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Considering the temporal when managing the spatial: a population range expansion impacts protected areas-based management for bottlenose dolphins

Ben Wilson[1,*], Robert J. Reid[2], Kate Grellier[1,3], Paul M. Thompson[3] and Philip S. Hammond[1]

[1] Sea Mammal Research Unit, Gatty Marine Laboratory, University of St. Andrews, St. Andrews, Fife, KY16 8LB, UK
[2] SAC Veterinary Science Division (Inverness), Drummondhill, Stratherrick Road, Inverness, IV2 4JZ, UK
[3] University of Aberdeen, Department of Zoology, Lighthouse Field Station, Cromarty, Ross-shire, IV11 8YJ, UK

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Abstract

Management of marine species has increasingly focused on key site protection. Initiatives to protect bottlenose dolphins, *Tursiops truncatus*, under the EU Habitats Directive reflect this trend. The boundaries of the Moray Firth candidate Special Area of Conservation (cSAC) were intended to include the main Scottish population's core range, following research conducted in the 1980s and early 1990s. However, during implementation, anecdotal sightings increased outside the cSAC. Here, the authors examine existing datasets to identify whether these reports reflect simply elevated awareness among public observers or real changes in distribution. Dolphins photo-identified in areas originally considered to be outside the population's range confirmed they originated from the protected population. These individuals became rarer within the cSAC during the 1990s. Scottish bottlenose dolphins kill harbour porpoises, *Phocoena phocoena*, and carcasses from these interactions also became more frequent outside the cSAC during the 1990s. These results indicate mobility of this 'resident' dolphin population on a timescale similar to that of the implementation of the European Directive designed to protect it. Consequently, this and other similar designations, may afford less protection than originally envisioned and the authors recommend, therefore, that the potential for long-term mobility should be actively incorporated into such management structures from the outset.

INTRODUCTION

Management efforts to conserve marine species are increasingly focusing on the protection of key areas and habitats (Agardy, 1994). The European Union's 'Habitats' (92/43/EEC) Community directive, for example, is currently under implementation and will lead to an extensive network of protected areas across the Union. Although the concept of marine protected areas (MPAs) for odontocetes (toothed whales, dolphins and porpoises) is desirable (Evans & Urquiola, 2001), from a pragmatic standpoint the large ranges and protracted life-history of many species poses particular difficulties.

The bottlenose dolphin, *Tursiops* sp., is perhaps one of the more promising species for this approach. Throughout their temperate and tropical range, coastal populations often occur in discrete locations either seasonally or year-round. In coastal waters around Britain, two relatively large resident populations are known and well studied (Evans, 1980), one in Cardigan Bay, Wales and the other in a large embayment off north-east Scotland called the Moray Firth (Fig. 1). Since bottlenose dolphins are listed in Annex II of the European Union's Habitats Directive, EU governments are required to consider these areas for the establishment of Special Areas of Conservation (SACs). These designations are intended to protect rare, endangered or vulnerable habitats and species through establishing a network of sites across the European Community. Accordingly, both areas used by the dolphins have been put forward as candidate SACs (cSACs) under the Natura 2000 scheme and management groups and plans are now in place (Scottish Natural Heritage, 1995; Ceredigion County Council *et al.*, 2001; Moray Firth Partnership, 2001). Of the two populations, the Moray Firth population is the most geographically discrete and better studied and so offers the best opportunity to examine the efficacy of a protected area approach.

The biological information that led to the determination of the area and boundaries for the Moray Firth cSAC was based primarily on data from ship-based sightings surveys in the 1980s but also from boat-based photo-identification work between 1989 and 1991. These data suggested that although other areas such as the southern Moray Firth were used (Lewis & Evans, 1993), the landward part of this large embayment (the inner Moray Firth) was occupied the most intensively by bottlenose dolphins (Fig. 1: Mudge, Crooke & Barrett, 1984; Wilson, Thompson & Hammond,

*All correspondence to: Dr Ben Wilson, The Behaviour@Sea Project, Marine Mammal Research Unit, University of British Columbia, 6248 Biological Sciences Road, Vancouver, V6T 1Z4, B.C. Canada. Tel: 001-604-822-9111; Fax: 001-604-822-8180; E-mail: bwilson@zoology.ubc.ca

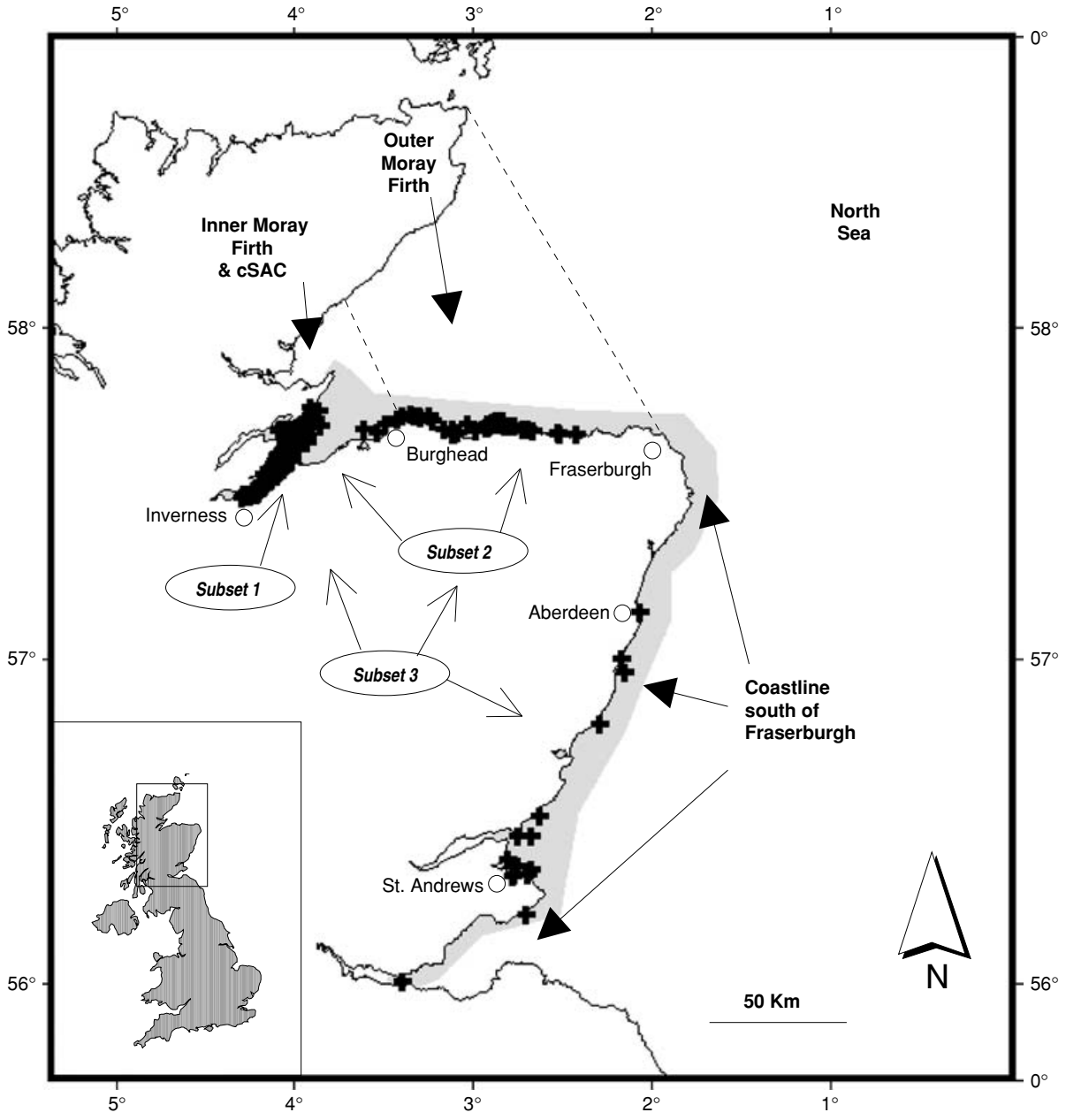

Fig. 1. Map of eastern Scotland showing the areas of survey effort (shading), dolphin sightings (crosses) and broad areas used by the three dolphin subsets. Inset shows location relative to the United Kingdom.

1997). Between 1990 and 1993, this area was occupied year-round and was visited annually by at least 90% of the total population (estimated at 129 individuals, standard error (SE) = 15: Wilson *et al.*, 1997; Wilson, Hammond & Thompson, 1999). Within this area, the distribution of individuals appeared to be stratified such that animals could be statistically ranked by their average location within the inner Moray Firth (Wilson *et al.*, 1997). Specifically, the individuals in the inner Moray Firth that were identified most often tended to be found nearer the head of the inner Moray Firth than occasionally and rarely seen individuals. The factors that led to this unusual stratification are as yet unknown as are the reasons why the inner Moray Firth appeared to be favoured by this population.

Although the majority of boat-based and opportunistic shore-based sightings of bottlenose dolphins take place in the inner Moray Firth (i.e. within the cSAC), animals are known to occur elsewhere. From 1991 onwards, reports of sightings by amateur observers along the southern shores of the outer Moray Firth (between Burghead and Fraserburgh: Fig. 1) became frequent (Lewis & Evans, 1993). In response to these accounts, photo-identification boat surveys in the inner Moray Firth were extended to cover these coastal waters (Table 1). Similarly, in the mid-1990s, anecdotal reports from coastal observers and mariners along the east coast of Scotland between Fraserburgh and St. Andrews began to increase (Weir & Stockin, 2001). For example, one skilled coastal observer

Table 1. Temporal and spatial distribution of survey effort

	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
Inner Moray Firth (cSAC)	14 (400)	38 (475)	38 (436)	23 (276)	27 (274)	43 (448)	19 (317)	14 (170)	14 (257)	13 (199)	10 (87)
Outer Moray Firth		3 (1)	9 (78)	2 (17)	18 (84)	8 (77)	9 (49)	4 (42)	1 (1)		
Coastline south of Fraserburgh			(5)*				5 (2)	5 (0)	2 (27)	5 (18)	8 (40)

Effort expressed as number of boat-survey days and total photo-identifications (summed ID recognitions per day) in brackets.
* Photo-identification pictures obtained without a boat survey.

off St. Andrews, who kept detailed notes from 1990, recorded bottlenose dolphins for the first time in 1992 and then every subsequent year with increasing frequency (I. Cumming, pers. comm.). Photo-identification surveys were likewise extended to this area in 1996 (Table 1).

While potentially pointing to an extension in the population's range, the temporal trends in reports coming from new areas must be treated with caution as Scottish bottlenose dolphins gained increasing media coverage and local observer interest during the 1990s. Unfortunately, too few observations were associated with quantified effort to discriminate between a true range extension or just the gradual exposure of an existing distribution.

In this study we use two other sources of information to test for evidence of a shift or extension in the range of the dolphin population during the 1990s. First, we use boat-based photo-identification data to examine the spatial structuring of individuals within the population and then look for changes in this structuring during the 1990s. Second, we examine data from an unusual source. Due to the nature of the marine environment, cetaceans typically do not leave the field-signs (droppings, tracks, burrows etc) that are routinely used to study terrestrial mammals. As a result, most information on distribution relies on direct sightings (Hammond *et al*., 2002; Reid, Evans & Northridge, 2003). However, off Scotland, bottlenose dolphins frequently attack and kill the more widespread and numerous harbour porpoises, *Phocoena phocoena* (Ross & Wilson, 1996). We therefore look at the recorded locations of stranded porpoise carcasses resulting from these attacks for evidence of a dolphin distributional change over time.

MATERIALS AND METHODS

Photo-identification studies

Between 1990 and 2000, 332 days of boat-based research effort were carried out in waters off eastern Scotland. Dolphins encountered on these surveys were photographed and the resulting pictures subjected to standard photo-identification analyses to identify individuals (Wilson *et al.*, 1999). Within the inner Moray Firth (the area of the cSAC), 253 systematic surveys (as detailed in Wilson *et al*., 1997) were carried out. Opportunistic effort was also carried out on 54 days in coastal waters of the outer Moray Firth (between Burghead and Fraserburgh, 1991–1998) and 25 days in the St. Andrews area (1996–2000: Table 1).

Sightings of a set of naturally well-marked individuals first identified between 1990 and 1992 and known to be surviving in 1998, 1999 or 2000, were examined to determine whether there was any evidence of changes in their ranging behaviour between 1990 and 2000.

For several spatial analyses, locations were expressed as linear through-water distances from Inverness (a coastal town at the head of the inner Moray Firth: Fig. 1). These same units were used in a previous study of area use in the Moray Firth between 1990 and 1993 (Wilson *et al.*, 1997) and therefore allow direct comparison with the longer time series featured in this study (1990–2000).

Harbour porpoise strandings

An ongoing study of stranded cetaceans has been carried out by the Scottish Strandings Scheme since 1990. The Scheme collates information and organises post-mortem examinations following standard protocols (Kuiken & Hartmann, 1991). For this study, records of harbour porpoises that stranded along the east coast of the Scottish mainland between 1990 and 2001 were compiled. Details from each post-mortem examination were retrospectively reviewed to determine whether animals showed the known characteristic signs of violent interactions with bottlenose dolphins (Ross & Wilson, 1996). Carcasses were excluded if they were sufficiently decomposed that the cause of death could not be determined.

RESULTS

Photo-identification studies

To investigate whether there had been changes in area use, we looked for individual bottlenose dolphins that were encountered throughout the study period. Of the total dolphins identified, 54 individuals identified between 1990 and 1992 continued to be re-sighted between 1998 and 2000; this set of animals represented 42% of the entire population as estimated in 1992 (Wilson *et al.*, 1999). On average, each of these individuals was seen in 9 out of the 11 years of the study (range 5–11 years). All members of

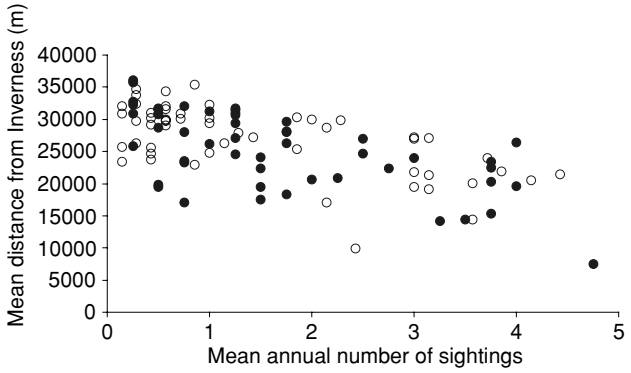

Fig. 2. Spatial stratification of locations by 54 individuals within the inner Moray Firth (cSAC). Mean of annual number of sightings of each individual are plotted against their mean locations in the inner Moray Firth. Filled circles depict data from 1990–1993 and open circles from 1994–2000.

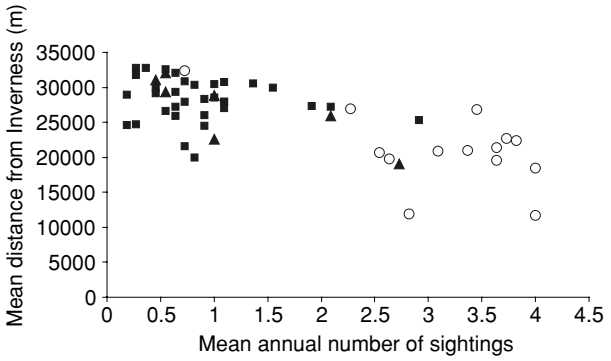

Fig. 3. Spatial distribution of 54 individuals in the inner Moray Firth (cSAC). Open circles depict animals only ever found in the inner Moray Firth (subset 1 animals); triangles depict individuals identified at other times in the outer Moray Firth (subset 2 animals); squares depict individuals found in all parts of the population's known range (inner and outer Moray Firth and coasts south of Fraserburgh: subset 3 animals).

the set were seen in the inner Moray Firth at some time during the 11 years of survey effort. Fourteen (26%) were only ever seen in the inner Moray Firth (termed subset 1 animals: Fig. 1). Seven (13%) were identified in both the inner and outer Moray Firth but nowhere else (subset 2). The remaining 33 (61%) had been seen in all parts of the population's known range (inner and outer Moray Firth and coasts south of Fraserburgh: subset 3). The average subset 1 animal was seen in 10 out of the 11 study years, subset 2 animals were identified on average in 8 of the years and subset 3 in 9.

Following a previous examination of dolphin distribution between 1990 and 1993 in the inner Moray Firth, an unusual spatial stratification pattern within the population was identified (Wilson *et al.*, 1997). In this, the number of days that each individual dolphin was seen was negatively correlated with its average location within the inner Moray Firth (expressed as distance from the town of Inverness). When re-calculated using the long-term set of 54 individuals identified in 1990–1992 and still alive in 1998–2000, we found that the previously described pattern was conserved throughout the time series. That is, data pooled for 1990–1993 and 1994–2000 showed similar relationships between sightings rate and average locations in the inner Moray Firth (Fig. 2). In addition, the individuals themselves appeared to be consistent in their relative distributions with respect to one another through time, with the mean location of each individual in the inner Moray Firth being highly correlated in 1990–1993 with its mean location in 1994–2000 (Spearman's Rank Correlation: $t = 4.8$, $n = 54$, $P < 0.0001$). In other words, throughout an 11 year period, the dolphins using the inner Moray Firth showed a consistent pattern of spatial structuring among themselves.

Because the surveys conducted in the inner Moray Firth were standardised across years with respect to spatial coverage, the observed stratification patterns should be representative. However, because survey coverage was opportunistic in other areas it was not possible to test for similar patterns elsewhere. Despite this, when the inner

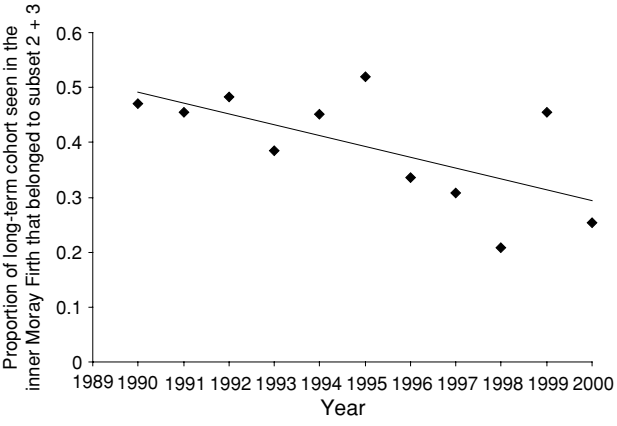

Fig. 4. Of the total long-term cohort of photo-identified dolphins, subsets 2 and 3 became a progressively smaller proportion of those identified in the inner Moray Firth between 1990 and 2000.

Moray Firth stratification patterns (described above) were re-examined with reference to whether or not individuals had been identified in other areas, two trends emerged (Fig. 3). First, subset 2 and 3 animals used parts of the inner Moray Firth significantly further from Inverness than subset 1 animals (median distance = 28.4 km versus 20.9 km, Mann–Whitney U test, $z = 4.0$, $P < 0.0001$). Second, subset 2 and 3 animals were identified significantly less frequently in the inner Moray Firth than the subset 1 animals (median number of sightings = 8 versus 37, Mann–Whitney U test, $z = -5.0$, $P < 0.001$).

If the range of the population expanded during the 1990s, we would predict that the frequency of subset 2 and 3 animals in the inner Moray Firth would decline with time as it is these animals that were found further afield. This was the case: the subset 2 and 3 animals became a significantly smaller proportion of the long-term cohort of individuals seen during systematic surveys in the inner Moray Firth over time (Ordinary Least Squares regression, $r^2 = 0.4$, $P < 0.05$: Fig. 4).

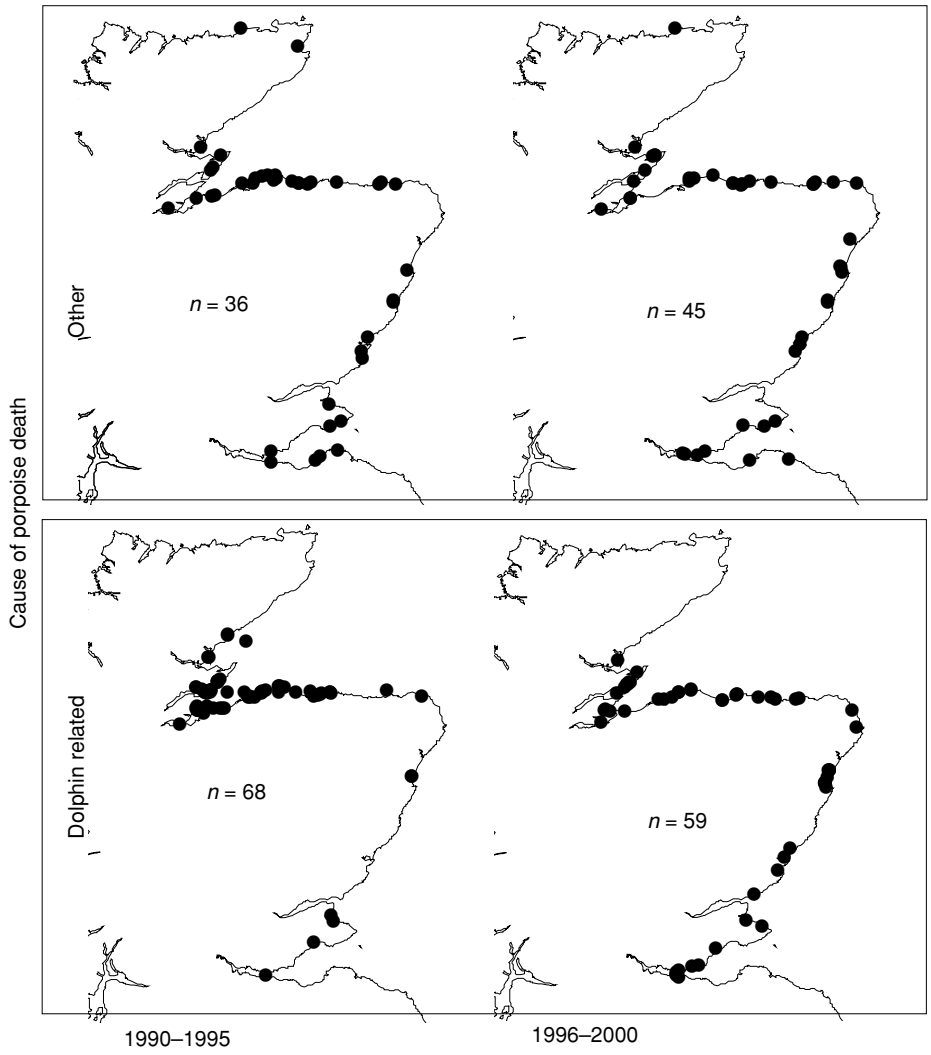

Fig. 5. Distribution of harbour porpoise carcasses recovered along the east coast of the Scottish mainland by the Scottish Strandings Scheme. Strandings were sorted into two categories: those that displayed signs consistent with attack by bottlenose dolphins (bottom maps) and those that died from other causes (top maps).

Subset 2 and 3 animals did not stop using the inner Moray Firth, however, and many appeared to make rapid long distance movements within the population's known range. One subset 3 individual, for example, was identified south of Aberdeen in June 1996 and re-identified off Burghead 52 h later. This represented a distance of 218 km and a minimum swimming speed of 4.2 km h^{-1}. In general, animals that used areas outside of the inner Moray Firth (subset 2 and 3 animals) appeared to move greater distances *between* sightings. For consecutive sightings 5 or less days apart, the median rate of travel by subset 1 animals was 0.071 km h^{-1} ($n = 14$ individuals) while for subset 2 and 3 animals it was significantly greater at 0.22 km h^{-1} ($n = 38$ individuals, Mann–Whitney U test, $z = -3.3$, $P < 0.001$). They also moved faster *during* sightings. Because the location at the start and end of each sighting was recorded, the rate of progress could be calculated. In the outer Moray Firth and along coasts south of Fraserburgh the median rate of progress was 7.6 km h^{-1} ($n = 47$) while in the inner Moray Firth it was approximately half this speed (3.9 km h^{-1}, $n = 754$, Mann–Whitney U test, $z = -3.9$, $P < 0.0001$).

Harbour porpoise strandings

Between 1990 and 2001, 227 harbour porpoises were recovered from beaches or found floating in the water near the east coast of mainland Scotland. Of these, 208 were sufficiently fresh for probable cause of death to be ascribed at post-mortem examinations. A total of 61% of these showed signs characteristic of violent interactions with bottlenose dolphins while the remaining animals had died of various other causes ranging from accidental capture in fishing nets to chronic disease. The numbers of stranded porpoises that died of the 'other' causes were similar in the period 1990–1995 and the period 1996–2000 (36 and 45, respectively). The spatial distribution of these porpoise strandings was also similar in the two time periods (Fig. 5) and when classified by their distance from Inverness was not significantly

different (1990–1995, median distance = 113 km; 1996–2000, median distance = 127 km: Mann–Whitney *U* Test, $z = -0.2$, $P = 0.84$). The numbers of strandings resulting from violent interactions with dolphins were also of similar magnitude before and after the start of 1996 (68 compared with 59) but the locations of these strandings varied significantly between the two periods, with the median stranding being 51 km from Inverness before 1996 and 126 km from Inverness after (Mann–Whitney *U* Test, $z = -4.5$, $P < 0.0001$). This difference stemmed from a low number of dolphin-related porpoise strandings on coasts south of the Moray Firth in the earlier years (Fig. 5).

DISCUSSION

Photo-identification offers a method for tracking the movements of individuals and trends in area use. One objective of our photo-identification study of bottlenose dolphins along the Scottish east coast in the 1990s was to photograph as many individuals from as wide a range of locations as possible. Effort was therefore targeted towards areas where dolphins were known to occur. In consequence, we increased the spatial range of our research effort in response to reports from the public during the 1990s. Because search effort was not systematic throughout the geographical range, we are unable to use these data to directly test the range extension hypothesis. However, our detailed investigation of the individuals identified on these surveys did reveal supporting evidence. Examination of data from a set of 54 distinctively marked animals first identified in the inner Moray Firth and known to have survived through the 1990s, revealed that the majority (74%) had subsequently been identified in the outer Moray Firth and that 61% had also been seen along the coasts south of Fraserburgh. Because these animals were chosen on the basis of the longevity of their natural marks and their survival rather than their behaviour, this pattern should be representative of the population as a whole. The animals that were found in the outer Moray Firth and coasts south of Fraserburgh had already been identified in the inner Moray Firth at the beginning of the 1990s, confirming that they had come from the previously termed Moray Firth population and not from other parts of the North Sea or the wider Atlantic.

Rather than shifting their range completely out of the inner Moray Firth (cSAC), the animals seen in other areas (subsets 2 and 3) continued to be seen in the inner Moray Firth. Thus, the population has expanded, rather than shifted, its range. When compared, the population also continued to display the unusual spatio-temporal stratification pattern within the inner Moray Firth, previously detected in the early 1990s (Wilson *et al.*, 1997). As such, the animals that were identified in areas outside the inner Moray Firth (subsets 2 & 3) occupied strata furthest from the headwaters. In addition, although they continued to use the inner Moray Firth throughout the 1990s, their proportion of the total long-term cohort seen on surveys in the inner Moray Firth declined significantly (Fig. 4). Whether these animals will continue to use the inner Moray Firth less and less, or will return to use it more regularly in the future remains to be seen.

The second line of evidence for a range extension comes from the stranded porpoise carcasses. Numbers that resulted from violent interactions with dolphins increased in the 1990s in areas outside the cSAC, while numbers that died of other causes did not. The small number of dolphin-related carcasses that stranded as far south as St. Andrews in the early 1990s suggest that some bottlenose dolphins did occur that far south, if only rarely, in this area before a larger influx later on.

We recognise that care must be taken with this kind of information. Attacking porpoises is a dolphin behaviour and changes in its frequency could result from several factors. For example, cultural transmission along a line of already established dolphins rather than the movements of the individuals themselves could have caused the pattern observed here. Without knowing which individual dolphins were responsible for the attacks, this possibility can, therefore, not be excluded outright. However, the discovery of similar violent interactions around the British Isles and North America (Dunn *et al.*, 1998; Jepson & Baker, 1998) suggests that these attacks are an established component of bottlenose dolphin behaviour and not simply a new or localised aberration. Another alternative is that an increase in the abundance of porpoises in the outer Moray Firth and coasts to the south could have inflated the probability of the two species encountering one another and hence the occurrence of violent interactions. However, changes in the distribution of porpoises should also be reflected in the distribution of porpoise carcasses that resulted from other causes. This, however, was not observed.

If the bottlenose dolphin range extension hypothesis is, therefore, accepted, the question of its cause(s) arises. One possibility is that the number of individuals in the population has increased and has forced the boundary of the population into new areas. The lack of evidence of influx from other populations (Wilson *et al.*, 1999) and the apparent negative population growth rate during this period (Sanders-Reed *et al.*, 1999) renders this possibility unlikely. A change in predation pressure also seems unlikely, since there is no evidence of predation occurring on these animals (Wilson, 1995). Instead, changes in prey resources seem most likely. Certainly the rapid and long-range movements observed outside the inner Moray Firth (cSAC) suggest that prey resources may be more widely dispersed and/or different in these newly exploited areas. Put in this context, the so far unexplained stratification pattern within the inner Moray Firth (cSAC) becomes more interesting. If many of the animals that use this area leave to forage up to 400 km away, why do others remain there permanently? Are these animals exploiting different prey or is there competition between dolphins leading to the exclusion of animals when prey become less abundant?

These ecological questions are highly relevant when current management initiatives are considered. SACs are intended to protect vulnerable species in particularly

important parts of their range. Such schemes are appropriate for site-faithful or sessile species but less so for highly mobile ones (Roberts, 2000). Bottlenose dolphins appear to fall between these extremes. The designation of the inner Moray Firth as a cSAC was based on information collected in the 1980s/early 1990s and, at the time, conferred protection across what was considered to be the majority of the population's known range. A decade on, as the management scheme is being implemented, the cSAC now covers a relatively small part of the population's range. Furthermore, because of the heterogeneity in individual ranging behaviour, the cSAC will afford individuals widely differing levels of protection. A population of large mammals of only 130 individuals is already expected to be highly vulnerable to extinction (Soulé, 1990). Affording protection to only a limited part of the population may have grave consequences since it is unlikely to allow the population to increase at the same rate as might be expected from more fecund species (Roberts, 1997).

The stratification among individuals found in the inner Moray Firth also has implications for population monitoring. If competition occurs between dolphins, the numbers present in the inner Moray Firth (and the cSAC) may have less to do with the total population size than its status as a preferred habitat. Thus, monitoring population status within the management area alone (as has been frequently suggested) would be inadvisable.

Despite many aspects of the ecology of the bottlenose dolphin population off eastern Scotland being poorly understood, arguably more is known about it than any other in temperate waters worldwide. The gradual changes in distribution seen in these animals over the period of a decade may also be common in other populations. However, due to the relative infancy of long-term population-based cetacean research, this remains unknown. As MPA development (from inception to research to consultation to implementation to establishment), is likely to occur within equivalent timeframes to the Scottish scheme, gradual changes in range by the animals will pose significant problems. It is imperative therefore, that policy structures associated with this, and similar schemes, include provision for such mobility.

In recent decades there has been substantial investment, formulation of methodologies and progress in describing the distribution of mammals and other top predators at sea. These have facilitated the identification of key hotspots and hence the application of the protected area approach (examples include the Stellwagen Bank National Marine Sanctuary, eastern US and the Ligurian Sea Cetacean Sanctuary, NW Mediterranean). However, our understanding of the oceanographic, biological or anthropogenic factors that drive these distribution patterns still remains basic. It is this desirable next stage of understanding that will potentially solve issues such as the temporal mismatch between distribution and management outlined in this study. Using the factors that drive distribution as a guide to the placement of boundaries will provide a biological rationale as well as a capability to proactively shift, extend or retract boundaries. Thus research into the mediating factors, as well as simply distribution itself, ought to be a focus of research associated with protected areas-based management. Ultimately, it is this understanding that will allow managers to correctly place these important boundaries around their moving targets.

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REFERENCES

Agardy, M. T. (1994). Advances in marine conservation: the role of marine protected areas. *Trends Ecol. Evol.* **9**: 267–270.

Ceredigion County Council, the Countryside Council for Wales, Environment Agency Wales, North Western & North Wales Sea Fisheries Committee, Pembrokeshire Coast National Park Authority, Pembrokeshire County Council, South Wales Sea Fisheries Committee, Trinity House & Dŵr Cymru Welsh Water (2001). *Cardigan Bay Special Area of Conservation management plan*. http://www.ceredigion.gov.uk/cbsac/ 213p.

Dunn, D., Barco, S., McLellan, W. & Pabst, A. (1998). Fatal blunt force trauma in ten Atlantic bottlenose dolphins (*Tursiops truncatus*) – Evidence of violent dolphin behavior and infanticide. *Vet. Pathol.* **35**: 435.

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

Evans, P. G. H. & Urquiola, E. (Eds) (2001). Protected areas for cetaceans. *Spec. Pub. Eur. Cetacean Soc*. **38**: 1–49.

Hammond, P. S., Berggren, P., Benke, H., Borchers, D. L., Collet, A., Heide-Jørgensen, M. P., Heimlich, S., Hiby, A. R., Leopold, M. F. & Øien, N. (2002). Abundance of harbour porpoises and other cetaceans in the North Sea and adjacent waters. *J. Appl. Ecol.* **39**: 361–376.

Jepson, P. D. & Baker, J. R. (1998). Bottlenosed dolphins (*Tursiops truncatus*) as a possible cause of acute traumatic injuries in porpoises (*Phocoena phocoena*). *Vet. Rec*. 1**43**: 614–615.

Kuiken, T. & Hartmann, M. G. (Eds) (1991). Cetacean pathology: dissection techniques and tissue sampling. *Special Pub. Eur. Cetacean Soc*. no. **17**.

Lewis, E. J. & Evans, P. G. H. (1993) Comparative ecology of bottle-nose dolphins in Cardigan Bay and the Moray Firth. In *European research on Cetaceans*, volume 7: 57–62. Cambridge: European Cetacean Society.

Moray Firth Partnership (2001). *The Moray Firth cSAC management scheme for bottlenose dolphins, consultation draft*. Dingwall: The Moray Firth Partnership.

Mudge, G. P., Crooke, C. H. & Barrett, C. F. (1984). *The offshore distribution and abundance of seabirds in the Moray Firth*. Report to Britoil. RSPB, Munlochy.

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

Roberts, C. M. (1997). Connectivity and management of Caribbean coral reefs. *Science* **278**: 1454–1457.

Roberts, C. M. (2000). Selecting marine reserve locations: optimality versus opportunism. *B. Mar. Sci*. **66**: 581–592.

Ross, H. M. & Wilson, B. (1996). Violent interactions between bottlenose dolphins and harbour porpoises. *P. Roy. Soc. Lond., ser. B.* **263**: 283–286.

Sanders-Reed, C. A., Hammond P. S., Grellier, K. & Thompson, P. M. (1999). *Scottish National Heritage Research, Survey and Monitoring Report* No. 156. Edinburgh: Scottish National Heritage.

Scottish Natural Heritage (1995). *Natura 2000: a guide to the 1992 EC Habitats directive in Scotland's marine environment*. Edinburgh: Scottish Natural Heritage.

Soulé, M. E. (1990). *Viable populations for conservation*. Cambridge: Cambridge University Press.

Weir, C. R. & Stockin, K. A. (2001). *The occurrence and distribution of bottlenose dolphins and other cetacean species in the coastal waters of Aberdeenshire, Scotland.* Oxford: Sea Watch Foundation.

Wilson, B. (1995). *The ecology of bottlenose dolphins in the Moray Firth, Scotland: a population at the northern extreme of the species' range*. PhD thesis: University of Aberdeen, Scotland.

Wilson, B., Thompson, P. M. & Hammond, P. S. (1997). Habitat use by bottlenose dolphins: Seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *J. Appl. Ecol.* **34**: 1365–1374.

Wilson, B., Hammond, P. S. & Thompson, P. M. (1999). Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecol. Appl*. **9**: 288–300.