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REVIEW

Integrating multiple data sources to assess the distribution and abundance of bottlenose dolphins *Tursiops truncatus* in Scottish waters

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ABSTRACT

1. The distribution, movements and abundance of highly mobile marine species such as bottlenose dolphins *Tursiops truncatus* are best studied at large spatial scales, but previous research effort has generally been focused on relatively small areas, occupied by populations with high site fidelity.
2. We aimed to characterize the distribution, movements and abundance of bottlenose dolphins around the coasts of Scotland, exploring how data from multiple sources could be integrated to build a broader-scale picture of their ecology.
3. We reviewed existing historical data, integrated data from ongoing studies and developed new collaborative studies to describe distribution patterns. We adopted a Bayesian multi-site mark-recapture model to estimate abundance of bottlenose dolphins throughout Scottish coastal waters and quantified movements of individuals between study areas.
4. The majority of sightings of bottlenose dolphins around the Scottish coastline are concentrated on the east and west coasts, but records are rare before the 1990s. Dedicated photo-identification studies in 2006 and 2007 were used to estimate the size of two resident populations: one on the east coast from the Moray Firth to Fife, population estimate 195 [95% highest posterior density intervals (HPDI): 162–253] and the second in the Hebrides, population estimate 45 (95% HPDI: 33–66). Interaction parameters demonstrated that the dolphins off the east coast of Scotland are highly mobile, whereas those off the west coast form two discrete communities.
5. We provide the first comprehensive assessment of the abundance of bottlenose dolphins in the inshore waters of Scotland. The combination of dedicated photo-identification studies and opportunistic sightings suggest that a relatively small number of bottlenose dolphins (200–300 individuals) occur regularly in Scottish coastal waters. On both east and west coasts, re-sightings of identifiable individuals indicate that the animals have been using these coastal areas since studies began.

INTRODUCTION

The widespread distribution of bottlenose dolphins *Tursiops truncatus* has made them an iconic species throughout many countries and cultures. Their tendency to inhabit both oceanic and coastal habitats has also brought them into conflict with a broad range of human activities (Wilson et al. 2000, Palka & Rossman 2001, Lusseau 2003, Dawson & Slooten 2005, Bailey et al. 2010). Consequently, most of the research currently being conducted on the species (http://www.iwcoffice.org/sci_com/scprogress.htm) is focused towards gathering data to inform conservation and management. For obvious reasons, the majority of this research has been carried out on the more accessible populations (Wells et al. 1987, Connor et al. 1992, Wilson et al. 1999). Conversely, populations that are at lower densities, have unpredictable distributions, are highly mobile or live in inaccessible locations have tended to receive less attention.

Distribution, movements and abundance of highly mobile marine species such as bottlenose dolphins are clearly best studied at relatively large spatial scales, but this can present enormous challenges. In North America the US

Mid-Atlantic Bottlenose Dolphin Catalog project (Urian et al. 1999) and in Europe the Pelagos Sanctuary Marine Protected Area project (Gnone et al. 2011) are excellent but rare examples of a large-scale approach. In the US study, data from individually identified bottlenose dolphins have been shared between independent research projects and at least 16 field sites to understand distribution and abundance of the dolphins that range along the western Atlantic coast of the United States (http://seamap.env.duke.edu/photoid/mabdc; Urian et al. 1999). This approach has revealed a complex mixture of movements among different components of the population(s), informing federal management and leading to the development of seasonally variable management units (Hohn 1997). In Europe, photo-identification data from 10 different research groups were analysed to estimate abundance, distribution and movements of bottlenose dolphins in the Mediterranean Sea Pelagos Sanctuary. Again, differences in movements were found: most dolphins showed high site fidelity but a few ranged widely. Two (sub)populations were identified, and designation of Special Areas of Conservation (SAC) was recommended (Gnone et al. 2011).

There is a potentially analogous scenario for populations of bottlenose dolphins off the Atlantic coasts of Western Europe. As with the coastlines of the Eastern United States, dolphins can be found along almost the entire coastline from Spain to the British Isles (Reid et al. 2003). The north of Scotland appears to be the northern extreme of the coastal range; instances of this species occurring at higher latitudes are rare (Wilson 1995). Some bottlenose dolphins occur further north but, being encountered off the shelf edge, these animals presumably belong to offshore rather than coastal populations (Skov et al. 1995). Within the coastal environment, our knowledge of the ecology of bottlenose dolphin populations in Western Europe is more fragmented than knowledge of the populations mentioned above. This is because key long-term research projects to date have been focused on a series of apparently isolated populations with high site fidelity to relatively small coastal areas (notably: the Sado Estuary, Portugal, Harzen 1998, dos Santos et al. 2005; Western Brittany, Guinet et al. 1993, Liret et al. 1995; Cardigan Bay, Pesante et al. 2008, Pierpoint et al. 2009; Shannon Estuary, Ireland, Ingram & Rogan 2002; and the Moray Firth, Scotland, Wilson et al. 1997, 2004, Hastie et al. 2006, Culloch & Robinson 2008, Bailey & Thompson 2009). These populations typically range in size from the low tens of individuals to the low hundreds (Liret et al. 1995, Wilson et al. 1999). However, while the majority of research effort has focused on these populations, the Western European coastal waters are also frequented by a number of less well-known groupings. Some of these have been seen regularly, others sporadically or over a number of years before disappearing (examples include groups in South West England, Wood 1998; Sound of Barra, Scotland, Grellier & Wilson 2003; Southern North Sea, Kayes 1985; English Channel, Williams et al. 1997). In addition, records from national sighting reporting schemes or other survey efforts suggest that other dolphins lack clear links to particular areas or recognized populations (Evans 1980, Reid et al. 2003).

Bottlenose dolphins in European waters are protected by a series of legislative agreements, particularly the European Union Habitats Directive (92/43/EEC), the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas and, in the United Kingdom, the Biodiversity Action Plan for Small Cetaceans (Anonymous 1995, Baxter 2001). In particular, the European Union Habitats Directive has focused effort to protect this species by spatial designations of SACs. Several of these have been set up in European waters and are located around the best known and most site-faithful groupings of dolphins (for example, Wales: Anonymous 2008a, Scotland: Anonymous 2009a). Because of the monitoring requirements for these sites, conservation research has been focused into these areas. Thus ongoing conservation efforts and research are biased against areas where the animals are more mobile, dispersed or typically only occur in small groups.

In this manuscript, we characterize the distribution, movements and abundance of bottlenose dolphins around the coasts of Scotland. In doing so, we aim to explore how data from multiple sources can be integrated to build a picture of the contemporary ranging patterns and abundances of several potential populations of dolphins inhabiting the area. To achieve this, we built upon what were previously unconnected research programmes and extended these with wider ranging research effort that was actively informed by opportunistic sightings from the public and boating communities.

METHODS

Study area

Scotland has a long and convoluted coastline with over 750 islands (Anonymous 2003). The largest island groups are Shetland and Orkney to the north and the Hebrides to the west. The islands feature complex coastlines, separated by sounds and firths with strong tidal currents. The north and west coast of Scotland have a fjordic coastline with a number of deep, narrow, sheltered sea lochs. The east coast features long stretches of coastline with little shelter and is dominated by two major estuarine embayments: the Firth of Forth and the Moray Firth (Baxter et al. 2008). The Moray Firth has the only SAC for bottlenose dolphins in Scotland, as designated in 2005 under the European Habitats Directive (92/43/EEC). The SAC encompasses the

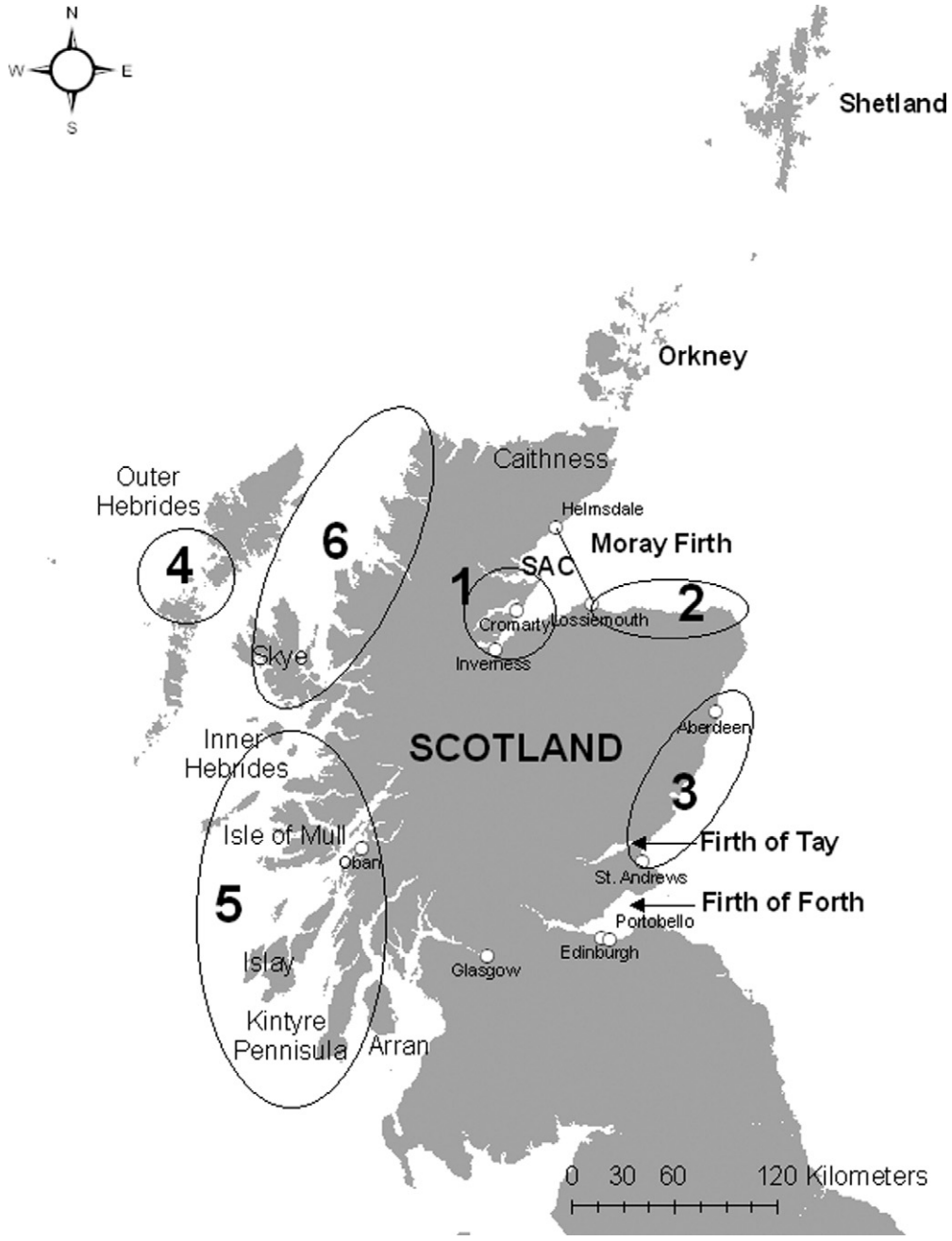

Fig. 1. Map of Scotland showing the key locations mentioned in the text and the areas used for the multi-site mark-recapture analysis of bottlenose dolphins (Area 1: Inner Moray Firth, Area 2: Southern Moray Firth, Area 3: Grampian/Fife Coast, Area 4: Sound of Barra, Area 5: South of Skye and Area 6: Skye and North).

waters of the Moray Firth west of a line drawn from Helmsdale on the northern coast to Lossiemouth on the south coast (Fig. 1).

Data sources for historical review

Our review of the historical distribution of bottlenose dolphins around Scotland was based on the collation of records from a wide variety of published and unpublished sources. Early sightings were sought from antiquarian books by naturalists describing Scottish fauna and flora. Since 1913, the Natural History Museum of London has recorded cetacean strandings, including bottlenose dolphins, around the coasts of England, Scotland and Wales (Harmer 1927, Fraser 1934, 1946, 1953, 1974, Sheldrick 1989, Sheldrick et al. 1994). The National Stranded Whale Recording Scheme was

set up in April 1990 for a coordinated investigation of the ecology and biology of cetaceans around Britain (http://www.nhm.ac.uk/research-curation/research/groups/nhm-cetacean-strandings-project/index.html). Since 1992, this scheme's work within Scotland has been carried out by the Scottish Agricultural College Veterinary Services (Inverness).

The Joint Nature Conservation Committee (JNCC) has integrated data from three main sources to produce an atlas of cetacean distribution (Reid et al. 2003). Firstly, this draws upon the European Seabirds at Sea data base, which contains year round cetacean records collected by JNCC and sister organizations in other European countries (Reid et al. 2003). Secondly, it includes effort-based data collected by the Sea Watch Foundation (see below). Finally, it includes data from the Small Cetacean Abundance in the North Sea (SCANS) surveys (Hammond et al. 2002). To create each of the distribution maps in the JNCC atlas, all data from 1979 to 1997 were converted to a common format and adjusted for effects of sea state upon detection rates, and only sightings that were related to effort were included (Reid et al. 2003).

The Sea Watch Foundation (formerly the UK Mammal Society Cetacean Group) has been collecting marine mammal sightings in UK and Irish waters since the mid-1960s from their network of observers including zoologists, ornithologists, fishermen, yachtsmen and the coastguard (Evans 1980, 1992, Evans et al. 2003). All sightings are entered into the Sea Watch National Database.

The Hebridean Whale and Dolphin Trust (HWDT) has collected bottlenose dolphin sightings from members of the public dating back to 1989. These records include casual sighting data that were collected from a number of different sources (Jeewoonarain et al. 1999, Mandleberg 2006) and sightings obtained from dedicated cetacean surveys conducted by the HWDT (see Embling et al. 2010).

In 2005, the SCANS-II survey was carried out to repeat and extend the SCANS survey conducted in 1994 (Hammond et al. 2002, Anonymous 2008b). This survey provided coverage of offshore as well as inshore areas of the continental shelf around Scotland. Additional data on offshore sightings were also available from JNCC through the Marine Mammal Observer programme that has been conducted since 1997 during seismic operations (Stone 2003).

Current abundance

Estimates of the abundance of bottlenose dolphins in Scottish coastal waters for 2006 and 2007 were obtained from mark-recapture analyses of an integrated data set, comprising individual recognition data from photo-identification studies by all the groups conducting dedicated research programmes in Scotland.

PHOTO-IDENTIFICATION DATA COLLECTION, PROCESSING AND QUALITY ASSURANCE

Data were available from studies conducted along the east coast of Scotland from (i) the University of Aberdeen in the inner Moray Firth (see Wilson 1995, Wilson et al. 1997, 2004 for survey details), (ii) the Cetacean Research and Rescue Unit along the southern coast of the Moray Firth (see Eisfeld 2003, Robinson et al. 2007 and Culloch & Robinson 2008 for survey details), (iii) the South Grampian Regional Group of the Sea Watch Foundation along the Aberdeen coast (see Stockin et al. 2006 and Weir et al. 2008 for survey details) and (iv) the University of St Andrews around the Firth of Tay (see Quick & Janik 2008 and Islas 2010 for survey details). Additional data from the Moray Firth were also available from the Whale and Dolphin Conservation Society surveys that were made from land-based observation points in the inner Moray Firth and from commercial dolphin watching vessels along the southern coast of the Moray Firth (Thompson et al. 2011).

Although details of data collection varied among research groups, all researchers carried out targeted photo-identification surveys during the summer months aimed at obtaining high-quality photographs from as many bottlenose dolphins as possible within their respective study areas. Systematic review and filtering of data (see below) minimized any differences in data quality resulting from differences in these studies' protocols.

In an additional collaborative study, the University of Aberdeen, University of St Andrews, Scottish Association of Marine Science and HWDT extended photo-identification efforts to coastal waters off the west and north coasts of Scotland in May to September, 2006 and 2007. Searching for animals was initially directed by our review of historic sightings, but sightings in these areas have typically been patchy in both space and time. To maximize the chance of obtaining photo-identification pictures of animals in these areas, we developed the existing HWDT sightings network to encourage real-time reporting of bottlenose dolphin sightings by the public and other marine users. We targeted promotion of the sightings network particularly in the less frequently surveyed parts of the west and north coasts of Scotland. Members of the public and wildlife tour operators were also encouraged to send in photographs of bottlenose dolphins. Although data quality can be a concern, photographs are verifiable and were subjected to rigorous quality control (see below).

All collaborators provided the best quality picture of each side of each of the well-marked dolphins (i.e. animals with dorsal fin nicks that could be identified from either the left or right side) photographed in 2006 and 2007. All pictures were graded for photographic quality according to criteria adapted from Wilson et al. (1999). Only high-quality photo-

Table 1. Number of well-marked individual bottlenose dolphins *Tursiops truncatus* identified in high-quality photographs by each collaborating research group and by members of the public in Scotland, UK, in photo-identification surveys in 2006 and 2007

Group	2006	2007
East coast of Scotland		
University of Aberdeen	45	47
University of St Andrews	48	44
Cetacean Research and Rescue Unit	51	29
Whale and Dolphin Conservation Society	39	43
Sea Watch Foundation (South Grampian Regional Group)	8	26
West coast of Scotland		
University of Aberdeen	18	22
Hebridean Whale and Dolphin Trust	5	3
Members of the public	4	13

graphs in which the dorsal fin comprised more than 10% of total image height, was in focus, was parallel to the photographer, and where the complete trailing edge of the fin was visible, were used in this analysis.

Photographs of animals identified during 2006 and 2007 were compared within and among studies to determine whether individuals had been seen in multiple study areas. The unique combination of nicks, tooth rake scars and pigmentation patterns on each dolphin were used to identify individuals (Würsig & Würsig 1977). A catalogue of individually recognizable bottlenose dolphins seen on the east coast of Scotland has been maintained by the University of Aberdeen and the University of St. Andrews since 1989. Each of the dorsal fin pictures obtained from other groups working on the east coast was initially compared with this catalogue by one experienced researcher. On the west coast of Scotland, the HWDT had also maintained a bottlenose dolphin photo-identification catalogue between 2001 and 2005 (Mandleberg 2006). Individuals were also identified during surveys conducted in the Sound of Barra in 1995 and 1998 (Grellier & Wilson 2003). Both these catalogues were reviewed, and individuals for which there were high quality pictures (as defined above) were kept for matching to more recent pictures obtained in all these areas during 2006 and 2007. Finally, these catalogues from the east and west coast were compared. All matches between research groups were confirmed by at least two experienced researchers (Table 1).

In addition, archive photographs of some particularly well-marked animals were made available by all collaborators. These data provided an opportunity to detect long-range movements that could be occurring over longer time-scales (Robinson et al. 2012). We compared archive photographs of well-marked animals from west coast and east coast studies to determine whether individuals had been seen in multiple study areas in earlier years.

ESTIMATION OF ABUNDANCE AND STUDY AREA INTERACTIONS

The multi-site mark-recapture framework described by Durban et al. (2005) was used to estimate abundance and movements of animals between study areas from data stratified into three areas on the east coast and three areas on the west coast of Scotland. A Scotland-wide analysis was not possible because of the lack of exchange of animals between the east and west coasts in 2006 and 2007 (see results). On the east coast: Area 1, the inner Moray Firth, included data from the University of Aberdeen boat-based surveys and the Whale and Dolphin Conservation Society land-based observations; Area 2, the Southern Moray Firth coast, included data from the Whale and Dolphin Conservation Society boat-based surveys and the Cetacean Research and Rescue Unit; and Area 3, the Grampian and Fife coast, included data from the Sea Watch Foundation and the University of St Andrews (see Fig. 1). On the west coast, data from our collaborative photo-identification study in 2006 and 2007 were integrated with those provided by the public and were assigned to three areas: Area 4, the Sound of Barra; Area 5, all waters to the south of Skye; and Area 6, all waters around Skye and to the north (see Fig. 1). Areas were chosen based on each collaborating group's established research sites, which represented good geographical separation throughout the known home range of bottlenose dolphins around Scotland.

Following Durban et al. (2005), simple contingency tables were constructed for the east and west coasts separately, the cells of which referred to discrete categories formed by the combination of the three study areas on each coast (Fig. 1). The corresponding cell counts denoted the number of well-marked individuals that were photographed in each combination of study areas (Table 2). A Bayesian statistical approach was used to fit hierarchical log-linear models for the cell counts in order to predict an estimate into the empty cell for the count of the number of missed individuals that were not identified at any of the areas, and therefore estimate overall abundance of well-marked animals (Durban et al. 2005). The general log-linear model contained effects for each study area, describing the relative number of individuals identified in each area, and parameters for the interaction between study areas, reflecting relatively high or low levels of movement of individuals between areas. Only study area interaction terms with significant deviation from zero interaction were incorporated in model selection. Different models could be produced by omission of one or more of these interaction effects and we produced a model averaged estimate for the total number of well-marked individuals (N), weighted by the relative plausibility of the candidate models. Model averaging and prediction was accomplished using Gibbs sampling Markov

Table 2. East and west coast cross-area contingency table used in the multi-site mark-recapture model showing the number of well-marked individual bottlenose dolphins identified each year (2006 and 2007) in different combinations of the three study areas (Y means that the individuals were seen in the areas; N means not seen, so for example, in 2006, 13 individuals were seen in areas 2 and 3, but these individuals were not seen in any other area). No dolphins were seen in both the east and west coasts of Scotland, UK, in 2006 or 2007. For locations of areas, see Fig. 1

East coast					West coast				
Inner Moray Firth (Area 1)	Southern Moray Firth (Area 2)	Grampian/Fife Coast (Area 3)	Number of well-marked dolphins		Sound of Barra (Area 4)	South of Skye (Area 5)	Skye and North (Area 6)	Number of well-marked dolphins	
			2006	2007				2006	2007
Y	N	N	7	20	Y	N	N	7	8
N	Y	N	2	1	N	Y	N	0	0
N	N	Y	28	40	N	N	Y	3	5
Y	Y	N	28	17	Y	Y	N	0	0
Y	N	Y	1	0	Y	N	Y	0	0
N	Y	Y	13	5	N	Y	Y	8	9
Y	Y	Y	9	10	Y	Y	Y	0	0
Total number of well-marked dolphins			88	93	Total number of well-marked dolphins			18	22

chain Monte Carlo (MCMC) methods implemented in WinBUGS software (Imperial College School of Medicine at St. Mary's, London, UK and Medical Research Council Biostatistics Unit, Cambridge, UK) (Lunn et al. 2000). This approach allows for data collected opportunistically and concurrently by different groups at different study sites based on practicalities rather than random design, as it estimates the geographical dependencies between sites (Durban et al. 2005).

To expand this estimate to the total abundance (P), data on the number of individuals with and without dorsal fin nicks seen on each trip were used to estimate the proportion of well-marked individuals in the population. Specifically, the number of well-marked individuals was treated as a binomial sample of the total number of individuals seen on each trip, with a common (average) binomial probability representing the proportion of well-marked individuals (θ). A flat Beta (1,1) prior distribution was adopted for θ with probability mass equally spaced between 0 and 1. The mark-recapture model for well-marked individuals N and proportion of well-marked individuals θ were linked to form a single probability model through the relationship $P = N/\theta$, and rounded to the nearest whole number (Durban et al. 2010). In this way, the uncertainty from both the mark-recapture and mark-rescaling components was combined by jointly sampling from each in the same MCMC run. The 95% highest posterior density intervals (HPDI) were also calculated directly from the MCMC output. In the absence of sufficient data on the proportion of well-marked animals from all areas, we estimated this proportion from the most comprehensive data sets collected by the University of Aberdeen within the Moray Firth and west coast and assumed this was constant on each coast.

RESULTS

Historical literature

Historical records confirm that bottlenose dolphins have been present in Scottish waters since at least the late 1800s (Herman 1992). However, until the late 20th century, sightings of this species appear to have been relatively rare. Running anticlockwise around the Scottish coast, reports of this species on the south east coast of Scotland were absent (Sim 1903). Evans (1892) recorded five to seven museum specimens from the Firth of Forth, including one stranded at Portobello in 1833–34. Most of the records from the Moray Firth area also suggest that bottlenose dolphins were seen less often than other species, particularly harbour porpoises *Phocoena phocoena* (Smiles 1876, Harvie-Brown & Buckley 1895, Taylor 1898, 1899). The first documented bottlenose dolphin stranding in the Moray Firth occurred in 1897 (Taylor 1899); another stranding of six individuals was reported in 1901 (Taylor 1902). Bottlenose dolphins are simply listed as present in lists of fauna from Caithness (Harvie-Brown & Buckley 1887). In Orkney, one stranding of two probable bottlenose dolphins was recorded in 1888 (Buckley & Harvie-Brown 1891). Neither Evans and Buckley (1899) nor Venables and Venables (1955) report this species as occurring in Shetland. In the Outer Hebrides (Harvie-Brown & Buckley 1888), bottlenose dolphins are included in a list of mammals occurring in the area. Similarly in the Inner Hebrides, there is only mention of a single sighting in contrast to frequent sightings of harbour porpoises (Harvie-Brown & Buckley 1892). A single stranding was recorded in a west coast sea loch in 1879 (Herman 1992).

Fig. 2. Locations of strandings of bottlenose dolphins around Scotland from 1929 to 2008, as recorded by the Scottish Agricultural College in Inverness and the Natural History Museum, London, UK.

Contemporary information

STRANDINGS

Since regular stranding records have been kept by the Natural History Museum of London, there have been 72 bottlenose dolphins reported stranded around the coast of Scotland between 1929 and 2008 (Fig. 2). Most of these animals were reported in the Moray Firth and the Hebrides, and the majority (78%) were in the 1990s and 2000s.

SIGHTINGS

The JNCC cetacean atlas presents the distribution of bottlenose dolphins in North-West Europe from 1979 to 1997. In Scotland, the highest sightings rates were in the north-east, specifically around the Moray Firth (Fig. 3). However, there were also sightings on the west coast (especially the Outer Hebrides) and a few south of Shetland.

Three sightings of bottlenose dolphins were recorded in Scottish waters during SCANS-II (Fig. 4). Marine Mammal Observers have also observed bottlenose dolphins in more offshore waters to both the west and east of Scotland during seismic operations (Fig. 4).

The Sea Watch Foundation and the HWDT provided sightings of bottlenose dolphins around the Scottish coast from July 1966 to October 2007 (Fig. 5).

Abundance estimates

EAST COAST

Totals of 88 and 93 well-marked individuals were identified from the highest quality photographs in the summers of

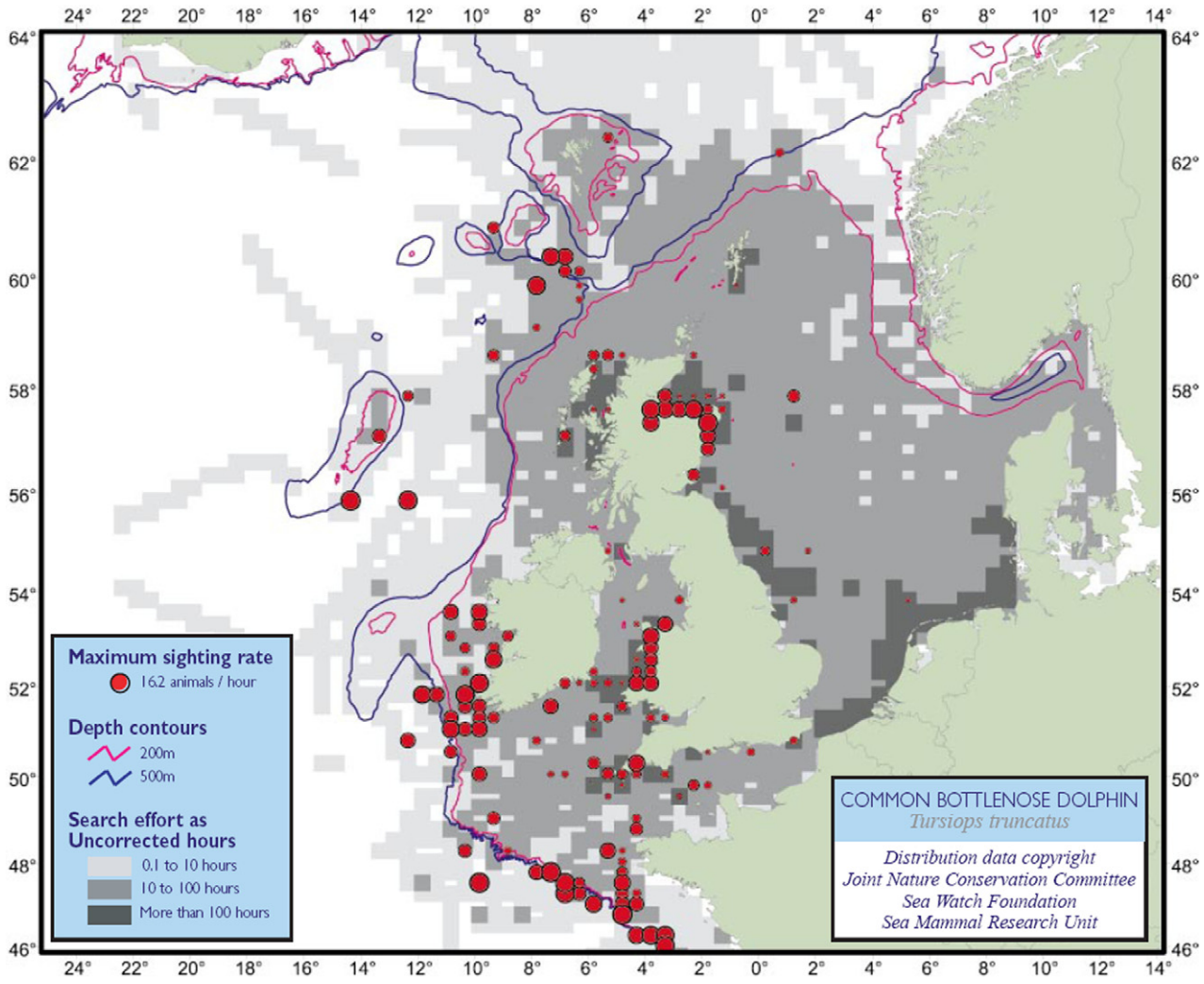

Fig. 3. Bottlenose dolphin distribution in North West Europe, from the Joint Nature Conservation Committee Cetacean Atlas. The map depicts grid cells (¼ International Council for the Exploration of the Seas rectangles, 15′ latitude × 30′ longitude) that are shaded; the greater the survey effort in the cell, the darker the shading. The size of the red dots (which represent sightings) indicates the relative sighting rate (reproduced from Reid et al. 2003).

2006 and 2007, respectively. In both 2006 and 2007, a high proportion of individuals (57%) were recorded in more than one of the three study areas (Table 2). Model-averaged posterior estimates of the total number of well-marked individuals in 2006 and 2007 were 104 and 136 (Table 3). Estimates of the proportion of well-marked animals in the population in 2006 and 2007 were 0.53 (95% HPDI: 0.48–0.58) and 0.60 (95% HPDI: 0.55–0.65), giving estimates of total abundance of 195 and 227, respectively, with 95% HPDI ranging between 162 and 384 (Table 3).

Of the 98 well-marked individuals identified in either 2006 or 2007, 36% were seen in the first 2 years of research carried out by the University of Aberdeen and University of St. Andrews in 1989 and 1990. Two individuals were seen in all 19 years of the study and 65% were seen in at least 10 individual years.

WEST COAST

Totals of 18 and 22 well-marked individuals were identified from the highest quality photographs in the summers of 2006 and 2007, respectively (Table 2). Of the 22 well-marked individuals seen in 2007, eight were from the Sound of Barra and 14 were seen in the Inner Hebrides. Model-averaged estimates of the total number of well-marked individuals in 2006 and 2007 were 25 and 30 (Table 3).

Fig. 4. Sightings of bottlenose dolphins around Scotland recorded during SCANS-II (Small Cetacean Abundance in the North Sea) in 2005 (circles) and during seismic surveys conducted between 1994 and 2006 (triangles).

Estimates of the proportion of well-marked animals in the population in 2006 and 2007 were 0.56 (95% HPDI: 0.43–0.69) and 0.67 (95% HPDI: 0.57–0.77), giving estimates of 45 in both years, with 95% HPDI ranging between 31 and 71 (Table 3).

Around the Sound of Barra, four of the individuals seen in 2006 and 2007 were first seen in 1995 and/or 1998 by Grellier and Wilson (2003). The first bottlenose dolphin photo-identification pictures we have from the Inner Hebrides were taken in 2001. Although three individuals seen in 2006 and 2007 in the Inner Hebrides were also seen in 2001 and 2002, these were in poorer quality photographs, and the majority of animals were identified from 2004 onwards.

Study area interactions

EAST COAST

There were notable movements of individuals between areas: 51 and 33 well-marked individuals were seen in more than one area in each year (2006 and 2007), and 9 and 10 individuals were seen in all three areas. In both years, the movement of individuals was greatest between the inner and southern Moray Firth (37 and 27 individuals), as indicated by the positive estimated interaction effects for these areas in the model (Table 4). There was a weaker positive interaction between the southern Moray Firth and the Grampian/Fife coast but less movement of individuals

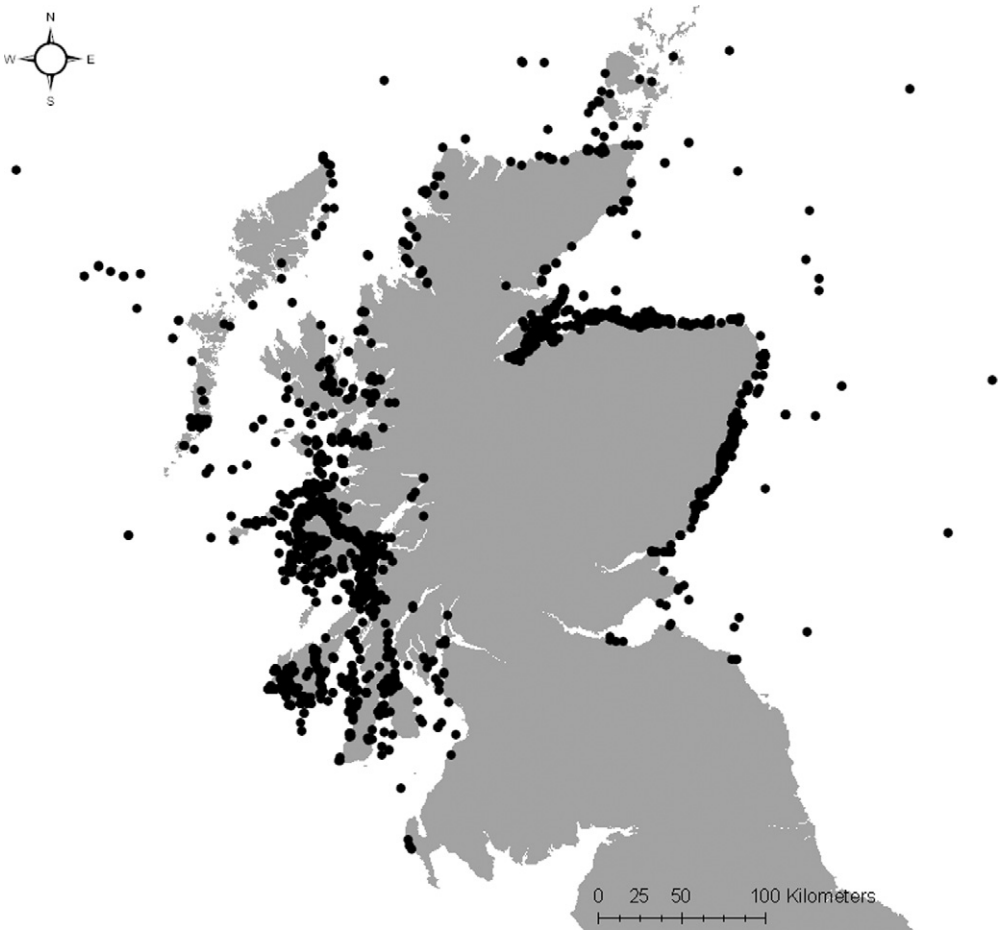

Fig. 5. Sightings of bottlenose dolphins around Scotland from 1966 to 2007, recorded by the Sea Watch Foundation and the Hebridean Whale and Dolphin Trust.

between the two areas (22 and 15 individuals in 2006 and 2007, respectively). Conversely, there was a strong negative estimated interaction effect between the inner Moray Firth and Grampian/Fife coast, indicating relatively low levels of movement (10 individuals) between these most geographically separate of areas. For 2007, there was a high probability of all the interaction effects being selected for inclusion in the model, but in 2006 there was little support for the southern Moray Firth and the Grampian/Fife coast interaction. The posterior distribution for this interaction effect overlapped zero, in contrast to the other interactions where the distribution covered only positive and only negative values (Table 4). The multi-site mark-recapture model incorporated these interaction terms and inclusion probabilities when using MCMC sampling to predict overall abundance (Durban et al. 2005).

Table 3. Model averaged estimates of a) the number of well-marked individuals (*N*) and b) the total number of all individual (*P*) bottlenose dolphins using the east and west coast of Scotland in the summers of 2006 and 2007. The 95% highest posterior density intervals (HPDI) are shown for each estimate

	2006		2007	
	Median	95% HPDI	Median	95% HPDI
a) Well-marked individuals (*N*)				
East coast	104	89–132	136	107–231
West coast	25	19–37	30	23–42
b) All individuals (*P*)				
East coast	195	162–253	227	175–384
West coast	45	31–71	45	33–66

Table 4. East coast of Scotland estimates of all study area interactions in the multi-site mark-recapture model describing the study area counts (Table 1). Estimates are presented as the median (95% highest posterior density intervals) of the posterior distribution for each parameter and the probability (*p*) of each possible interaction being selected for inclusion in the model. The upper diagonal denotes interactions for 2006 and the lower for 2007

	Inner Moray Firth (Area 1)	Southern Moray Firth (Area 2)	Grampian/Fife Coast (Area 3)
Inner Moray Firth (Area 1)		1.4 (0.5, 3.4) $p = 0.99$	–1.3 (–3.3, –0.5) $p = 1.0$
Southern Moray Firth (Area 2)	2.0 (0.9, 6.0) $p = 1.0$		–0.2 (–1.9, 0.5) $p = 0.3$
Grampian/Fife Coast (Area 3)	–0.2 (–1.7, –0.2) $p = 0.8$	1.0 (0.2, 3.4) $p = 0.95$	

WEST COAST

There was movement of individuals only between Skye and north and south of Skye: 8 and 9 well-marked individuals were seen in both of these areas in 2006 and 2007, as indicated by the positive interaction between them. There was a negative interaction between Skye and north and the Sound of Barra, with no movement between these areas (Table 5). Both these interactions had a high probability of inclusion in the model, but there was little utility to adding an interaction between the south of Skye and Sound of Barra areas, as the low numbers of dolphins identified in both these areas led to very imprecise estimates of the distributions for interaction effects, which significantly overlapped with zero.

DISCUSSION

Historic and contemporary sightings from naturalists and members of the public can provide a useful indication of the broad scale distribution of bottlenose dolphins around the Scottish coast. However, inferences from these data are constrained both by uncertainty over the reliability of species identification and by spatial and temporal variation in sightings effort. Data on strandings are generally less vulnerable to misidentification issues but are also potentially biased due to the lower likelihood of reporting on remote coasts and the relevance of the location of stranding relative to living distribution.

Historical literature sources provide little evidence for the occurrence of bottlenose dolphins in Scottish waters. There are no known archaeological sites in Scotland, and naturalists' reports suggest that the occurrence of bottlenose dolphins in the late 1800s was sporadic compared with that of other species such as harbour porpoise, killer whales *Orcinus orca* and pilot whales *Globicephala* sp. Nevertheless, it is clear from our review of more recent strandings and sightings that bottlenose dolphins are now present both in offshore waters and throughout most Scottish inshore waters. Reid et al. (2003) provide the most robust effort-corrected data set for comparing density in different areas, although their analysis is restricted to data collected before 1998. Their data (Fig. 3) highlight the high relative densities along the east coast of Scotland and the occurrence of dolphins further offshore along the shelf edge. Sightings around the rest of the Scottish coastline were rare in this data set (Fig. 3), but search effort was also relatively low. Additional sightings from the Sea Watch Foundation and the HWDT (Fig. 5), many of them reported since 1997, provide evidence of widespread occurrence of bottlenose dolphins in the Inner Hebrides. There have been relatively few reports of bottlenose dolphins on the north coast of mainland Scotland or around Orkney and Shetland (Figs 4 and 5), and some of these sightings are by members of the public (Fig. 5) where there is less certainty over species identification. Confusion with species such as Risso's dolphin *Grampus griseus* and white-beaked dolphin *Lagenorhynchus albirostris* that are more commonly seen in these areas (Reid et al. 2003) is of particular concern. Despite efforts to solicit additional reports from the north coast, only one sighting was reported from this area during 2006 and 2007. Photographs submitted by members of the public confirmed that individuals that we recorded on the west coast in 2006 and 2007 were subsequently recorded on the north coast in 2008 (University of Aberdeen unpublished data).

Variation in the effort underpinning these sightings constrains the extent to which these data truly indicate geographical variation in the density of bottlenose dolphins.

Table 5. West coast of Scotland estimates of all study area interactions in the multi-site mark-recapture model describing the study area counts (Table 1). Estimates are presented as the median (95% highest posterior density intervals) of the posterior distribution for each parameter and the probability (*p*) of each possible interaction being selected for inclusion in the model. The upper diagonal denotes interactions for 2006 and the lower for 2007

	Sound of Barra (Area 4)	South of Skye (Area 5)	Skye and North (Area 6)
Sound of Barra (Area 4)		–1.2 (–9.8, 6.6) $p = 0.4$	–5.9 (–17.9, 0.2) $p = 0.8$
South of Skye (Area 5)	–0.9 (–9.6, 6.9) $p = 0.3$		6.5 (0.3, 17.9) $p = 0.8$
Skye and North (Area 6)	–6.7 (–18.7, –0.4) $p = 0.8$	6.4 (0.2, 17.5) $p = 0.8$	

Similarly, temporal variation in sighting effort makes it difficult to assess how the occurrence of dolphins in different areas may have changed over time. Over the last two decades, sightings have only been consistently reported from two areas: the east coast of Scotland (Wilson et al. 2004, Anderwald et al. 2010) and the Sound of Barra (Grellier & Wilson 2003). The east coast has one of the highest human population densities of the Scottish coast, but the Sound of Barra is one of its most remote areas. Regular reports of sightings in both these areas from members of the public provide some support for the assumption that the regular occurrence of dolphins in any part of the Scottish coast is now unlikely to remain undetected. Bottlenose dolphins have also been reported in many other remote areas of Scotland (see Fig. 5), but the temporal pattern of these sightings appears much more patchy, and there is no evidence of predictable sightings at the same location either within or between years.

Estimates of abundance

We draw together all available photo-identification data to produce the first comprehensive estimates of abundance of bottlenose dolphins in inshore waters of mainland Scotland and the Western Isles.

EAST COAST

Our 2006 estimate (195, 95% HPDI: 162–253) provides the most precise indication of the current size of the Scottish east coast bottlenose dolphin population (Table 3). This result is similar to that produced by Durban et al. (2005), who used a smaller data set from the same areas to demonstrate the methodology used here and estimated this population as 85 (95% HPDI: 76–263) well-marked dolphins in 2001, compared with our estimate of 104 (95% HPDI: 89–132) well-marked dolphins in 2006.

Previous studies of bottlenose dolphins in Scottish coastal waters have been focused on the east coast population, particularly in the Moray Firth. The integration of photo-identification data collected by all research groups working on this population has provided an abundance estimate that was higher than the first, and most commonly used, estimate for this population, of 129 in 1992 (Wilson et al. 1999). However, it is important not to over-interpret the significance of this difference. Wilson et al. (1999) used Chao et al.'s (1992) M_{th} model, implemented in the programme CAPTURE (Rexstad & Burnham 1991). Also, the 95% confidence intervals of the 1992 estimate (110–174) overlap with the 95% HPDI for our most precise recent estimate (162–252). Unfortunately, data collection methods in each collaborating research group did not allow a direct comparison of methodologies. Further work is required to determine whether or not the overall size of the east coast population has changed over this period. However, assessment of this is complicated by the fact that the geographical range of this population has changed over the last 20 years (Wilson et al. 2004), and survey effort in different areas has also changed in response to this. Consequently, these two sets of estimates differ both in the detail of data collection and in the statistical approach to estimation. The 2006 estimate may be higher because survey design in the earlier studies resulted in an estimate that was negatively biased, because of differences in the mark-recapture model used for the two estimates, because our new estimate covers more of the home range of this population, or because the population has increased over the last two decades.

WEST COAST

For the west coast, our estimates for 2006 (45, 95% HPDI: 31–71) and 2007 (45, 95% HPDI: 33–66) are identical, but the estimate for 2007 is slightly more precise and we consider this to be the best estimate of the number of bottlenose dolphins in the area. The only previous estimate for this area is from the Sound of Barra, where Grellier and Wilson (2003) estimated 6–15 individuals from data collected in 1995 and 1998. This compares well with our data from 2006 and 2007, which indicated that a total of 13–15 individuals used the waters around the Sound of Barra.

SCOTTISH BOTTLENOSE DOLPHIN ABUNDANCE IN A WIDER CONTEXT

Estimates from larger scale surveys illustrate that our estimates for mainland Scotland and the Western Isles are a small proportion of the populations living in European waters. The SCANS-II line transect survey estimate of bottlenose dolphin abundance in European Atlantic continental shelf waters from 62°N to the Straits of Gibraltar in 2005 was 12645 (95% CI: 7500–21300; Anonymous 2008b). This survey was not designed to estimate abundance in small areas, so no direct comparison is possible with our estimates. However, SCANS-II estimates from survey blocks that included Scottish waters (including Orkney and Shetland) were of the same order of magnitude (100 s) as our estimates. In 2007, offshore surveys of waters (deeper than 200 m) to the west of the SCANS-II survey area produced an estimated 19295 (95% CI: 11842–31440) bottlenose dolphins, 5700 (95% CI: 2900–11100) in waters north of 53°N, including offshore Scottish waters (Anonymous 2009b). In both these surveys, researchers were unable to correct for animals missed on the transect line in analyses, so the estimates are negatively biased.

This estimate of just 200–300 bottlenose dolphins in Scottish coastal waters contrasts with the estimates of the

number of offshore animals, an order of magnitude larger, that have been obtained through these large-scale surveys. The relationship between offshore groups and those occurring in coastal waters remains uncertain, although more detailed studies in the NW Atlantic suggest that inshore and offshore populations are often ecologically and genetically discrete (Hoelzel et al. 1998). Nevertheless, some offshore animals may occasionally strand on Scottish coasts and this is a potential confounding factor when using samples from stranded individuals to explore population structure.

Study area interactions

EAST COAST

There was significant movement of individuals between all the east coast study areas, and a number of individuals were seen in all three areas. However, the results show a higher rate of exchange of dolphins between the two geographically closest areas (inner and southern Moray Firth).

Although these results do not provide information on the ranging patterns of individual dolphins, they clearly demonstrate that the population of bottlenose dolphins off the east coast of Scotland is highly mobile: individuals range from the inner Moray Firth to Fife. However, one confirmed sighting in 2007 of a group near Whitley Bay and the Tyne river mouth suggests that individuals occasionally range further south (Thompson et al. 2011). This population cannot, therefore, be subdivided into separate units based on area alone. The results of genetic analyses (Parsons et al. 2002, Thompson et al. 2011) show some but not complete isolation between animals found on the east and west coasts and elsewhere in Britain and Ireland. Together, these results confirm that the east coast population should continue to be considered as a single separate unit for management purposes.

WEST COAST

In both years the majority of individuals were observed in waters around Skye and to the north, and few individuals were seen south of Skye and in the Sound of Barra. Despite observations of significant movements of dolphins throughout the west coast, none of the individuals identified in the Sound of Barra was seen elsewhere. This suggests that there are two discrete communities of bottlenose dolphins on the west coast of Scotland, which we recommend should be considered as separate units for management purposes, pending further study.

SCOTTISH BOTTLENOSE DOLPHIN MOVEMENT

Photographs of well-marked dolphins from 2006 and 2007 from all collaborating organizations and comparisons of the east and west coast catalogues, maintained by the University of Aberdeen and the HWDT, respectively, produced no matches, suggesting that there is no movement of bottlenose dolphins between the east and west coast of Scotland. However, archive photographs from previous years did provide evidence for such movement. Seven individuals that were photographed along the southern shore of the outer Moray Firth by the Cetacean Research and Rescue Unit in 2001 were later recorded on the west coast by the HWDT between 2002 and 2005 and by the University of Aberdeen in 2006 and 2007 (Robinson et al. 2012). Furthermore, subsequent comparisons have shown that five of these dolphins could also be matched with bottlenose dolphins photographed around the coasts of the Republic of Ireland (Robinson et al. 2012). These photographic matches support the results of the genetic analysis in showing only partial isolation between dolphins found around the Scottish coasts (Parsons et al. 2002, Thompson et al. 2011).

CONCLUSIONS

Existing data indicated a wide but patchy distribution of bottlenose dolphins in Scottish waters. This review based on the combination of historical records, dedicated photo-identification studies and third party reports has allowed us to expand our research efforts and examine distribution and abundance even in areas with low density, where animals are unpredictable and highly mobile. Our study suggests that a relatively small number of bottlenose dolphins (200–300 individuals) occur regularly in Scottish coastal waters. Multi-site mark-recapture estimates indicate that the numbers on the east coast are approximately five times higher than those on the west coast. On both coasts, re-sightings of identifiable individuals indicate that some of the animals recorded during our surveys in 2006 and 2007 have been using these coastal areas since studies began in 1989 on the east coast and 1995 on the west coast. The number of animals using other parts of the Scottish coastline, for example the north coast, appears to be low, but further investigation of the occurrence of dolphins on this coast may now be justified given recent evidence of movement between east and west coasts and the strategic importance of this area for marine renewable energy developments.

Our study suggests that there are three parapatric communities of bottlenose dolphins in Scottish coastal waters, each of a different size and with marked contrasts in their ranging patterns. On the west coast, there are two small and socially segregated communities of dolphins, one of which includes approximately 15 individuals that have only been recorded in the waters around the Sound of Barra, whereas the other is double that size and ranges more widely throughout the Inner Hebrides and mainland coasts. On the

east coast, there is a population of nearly 200 interacting dolphins between the Moray Firth and Fife, with individual differences in ranging behaviour and site fidelity.

Analyses of photo-identification data from multiple studies have also shown that bottlenose dolphins can make long-distance movements between the east and west coasts of Scotland, and further exchange between Scottish and Irish waters has recently been revealed (Robinson et al. 2012). Whether these movements represent exchange between different coastal communities or interaction with more widely ranging offshore animals remains uncertain, but this finding suggests that it would be worthwhile to continue making comparisons between photo-identification catalogues from Scottish and other European waters. Importantly, this finding also highlights the value of maintaining long-term research effort in each of these areas. Without the long-term archives available through previous projects, these rare movements would not have been detected. However, considerable resources would be required to maintain long-term photo-identification studies throughout Scottish coastal waters, and monitoring programmes of this kind are only likely to be sustainable if they are integrated into broader research projects and collaborations, education programmes or ecotourism operations.

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