeros were entered for year/region combinations with no stranding records and the response variable was thus expressed as presence/absence. A binomial distribution was assumed and the final model was chosen based on the lowest AIC value obtained (providing that all explanatory variables included had individually significant effects). The analyses were carried out using Brodgar v. 2.4.8 (Highland Statistics, www.brodgar.com).

The information available with each stranding report varied, particularly in the early years, but body length was recorded for 82% of stranded animals, and sex for 52% of the animals. Animals smaller than 160 cm in length were classified as calves and those greater than 240 cm as mature adults (Kinze *et al.*, 1997). Seasonal and spatial patterns in the size and sex data were analysed using GAMs and χ^2 tests.

HABITAT USE

A total of 95 boat surveys was carried out between May 2002 and September 2005, covering a distance of 4123 km (Figure 1). Thirty of these surveys were summer evening trips, seven followed the St Cyrus route, and the remaining surveys followed the Aberdeen route. Fifty-one white-beaked dolphin sightings were recorded in total and the boat skipper recorded an additional 33 sightings, which were included for the second part of the analysis.

The boat survey data were entered into a GIS (ArcView 3.1, Environmental Systems Research Institute, Inc.) and data were extracted to quantify the characteristics of habitats used by white-beaked dolphins (see below). Generalized additive models were used to quantify factors affecting dolphin presence. Due to the large number of zero values, a two-stage modelling approach was applied (McCullagh & Nelder, 1989; Barry & Welsh, 2002; Cañadas *et al.*, 2005; Canning, 2007):
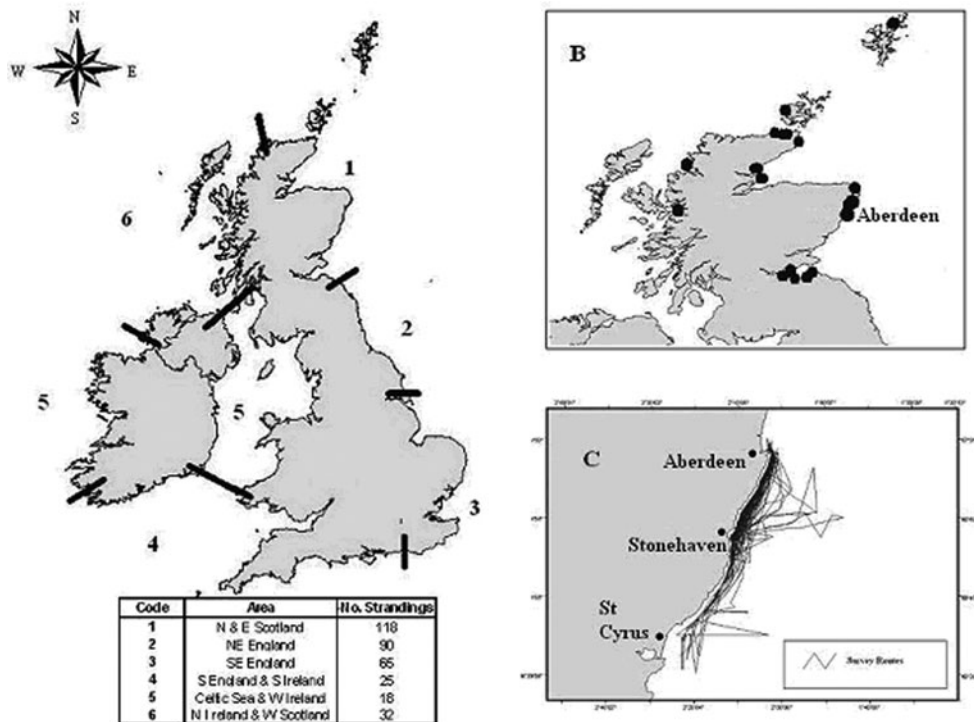
Fig. 1. Map of the British Isles, showing boundaries of the geographical regions used for analysis of distribution based on strandings data. Inset B, stranding locations of white-beaked dolphins used in stomach contents analysis. Inset C, summary of boat survey routes along the north-east Scottish coast for analysis of habitat use.

Model 1

To examine the relationship between white-beaked dolphin presence/absence and physical environmental characteristics within the survey area, the area was divided into 500 m grid-squares using MapInfo Professional 5.0 and ArcView 3.1. The explanatory variables examined were depth, slope, aspect, sediment type and survey effort, with a value for each variable calculated for all grid squares. Depth was assigned using the DigiBath 250 dataset and sediment type was determined from British Geological Survey sediment data. Aspect, slope, survey effort and dolphin presence/absence were calculated using ArcView. Aspect was divided into north and east components to avoid use of a circular variable. Bearings in degrees were converted to radians. Northerly and easterly components of aspect are then given by cos (bearing) and sin (bearing) respectively. Sediment type was assigned nominal values to allow its input into the model. A binomial GAM was fitted using dolphin presence as the response variable. Cross validation was applied and the best model was selected using a forwards and backwards selection procedure, based on the lowest AIC, ensuring that all explanatory variables retained in the final model were individually statistically significant.

Model 2

A second model was applied to look for relationships between dolphin abundance (given presence) and temporal and physical variables. Since each presence (as opposed to absence) record was associated with a specific time and location it was possible to examine effects of additional environmental variables. Depth, slope, aspect and sediment type were calculated as before, based on the starting position for each

sighting. Depth was then adjusted for the tidal height at the time of the sighting. The direction of tidal flow at that time (expressed as north or south) and the strength of that stream (knots) were calculated using Admiralty Total Tide v. 5.1 (UK Hydrographic Office). Time of sighting was expressed as the number of continuous minutes since midnight.

To look at the impact of fresh water entering the system, the distance of each sighting to the nearest large river was calculated using ArcView. The number of days to the nearest full or new moon for each sighting was also included to examine the possibility that sightings were associated with the tidal front, the distance of which from the shore would be affected by the lunar cycle. A mean daily value for sea surface temperature for each sighting was also included (recorded by Fisheries Research Services at a recording station in Findon, halfway between Stonehaven and Aberdeen). Aspect had to be omitted from the modelling process, as there was not enough variation in this dataset. Sediment type and direction of tidal flow were entered as nominal values. The response variable was number of adults per sighting and a Poisson distribution was assumed. Cross validation was applied and the best model was again selected based on the lowest AIC and significant values for individual explanatory variables.

GROUP SIZE

The boat survey sighting data were examined for monthly and yearly variations in median group size (number of adults) using Kruskal–Wallis tests. Variation between group size in relation to the presence or absence of calves was also examined using a Kruskal–Wallis test. The number of sightings per unit effort (SPUE) and total number of individual

animals per unit effort (IPUE) were calculated for the years 2002–2005 to allow comparison with previous data collected in the area (Weir *et al.*, 2007), regression analysis was used to look for trends.

DIETARY ANALYSIS

Twenty-two of the white-beaked dolphins stranded around Scotland were of a suitable condition to allow dietary analysis. Seventeen were recovered from the east coast, two from the west coast and the rest from the Northern Isles (Figure 1). Nearly half of the dolphins whose stomach contents were examined had stranded during the summer (June–August). The overall importance of each prey type in the diet was summarized using three standard measures: (1) frequency of occurrence (i.e. the number of stomachs in which a prey category occurred); (2) proportion of the total number of prey; and (3) proportion of total prey wet mass.

Although prey mass provides the best proxy for the energetic importance of each prey type, not all prey remains could be used to estimate prey size and the mass data are therefore slightly less complete than data on prey numbers or presence (see results). No explicit 'weighting' was applied to individual stomach samples. Thus when calculating the overall diet, the contribution of each stomach is proportional to the total estimated number or reconstructed mass of the prey contained therein.

RESULTS

Geographical and temporal patterns in strandings

The majority of white-beaked dolphins stranded in the UK are found around Scotland and along the east coast of England. There were fewer strandings in the south compared to the north and central areas along both coasts, although this difference is not statistically significant ($\chi^2 = 3.6$, 2df, $P = 0.17$). If these data are broken down according to season, significantly fewer white-beaked dolphins were stranded along the southern coastal areas during the summer months and significantly more during the winter ($\chi^2 = 28.12$, 15df, $P = 0.02$).

Considering the number of white-beaked strandings per decade as a proportion of all strandings, there was a dip during the 1940–1950s and then a steady decline in relative numbers since the 1970s. A linear regression fitted to the latter data shows a significant negative trend (number of strandings = $-0.014 \times$ decade, $+ 0.163$, $R^2 = 0.92$; Figure 2).

When the geographical regions were grouped according to latitude, a strong decline in numbers reported since the 1970s was observed in the central and southern regions while a small increase was observed in the northern region (Figure 3).

Friedmans tests indicated that there was a significant difference in the numbers of strandings reported by latitude ($S = 7.4$, 2df, $P = 0.025$) but not by decade ($S = 12.67$, 9df, $P = 0.178$). If the data from the 1970s are looked at in isolation by geographical region, the number of strandings for all regions except region 1 (north-east Scotland) goes down, although this effect is not significant for either region or decade.

The GAM fitted to data on presence/absence of reported strandings by year and by region explained 16.5%
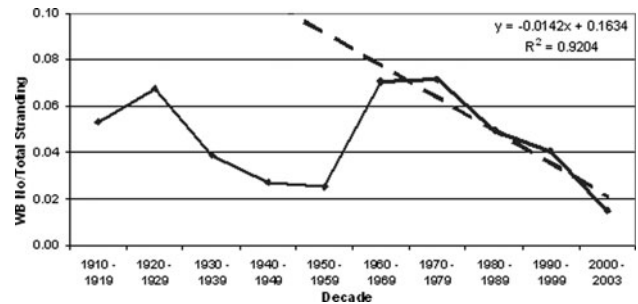

Fig. 2. Number of white-beaked dolphins reported stranded around the UK and Ireland each decade between 1920 and 2003, expressed as a proportion of all cetacean stranding reports. The dashed line represents the regression curve for the decades 1970–2000 showing a steady decline in reports of this species during that time.

of deviance and showed a strong non-linear inter-annual trend (5.6df, $P < 0.001$). This trend was generally upwards, with a dip around 1950, but is uncorrected for changing effort (since annual, by-region effort indices are not available). Although the effect of region was not significant, there was a significant year–region interaction for north-east Scotland (region 1, $P = 0.005$) indicating that this region has a different temporal trend when compared to the other regions.

There is a slight bias towards females in the strandings data: for all the stranding data combined, the sex ratio is 1.22. Among animals >240 cm in length, the sex ratio is 1.11 females per male for Scotland and 1.36 for England. The sex ratio for the east coast of Britain is 1.13 as compared to 1.46 for the west coast.

Of the stranded animals smaller than 160 cm length (calves), 67% were found in Scotland and 81% on the east coast of Britain. Seventy-one per cent of all calves were stranded between June and September. The calves that stranded outside this time period were all greater than 130 cm in length except for one reported in May (100 cm) and another in October (120 cm). Considering data for Scotland (where the majority of calves are reported) alone, these trends are stronger, with 82% of calves stranding between June and September and all but one calf stranded outside of this period being greater than 140 cm in length. A GAM fitted to length data for stranded animals explained 12.5% of deviance and indicated a significant linear decline
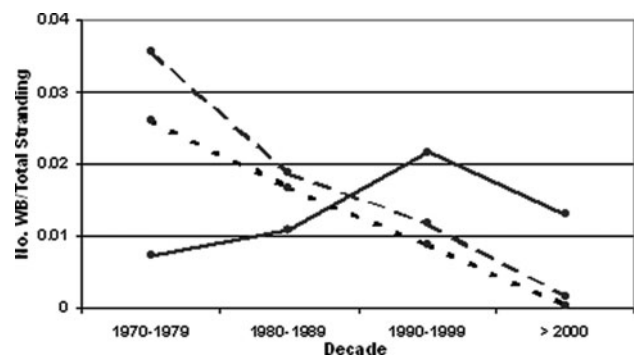

Fig. 3. Number of stranded white-beaked dolphins since the 1970s, grouped according to latitude showing an increase in reports in the north and a decrease in the southern areas. Solid line, north (regions 1 and 6); dashed line, central (regions 2 and 5); dotted line, south (regions 3 and 4; refer to Figure 1).

in length with year ($P < 0.001$) as well as significant regional differences: average length of stranded animals in regions 2, 3, 5 and 6 was significantly greater than in region 1, consistent with this region having a higher proportion of calves among the strandings. No satisfactory GAM could be fitted to the sex data (i.e. there were no significant interannual or regional trends).

When the month-to-month patterns of occurrence for strandings of (a) males, (b) females and (c) calves are compared, there is a significant difference ($\chi^2 = 41.92$, 22df, $P = 0.006$) with adult female (>240 cm) and calf strandings peaking in July and adult male (>240 cm) strandings peaking in August (Figure 4).

Temporal trends in sightings

Although boat surveys were conducted all through the year, all white-beaked dolphin sightings were reported between June and August except for a single sighting in September 2004. Group size ranged from 1 to 18 with an overall average of 4.2 (N = 84, SD 2.77). The median group size did not vary significantly between months (Kruskal–Wallis H = 4.46, 2df, $P = 0.098$), or between years (H = 3.26, 3df, $P = 0.35$). Calves were recorded only during July and August, with 30% of the sightings from these months including calves. Median group size for groups with and without calves was not significantly different (H = 1.62, 1df, $P = 0.205$).

Overall SPUE did not vary greatly between years or studies (Table 1) but a steady decrease in the IPUE was observed for the duration of this study and when compared to the previous study (see Table 1: IPUE = $-0.12 \times$ year $+ 1.04$, $R^2 = 0.76$).

Habitat use

Using the 51 sightings recorded during the boat surveys, the final model for white-beaked dolphin presence in relation to habitat type (model 1) explained 31.6% of deviance and included effects of slope ($P = 0.02$), northerly aspect ($P = 0.04$), easterly aspect ($P = 0.01$) and survey effort ($P = <0.01$). Slope, northerly and easterly aspects showed linear relationships with dolphin presence and so were included as parametric terms. The trend was for steeper north-facing slopes to have a negative effect on dolphin presence and for east facing slopes to have a positive effect.

All 84 sightings were included in the second model (for group size) and the final model explained 43.7% of the variation between group sizes, with temperature being the only significant explanatory variable ($\chi^2 = 61.79$, 8.7df, $P = <0.01$). The trend, although non-linear, was for smaller group sizes to be seen at higher temperatures (Figure 5).

Dietary analysis

A wide variety of prey species were identified, with fish representing more than 95% of the diet by number and by reconstructed weight (Table 2). Haddock and whiting were the most important prey species in the diet, representing 43% and 24% respectively of the total reconstructed weight. Cod comprised 11% of the total weight while herring and mackerel together make up less than 1%. Most of the haddock eaten were estimated to be of 265–285 mm total body length (although haddock in stomachs ranged from 105 to 485 mm) as compared to 155–165 mm for whiting (total fish length ranged from 65 to 365 mm).

DISCUSSION

The summer peak in the stranding data coincides with the increase observed in inshore sightings (this study and Reid *et al.*, 2003) and in both cases the vast majority of reports are from the North Sea. Stranding data for the eastern edge of the North Sea have suggested a segregation of the sexes (Kinze *et al.*, 1997). The same cannot be said for the UK and Irish stranding data, although the overall sex ratio was slightly female-biased. There is however, a significant difference in the months of peak occurrence of strandings for males and females, suggesting that females may move inshore first with males following later.

The distribution of calf strandings, and the pattern of sightings recorded during the boat surveys, reinforce the summer calving theory first described in 1974 by Fraser. Calves were recorded only during the boat surveys in July and August and nearly all of the stranded calves were reported between June and September. The few calves that stranded outside this period were greater than 130 cm in length, indicating that they were several months old. The peak in calf strandings coincides with the peak in female strandings, leading us to suggest that the females may be coming inshore to give birth. Neither haddock nor whiting (the predominant prey species in the stomach contents) exhibit an in/offshore
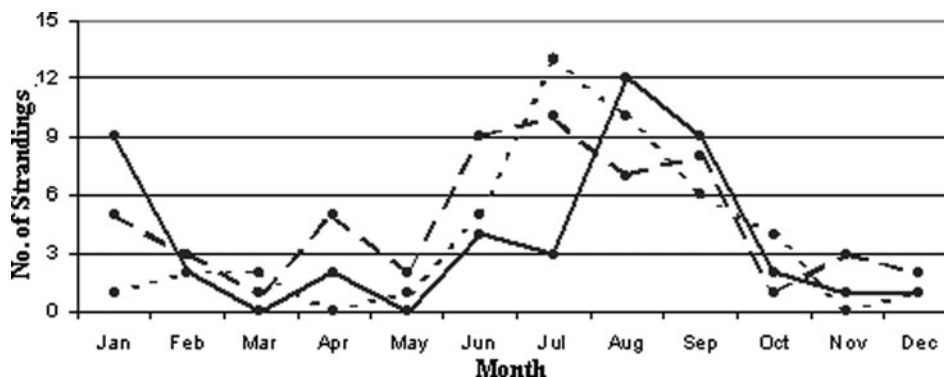

Fig. 4. Number of stranded white-beaked dolphins found around Britain and Ireland in each calendar month according to length and sex. Dotted line, calf (<160 cm long); solid line, male (>240 cm long); dashed line, female (>240 cm long). The peak in occurrence for each of the three size groups was significantly different ($\chi^2 = 41.92$, $P = 0.006$, 22df).

Table 1. Sightings per unit effort (SPUE) and number of individuals per unit effort (IPUE) for the years 2002–2005. Unit effort is 60 minutes. Data collected during 1999–2001 (Weir *et al.*, 2007) are also included for comparison. Regression analysis suggested a steady decline in the number of animals sighted between 1999 and 2005 (IPUE = 0.12 × year + 1.04, R^2 = 0.76).

Year	SPUE	IPUE
2002	0.14	0.72
2003	0.21	0.79
2004	0.13	0.69
2005	0.11	0.35
1999–2001	0.20	0.91
2002–2005	0.15	0.67

Table 2. Overall importance of the prey categories identified from the stomachs of white-beaked dolphins stranded around Scotland 1992–2003. Importance is expressed as % frequency of occurrence (%F), % number (%N) and %-reconstructed weight (%W).

Prey category	%F	%N	%W
All Fish	77.3	95.41	95.85
Herring (*Clupea harengus*)	9.1	0.23	0.07
All Clupeidae	9.1	0.23	0.07
Cod (*Gadus morhua*)	11.15	2.02	11.15
Haddock (*Melanogrammus aeglefinus*)	40.9	20.05	43.25
Haddock/Saithe/Pollack	18.2	1.64	2.03
Whiting (*Merlangius merlangus*)	59.1	35.28	23.55
Trisopterus spp. (*T. esmarkii, T. minutus, T. luscus*)	31.8	5.05	0.38
Forkbeard (*Phycis blennoides*)	4.5	0.08	0.55
Rocklings	4.5	1.48	0.12
Tadpole fish (*Raniceps raninus*)	9.1	0.54	0.09
All Gadidae	72.7	87.78	93.42
Hake (*Merluccius merluccius*)	4.5	0.16	0.43
Grey gurnard (*Eutrigla gurnardus*)	4.5	0.08	–
Scad (*Trachurus trachurus*)	13.6	2.02	1.47
Labridae	9.1	0.39	0.09
Sandeels (*Ammodytes* spp.)	22.7	1.94	0.07
Gobiidae	13.6	1.01	–
Mackerel (*Scomber scombrus*)	4.5	0.08	0.06
Long rough dab (*Hippoglossoides platessoides*)	13.6	0.24	0.05
Sole (*Solea solea*)	4.5	0.08	0.01
All Flatfish	54.5	0.87	0.24
Unidentified Fish	22.7	0.85	–
All Cephalopoda	31.8	3.89	4.15
Sepiolidae	18.2	2.25	0.05
Octopus (*Eledone cirrhosa*)	18.2	1.55	4.09
Unidentified Cephalopoda	4.5	0.08	–
Other Mollusca	13.6	0.23	–
Crustacea	18.2	0.31	–
Polychaeta	9.1	0.16	–

migration suggesting that white-beaked dolphins are not following a prey source into coastal waters during the summer months. Calving in coastal waters would presumably offer greater protection to the mothers with there still being plenty of prey available, as suggested for bottlenose dolphins (Scott *et al.*, 1990; Wilson *et al.*, 1997). Male bottlenose dolphins are also known to form separate groups from females and calves (Wells *et al.*, 1980; Wells, 1991; Connor *et al.*, 2000; Möller *et al.*, 2001) with the males moving between female groups in order to mate (Wells *et al.*, 1980). Little is known about the reproduction behaviour of the white-beaked dolphin but it may be that the males follow the females inshore in order to mate after they have calved. Only a small number of stranded animals around Scotland have been examined for reproductive state and of these, only two were sexually mature and reproductively active (J. Learmonth, personal communication). These were both male and they stranded in july and august.

Initial examination of the geographical distribution of the strandings data pointed to a possible link with sea depth, as fewer white-beaked dolphins were reported stranded around the south of England where the adjacent waters are generally shallow. However, when season is taken into consideration a
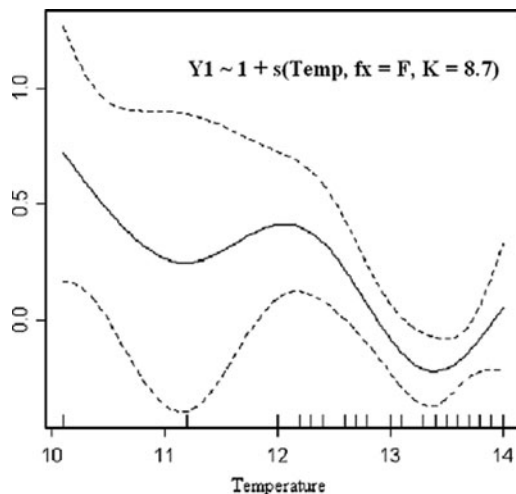

Fig. 5. Formula used to obtain the optimal group size model and the partial plot showing the relationship between group size and temperature. While the first half of the graph is uninformative due to a lack of data points, the overall trend is for a decline in group size with increasing temperature. (Dotted lines represent 95% confidence limits. Note: graph was further smoothed to allow easier interpretation).

different pattern emerges, with significantly fewer strandings in the south during the summer than in the winter, suggesting that white-beaked dolphin distribution may be linked to sea temperature rather than a physical factor such as depth. The habitat study in north-east Scotland highlighted temperature as having a significant effect on local abundance, with smaller group sizes being associated with higher sea surface temperatures. The waters to the south of Britain (particularly in the North Sea where the majority of sightings occur) are always warmer than those in the north, particularly during the summer when the temperature variation is more extreme (Becker & Pauly, 1996). White-beaked dolphin distribution around the UK may thus be generally restricted to cooler more northerly areas, especially during the summer months.

Regression analysis, taking into account changes in observer effort, suggested a steady decline in white-beaked dolphin strandings around the UK since the 1970s. The dip in incidence of strandings during the 1940s and 1950s can probably be attributed to the Second World War. The GAM results highlighted a difference in the inter-annual trend in incidence of white-beaked dolphin strandings between north-east Scotland and other UK regions. The number of strandings in north-east Scotland has been going up since the 1970s while the numbers in all other areas have gone down. A decline in white-beaked dolphin abundance on the west

coast of Scotland has previously been reported (MacLeod *et al.*, 2005), with a suggested link to rising sea temperatures. Results from the present study suggest that this decline is more widespread, with the number of reported strandings declining in recent decades for all regions except the north-east of Scotland. The increase here, where seawater temperatures tend to be colder than elsewhere around the UK, may reflect displacement of animals from other UK regions.

The strandings data series analysed did not extend beyond 2003 but the decline in IPUE (individuals sighted per unit effort) observed during the boat surveys off north-east Scotland since 1999, suggests that abundance may now also be declining in this region. As discussed by MacLeod *et al.* (2005), global warming may ultimately have a dramatic effect on the distribution and abundance of this species.

A previous study based on the Aberdeenshire coast (Weir *et al.*, 2007), reported a significant effect of sea depth on presence of this species. In contrast, this study found slope and aspect to be more important. The present study area is characterized by a predominantly sandy seabed, with relatively shallow water depths, although Aberdeen Bay is shallower than the area immediately to the south of Aberdeen. Significant effects of depth, seabed slope and aspect on dolphin presence may indicate that white-beaked dolphins favour particular locations. Continued survey effort, increasing the sample size for observations, would allow clarification of the direct or indirect effect of habitat type on white-beaked dolphin sightings in this area. Ultimately, however, it may be more informative to study the distribution of their prey. Haddock and whiting, the two predominant prey species found in the stomach contents analysed here, are both widespread in the study area, suggesting that the dolphins may be following prey rather than targeting specific habitats.

Earlier observations have suggested an association between white-beaked dolphins and herring and mackerel (Harmer, 1927; Fraser, 1946; Evans, 1980, 1987), at least on the west coast of Scotland, although neither species was frequent in the stomachs analysed here. Herring abundance in the North Sea has recently returned to levels not seen since the 1970s (ICES, 2005) and, although mackerel are presently regarded as overexploited (ICES, 2005), the mackerel stock is still very large (close to 2 million tonnes). In 2004, the haddock spawning stock in the North Sea was relatively large (around 290,000 tonnes). In contrast, whiting abundance appears to have decreased markedly since 1990 with the North Sea stock believed to be at or near an all-time low (ICES, 2005). These figures, however, describe the overall stock situation and are not informative about the local spatial distribution of fish populations. At present it is not possible to say which species of fish the dolphins actually encountered. Feeding strategies may differ between the east and west coast, but again the present dataset precludes a more detailed analysis (only two of the stomachs examined originated on the west coast). It is also possible that white-beaked dolphins feed on herring and mackerel mainly in offshore waters, where any animals that die are less likely to appear in the strandings record than animals which have been living and feeding closer to the shore.

The analysis here suggests that white-beaked dolphin distribution is restricted by temperature and that their distribution around the UK has steadily been shrinking northward, very probably as a response to rising sea temperatures. Bearing in mind recent changes in their distribution on the west coast of Scotland, the possible effects of sea temperature implied by our and previous findings and the generally observed rises in sea temperature, particularly in recent years, there is an urgent need to obtain a clearer understanding of the distribution and ecology of this species. The suggestion that they are using inshore areas to breed requires further confirmation and the small-scale diet and habitat studies reported here highlight the need for robust biological information to inform the processes of inshore management so as to mitigate adverse anthropogenic affects.

REFERENCES

Barry S.C. and Welsh A.H. (2002) Generalised additive modelling and zero inflated count data. *Ecological Modelling* 157, 179–188.

Becker G.A. and Pauly M. (1996) Sea surface temperature changes in the North Sea and their causes. *ICES Journal of Marine Science* 53, 887–898.

Canning S.J. (2007) *Cetacean distribution and habitat use along the east coast of Scotland.* PhD thesis, University of Aberdeen, Aberdeen, Scotland.

Cañadas A., Sagarminaga R., Stephanis R., de Urquiola E. and Hammond P.S. (2005) Habitat preference modeling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. *Aquatic Conservation* 15, 496–521.

Clarke M.R. (1986) *A handbook for the identification of cephalopod beaks.* Oxford: Clarendon Press.

Connor R.C., Wells R.S., Mann J. and Read A.J. (2000) The bottlenose dolphin: social relationships in a fission-fusion society. In Mann J. *et al.* (eds) *Cetacian societies: field studies of dolphins and whales,* Chicago: University of Chicago Press, pp. 91–126.

Evans P.G.H. (1980) Cetaceans in British waters. *Mammal Review* 10, 1–52.

Evans P.G.H. (1990) Whales dolphins and porpoises. The Order Cetacea. In Harris S. and Corbet G.B. (eds) *The handbook of British mammals,* Oxford: Blackwell, pp. 299–235.

Evans P.G.H. (1992) Status review of cetaceans in British and Irish waters. Oxford: UK Mammal Society Cetacean Group.

Evans P.G.H., Anderwald P. and Baines M.E. (1987) *UK Cetacean Status Review.* Report to English Nature and Countryside Council for Wales pp. 160. Oxford: Sea Watch Foundation.

Fraser F.C. (1934) *Report on Cetacea stranded on the British coasts from 1927 to 1932.* No. 11. London: British Museum (Natural History).

Fraser F.C. (1946) *Report on Cetacea stranded on the British coasts from 1933 to 1937.* No. 12. London: British Museum (Natural History).

Fraser F.C. (1953) *Report on Cetacea stranded on the British coasts from 1938 to 1947.* No. 13. London: British Museum (Natural History).

Fraser F.C. (1974) *Report of Cetacea stranded on the British Isles from 1948 to 1966.* No. 14. London: British Museum (Natural History).

Hammond P.S., Berggren P., Benke H., Borchers D.L., Collet A., Heide-Jørgensen M.P., Heimlich S., Hiby A.R. and Leopold M.F. (2002) Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. *Journal of Applied Ecology* 39, 361–376.

Härkönen T.J. (1986) *Guide to the otoliths of the bony fishes of the northeast Atlantic.* Hellerup: Danbiu ApS.

Harmer S.F. (1927) *Report of Cetacea stranded on the British Isles from 1913 to 1926.* No. 10. London: British Museum (Natural History).

ICES (2005) *Working group on the assessment of demersal stocks in the North Sea and Skagerrak (WGNSSK).* ICES CM 2006/ACFM:09

Katona S.K., Rough V. and Richardson D.T. (1983) *A field guild to the whales porpoises and seals of the Gulf of Main and eastern Canada – Cape Cod to Newfoundland.* New York: Charles Scriber's.

Kinze C.C., Addink M., Smeenk C., Hartmann M.G., Richards H.W., Sonntag R.P. and Benke H. (1997) The white-beaked dolphin (*Lagenorhynchus albirostris*) and the white-sided dolphin (*Lagenorhynchus acutus*) in the North and Baltic Seas: review of available information. *Report of the International Whaling Commision* 47, 675–681.

MacLeod C.D., Bannon S.M., Pierce G.J., Schweder C., Learmonth J.A., Reid R.J. and Herman J.S. (2005) Climate change and the cetacean community of northwest Scotland. *Biological Conservation* 124, 477–483.

McCullagh P. and Nelder J. (1989) *Generalized linear models.* New York: Chapman & Hall.

Möller L.M., Beheragaray L.B., Krützen M. and Harcourt R.G. (2001) Alliance membership and kinship in wild bottlenose dolphins (*Tursiops truncatus*) off south-east Australia. *Proceedings of the Royal Society B* 268, 1941–1947.

Northridge S., Tasker M., Webb A., Camphuysen K. and Leopold M. (1997) White-beaked *Lagenorhynchus albirostris* and Atlantic white-sided dolphin *L. acutus* in Northwest European and US North Atlantic waters. *Report of the International Whaling Commision* 47, 797–805.

Northridge S.P., Tasker M.L., Webb A. and Williams J.M. (1995) Distribution and relative abundance of harbour porpoise (*Phocoena phocoena* L.), white-beaked dolphins (*Lagenorhynchu alnirostris* Gray) and minke whales (*Balaenoptera acutorostrata* Lacepède) around the British Isles. *ICES Journal of Marine Science* 52, 55–66.

Reeves R., Smeenk C., Kinze C.C., Brownell R.L. Jr and Lien J. (1999) White-beaked dolphn *Lagenorhynchus albirostris*, Gray 1846. In *Handbook of marine mammals* vol. 6, pp. 1–30. Academic Press.

Reid J.B., Evans P.G.H. and Northridge S.P., ed. (2003) *Atlas of cetacean distribution in north-west European waters.* Peterborough: Joint Nature Conservation Committee.

Santos M.B., Pierce G.J., Learmonth J.A., Reid R.J., Ross H.M., Patterson I.A.P., Reid D.G. and Beare D. (2004) Variability in the diet of harbour porpoises (*Phocoena phocoena*) in Scottish waters 1992–2003. *Marine Mammal Science* 20, 1–27.

Scott M.D., Wells R.S. and Irvine A.B. (1990) A long term study of bottlenose dolphins on the west coast of Florida. In Leatherwood S. and Reeves R.R. (eds), *The bottlenose dolphin* San Diego: Academic Press Inc, pp. 235–244.

Sheldrick M.C. (1989) Stranded whale records for the entire British coastline 1967–1986. *Investigations on Cetacea* XXII, 298–329.

Sheldrick M.C., Chimonides P.J., Muir A.I., George J.D., Reid R.J., Kuiken T., Iskjare-Ackley C. and Kitchener A. (1994) Stranded cetacean records for England Scotland and Wales 1987–1992. *Investigations on Cetacea* XXV, 259–283.

Tollit D.J., Steward J.M., Thompson P.M., Pierce G.J., Santos M.B. and Highes S. (1997) Species and size differences in digestion of otoliths and beaks; implications for estimates of pinniped diet composition. *Canadian Journal of Fisheries and Aquatic Sciences* 54, 105–119.

Tomlin A.G. (1967) Mammals of the U.S.S.R. and adjacent countries. In Heptner V.G. (ed.) *Cetacea*, vol. IX Moscow: Nauk USSR.

Watt J.G., Pierce G.J. and Boyle P.R. (1997) *Guide to the identification of North Sea fish using premaxillae and vertebrae 1997. Co-operative Research Report no. 220.* Copenhagen: International Council for the Exploration of the Sea.

Weir C.A., Stockin K.A. and Pierce G.J. (2007) Seasonal occurrence of the harbour porpoise white-beaked dolphin and minke whale in coastal Aberdeenshire (UK) waters western North Sea. *Journal of the Marine Biological Association of the United Kingdom* 87, 327–338.

Wells R.S. (1991) The role of long-term study in understanding the social structure of a bottlenose dolphin community. In Pryor K. and Norris K.S. (eds) *Dolphin societies discoveries and puzzles.* Berkley: University of California Press, pp. 199–226.

Wells R.S., Irvine A.B. and Scott M.D. (1980) The social ecology of inshore odontocetes. In Herman L.M. (ed.) *Cetacean behaviour: mechanisms and functions*, New York: John Wiley and Sons, pp. 263–317.

and

Wilson B., Thompson P.M. and Hammond P.S. (1997) Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology* 34, 1365–1374.

Correspondence should be addressed to:
Sarah J. Canning
School of Biological Sciences (Zoology)
University of Aberdeen
Tillydrone Avenue
Aberdeen
Scotland, AB24 2TZ, UK
email: s.j.canning@abdn.ac.uk