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Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland

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Summary

1. This study investigated the distribution of a population of bottlenose dolphins *Tursiops truncatus* resident in the Moray Firth off north-eastern Scotland. Results add to existing information from studies in tropical areas to provide a better understanding of area use in this species.
2. Boat-based surveys and photo-identification techniques were used to study the distribution and movements of individually recognizable dolphins over a 3-year period.
3. Dolphins were seen in all months of the year, but there were consistent seasonal fluctuations in the number of individuals present. Numbers were low in winter and spring and peaked in summer and autumn.
4. Dolphins were seen throughout the survey area but were concentrated in three regions. Each had similar topographic features being centred on deep, narrow channels subject to strong tidal flows.
5. Area use by dolphins changed with season. The outer part of the inner Moray Firth study area was used for most of the year and areas closer to the head of the firth were used seasonally.
6. The summer increase in numbers of dolphins in the inner Moray Firth was not simply due to incomers diluting an already resident population. Instead, there was a stratified movement of all individuals. This persistent geographical stratification suggests that competition between individuals or social groupings may shape spatial distribution in this population.
7. Individuals exhibited rapid movements across the population's range. For instance, one individual was sighted at locations 190 km apart within a 5-day period.
8. In terms of conservation, the high use of areas at the mouths of the inner firths warrants special attention. Furthermore, the stratification patterns amongst dolphins suggest that individuals do not move freely within the inner Moray Firth and therefore may be unable to move away from localized disturbance or pollution.

Key-words: cetaceans, conservation, North Sea, photo-identification, temperate.

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Introduction

There has been widespread concern over the status of small cetaceans in European waters, especially species such as the bottlenose dolphin *Tursiops truncatus*, Montagu 1821, which inhabits coastal areas that are most likely to be affected by human activities (Kayes 1985; Thompson 1992). Bottlenose dolphins occur regularly in a number of areas throughout Europe (Evans 1980; Hussenot 1980; dos Santos & Lacerda 1987) but their distribution is believed to have contracted during the last century, particularly in the North Sea (Evans 1980; Verwey & Wolff 1982). Empirical data on trends in abundance of these and other small cetacean populations are lacking, but it is clear that bottlenose dolphins are now recorded regularly in only one North Sea area: the Moray Firth (57°40′N, 3°30′W), off north-east Scotland (Hammond & Thompson 1991). This species is listed in Annex II of the 1992 EC 'Habitats Directive' (Council directive 92/43/EEC), and the Moray Firth has been put forward as a possible Special Area of Conservation (pSAC) to be included in the suite of Natura 2000 sites (SNH 1995). The aim of these actions is to improve the conservation status of this species in European waters.

The success of designated areas depends critically upon the quality of information available, not only for defining boundaries to such areas but also to understanding how these areas are used by the animals and what factors affect their distribution and abundance. Such data can also provide a key to understanding other aspects of the population's ecology such as social structure (Emlen & Oring 1977), foraging strategies (Holbrook & Schmitt 1992) or disease processes (Heide-Jørgensen *et al.* 1992; Hess 1994).

Bottlenose dolphins have an extensive distribution, occur in almost all temperate and tropical seas, and are found in a wide range of habitats (Leatherwood & Reeves 1983a). Our understanding of habitat preferences and distribution patterns is, however, limited as most studies have been conducted in tropical coastal habitats (Leatherwood 1979; Wells, Scott & Irvine 1987; Corkeron 1989; Mullin *et al.* 1990; Acevedo 1991) or on an oceanic scale (Kenney 1990; Scott & Chivers 1990). What these studies have shown is that bottlenose dolphins can exhibit extremely variable distribution patterns. Some populations are entirely resident within confined areas (Wells, Scott & Irvine 1987), others are migratory (Kenney 1990) whilst others appear to be nomadic (Tanaka 1987). This variability suggests that it would be unwise to predict the distribution patterns of bottlenose dolphins using temperate coastal habitats. If we are to develop effective conservation strategies for bottlenose dolphins in the North Sea, these therefore need to be based on studies carried out in this area.

Broadening the range of environmental conditions within which this species has been studied will also increase the potential to develop a more general understanding of the factors influencing distribution patterns in coastal small cetaceans. It has been suggested, for example, that bottlenose dolphins inhabiting seasonal, higher latitude, areas are more likely to exhibit migratory behaviour (Shane, Wells & Würsig 1986). The population of bottlenose dolphins in the Moray Firth is small and at the northern extreme of the species range (Wilson 1995) and thus offers an extreme example for studies of this nature.

In this paper, we present results from a 3-year study of the distribution of individually recognizable bottlenose dolphins in the Moray Firth. Our primary aim was to apply these data to identify the key areas used by dolphins within the Firth and to assess whether these changed seasonally or between years. In addition, we used information on the distribution of individual dolphins to explore the factors which influence the population's overall distribution. Finally, we discuss the implications of these data for conservation strategies aimed at this population.

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Methods

STUDY AREA

The Moray Firth is a large embayment in the north-east of Scotland, covering approximately 5230 km^2 (Fig. 1). Its south-western part is known as the inner Moray Firth (see Fig. 1, inset) and has four smaller firths branching off it. These include the Inverness and Cromarty Firths. Of the 12 major rivers discharging freshwater into the Moray Firth, 10 discharge into the inner Moray Firth. These produce estuarine conditions which gradually decrease to the north and east (Adams & Martin 1986). Mean surface water temperatures in the inner Moray Firth vary from more than 12·5°C in mid summer (August) to less than 5·5°C in winter (February–March; Adams & Martin 1986). Occasionally, surface waters in the extreme inner Moray Firth freeze.

BOAT SURVEYS

Between 1990 and 1993, boat surveys were carried out along a pre-defined 42 km one-way course in the inner Moray Firth (Fig. 1). This route was selected as it covered a large part of the inner Moray Firth and included areas that dolphins were thought to use regularly (Hammond & Thompson 1991). The route length was limited so that it could be completed with sufficient daylight in a single day. Surveys which completed the whole route were termed 'full' and those that were aborted due to deterioration of the weather were categorised as 'part'. Ten full and three part surveys were conducted in the summer of 1990 and a minimum of two full surveys were carried out twice a month for two periods of 12 months (March 1991–February 1992, 25 full and 16 part; March 1992–February 1993, 25 full and 14 part). These 12-month blocks of survey effort are referred to as 1991/92 and 1992/93, respectively. An additional 13 surveys were conducted up to 250 km outside the inner Moray Firth and did not follow a pre-defined route.

All surveys in the inner Moray Firth were conducted in a 5·5 m fibreglass boat fitted with a 50 hp outboard engine. Three to five crew acted as observers, looking ahead and to 90 degrees either side of the trackline to a distance of approximately 1·5 km. Surveys were only carried out in clear and calm conditions (Beaufort sea state three or less) and, when searching, at boat speeds of typically 25–30 km h^{-1}. Boat speeds were occasionally reduced to 12–15 km h^{-1} in poor weather (i.e. on part surveys) or on those outside the inner Moray Firth. When dolphins were sighted, the time, location and number of individuals were recorded. Locations were established using a Decca

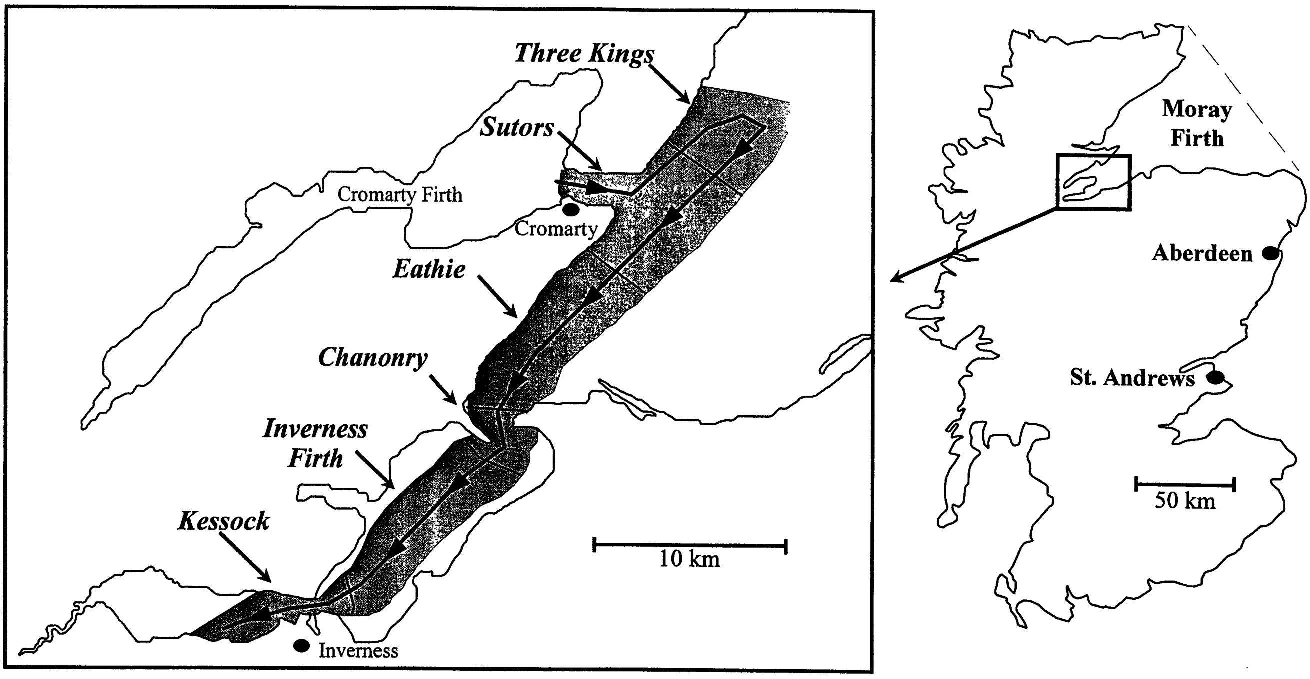

Fig. 1. Map of the Scottish mainland showing the location of the inner Moray Firth, the full survey route and the area covered by surveys (shaded). For analyses, the survey area was divided into the six zones indicated.

navigation system, compass fixes or, when close to shore, visual estimation from local land marks.

IDENTIFICATION OF INDIVIDUAL DOLPHINS

During an encounter with dolphins, photographs of their backs and dorsal fins were taken as they surfaced to breathe. Pictures were taken with an SLR, autofocus camera, 70–300 mm zoom lens and ISO 200 or 400 colour transparency film (Wilson 1995). Later, these photo-identification pictures were used to identify individual dolphins from the unique combination of scars and patterns of pigmentation on each animal (Würsig & Würsig 1977; Wilson 1995). The sex of some animals was determined by observation of the genital area (male or female), consistent association with a calf (female) or by heavy scarring and absence of a calf (probable male, Smolker *et al.* 1992; Tolley *et al.* 1995; Wilson 1995).

ANALYSES OF SPATIAL DATA

Analyses of the spatial distribution were based on the location of each group of dolphins when first seen. This was to avoid any potential bias created by the subsequent presence of the boat.

Areas of high density of sightings were identified using the harmonic-mean model (Dixon & Chapman 1980) and calculated using MCPAAL computer software (National Zoological Park, Smithsonian Institute, Washington, USA). This technique calculates isopleths around one or more centres of animal activity, determined using reciprocal mean distance deviation statistics. It has the advantage over other techniques of being able to define ranges of any shape and is thus suited to examining animal activity in heterogeneous environments (Dixon & Chapman 1980).

Changes in the use of the inner Moray Firth were examined by splitting the survey area into six zones (Fig. 1). Because the survey area was linear in nature, locations were also expressed as distances from Inverness, the town situated at the south-western end of the survey area.

Results

SEA STATE AND OBSERVER EFFORT

The number of dolphin schools seen on each survey was not affected by the accepted variations in sea conditions, nor the observer effort that occurred during the study. For example, no relationship was found between the mean sea state of each survey (which varied from 0 to 3) and the number of schools observed (Spearman's rank correlation, $r_s = 0{\cdot}15$, 55 d.f., $P = 0{\cdot}13$). Similarly, there were no significant effects on the number of sightings by having four or five observers rather than the minimum three (Separate variance t-test, $P = 0{\cdot}22$, $n = 39{\cdot}9$).

OVERALL DISTRIBUTION

Sightings of dolphins on full surveys occurred throughout the inner Moray Firth survey area but were not evenly distributed (Fig. 2). Harmonic-mean analyses highlighted three areas as being favoured. The first, in the Kessock zone and the second, in the

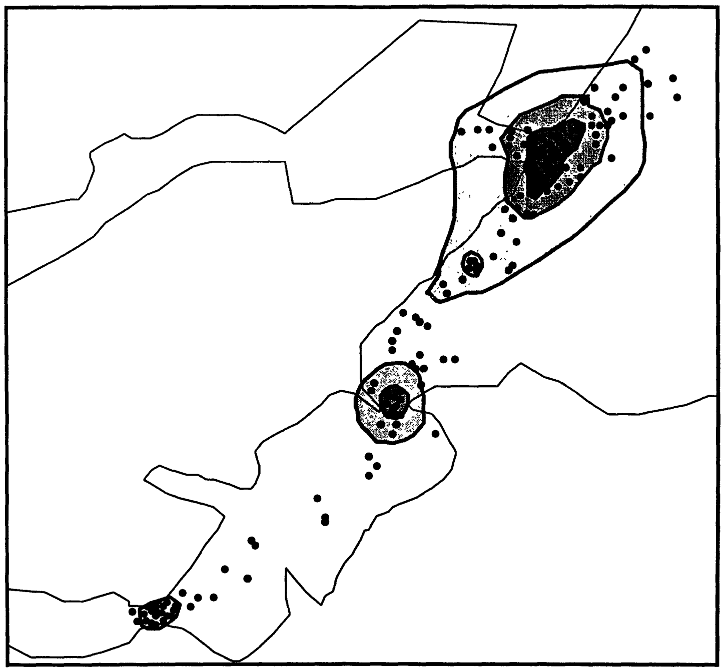

Fig. 2. The distribution of sightings in the inner Moray Firth survey area. Data were collected during full surveys in 1991/92 and 1992/93. Each sighting of a school is indicated with a point ($n = 151$). Harmonic-mean isopleths were drawn around 75% (light grey), 50% (medium grey) and 25% (dark grey) of the locations.

Chanonry zone were relatively discrete and located at constrictions in the inner Moray Firth. The third was more complex, covering a wider area that encompassed the Sutors and northern part of the Eathie zone. Within this area, however, the main concentration of sightings again occurred at a constriction of the water's course. Of these three areas, the third (Sutors/Eathie zone) was used by the most individuals. For example, an area within the core of the Sutors/Eathie concentration equivalent to the size of the Kessock concentration (1·8 km^2) yielded sightings of 62% of the whole dolphin population during full surveys in 1991/92 and 1992/93. Only 36% of the population was seen in an equivalent area in the Chanonry zone and only 24% seen in the Kessock concentration.

SEASONAL CHANGES IN DISTRIBUTION

On full surveys, dolphins were seen in the inner Moray Firth in every month of the study, but there were wide seasonal changes in the number of individuals observed. The greatest numbers occurred from May to September and the lowest from October to April (Fig. 3). These seasonal trends were similar in both years such that there was a strong correlation between the relative number of individuals seen in each month of 1991/92 and in the same month of 1992/93 (Spearman's rank correlation, $r_s = 0{\cdot}65$, 10 d.f., $P < 0{\cdot}05$).

The use of different parts of the inner Moray Firth also varied seasonally (Fig. 4). Sightings of individuals on full surveys occurred in the Sutors zone in all but 2 months of the year, with 81% occurring over a 5-month period, May–September. The use of other zones was more seasonal. No sightings occurred in the Chanonry zone for 5 months of the year and peak use (80% of sightings) was concentrated into a 4-month period between June and September. Kessock was used more seasonally still, with 81% of sightings concentrated into June, July and August.

DISTRIBUTION AND MOVEMENTS OF INDIVIDUALS

The frequency with which identifiable animals were seen in the inner Moray Firth varied greatly. Some were seen often; one adult female (No. 85) was encountered on 38% of all surveys. Others were observed more rarely; many were seen only once (Fig. 5).

The frequency of occurrence of each individual in the inner Moray Firth was similar from one year to the next such that pairing each animal's frequency value from surveys (full and part) in the inner Moray Firth in 1991/92 and 1992/93 produced a strong positive correlation (Spearman's rank correlation, $r_s = 0{\cdot}61$, 213 d.f., $P < 0{\cdot}001$). This shows that some individuals used the inner Moray Firth on a regular basis, whilst others were present less often.

Individual dolphins were divided subsequently into four arbitrary categories based on their frequency of sighting. Individuals placed in the '*common*' category were those seen in the inner Moray Firth the most often, i.e. on 20 or more surveys in 1991/92 and 1992/93. Those in the '*frequent*' category were seen on 12–19 surveys; '*occasional*' on 5–11 surveys; and '*rare*' on fewer than 5 surveys (Fig. 5). Although it was not

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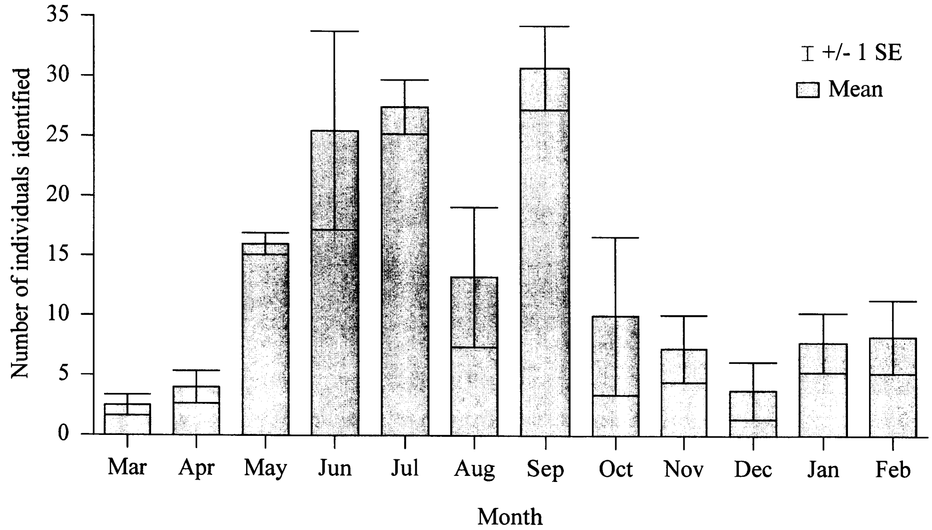

Fig. 3. The number of individual dolphins observed per month in the inner Moray Firth. Values were drawn from each full survey in 1991/92 and 1992/93 (n = 48).

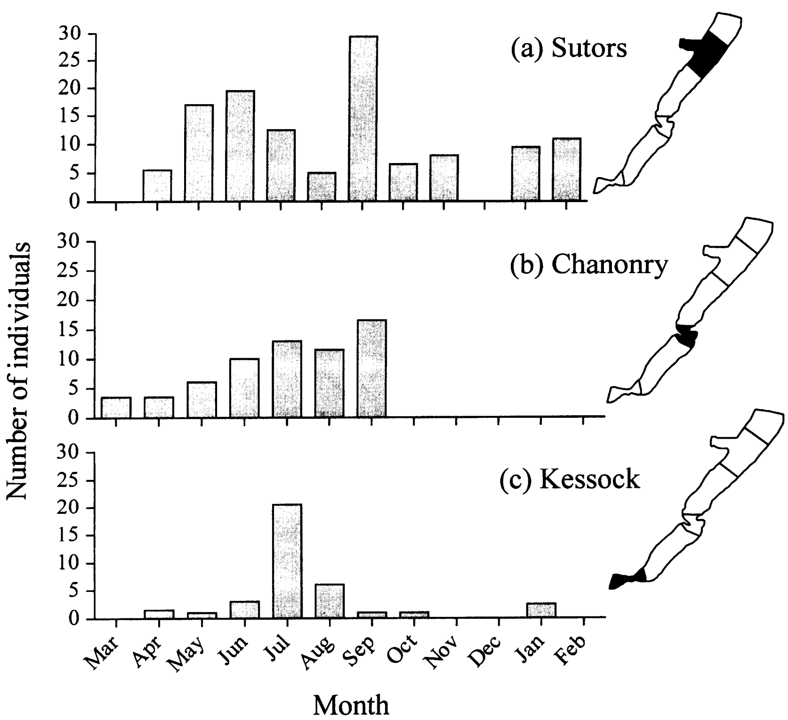

Fig. 4. Seasonal variations in the number of individual dolphins observed in three zones of the inner Moray Firth. Data were drawn from full surveys in 1991/92 and 1992/93 (n = 48).

possible to deduce the sex of all animals, each category contained adult females and probable males, as well as juveniles and calves.

When the monthly locations of animals in the common, frequent and occasional categories were plotted against their distance from Inverness (Fig. 6) two trends became apparent. First, occasional animals were consistently seen furthest from Inverness in all seasons. Common animals were always closest to Inverness with frequent animals falling between the two groups. Secondly, there was a seasonal shift in these distribution patterns, with all individuals being found nearer to Inverness in mid summer (July and August). These seasonal movement patterns were repeated in both 1991/92 and 1992/93 such that there was a strong positive correlation between each animal's mean monthly distance from Inverness in 1991/92 and in 1992/93 (Spearman's rank correlation, $r_s = 0{\cdot}41$, 160 d.f., $P < 0{\cdot}0001$).

In addition to these seasonal movement patterns in the inner Moray Firth, some individual dolphins also made wide-scale movements of at least 220 km from the inner Moray Firth. Adult No. 60, for example, was photographed off Aberdeen on 2 June 1992 and then again in the inner Moray Firth on 7 June 1992. It had travelled over 190 km in less than 5 days (mini-

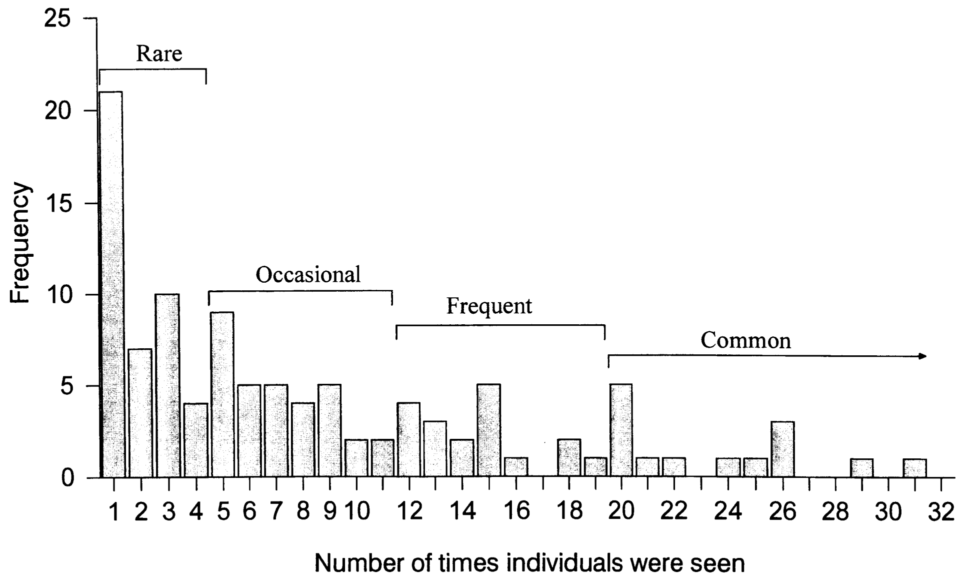

Fig. 5. Frequency distribution of the number of times that each individual dolphin was seen in the inner Moray Firth during 1991/92 and 1992/93.

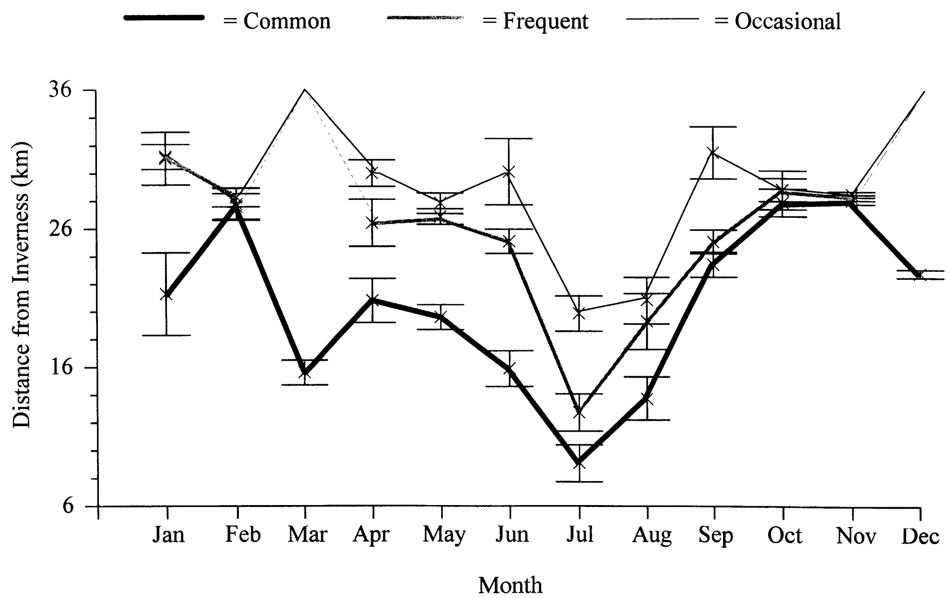

Fig. 6. Seasonal changes in the distribution of individual dolphins in the inner Moray Firth. Monthly mean locations (crosses) with single standard errors are shown for three groups of animals. Data were collected during all surveys between 1990 and 1993. Locations are expressed as distance from Inverness. In months when animals in a category were not seen they were assumed to be north or east of the survey area (i.e. more than 36 km from Inverness, dotted lines).

mum average speed, 1·58 km h^{-1}). Another adult (No. 19), was photographed at two separate locations 65 km apart on two consecutive days in 1994. If it had swum directly from one location to the other it would have travelled at an average speed of 2·9 km h^{-1}.

Discussion

OVERALL DISTRIBUTION

Sightings of dolphins on full surveys in the inner Moray Firth were not distributed evenly, but were clumped in three areas (Fig. 2). We have identified three possible sources of bias which could have affected our results. First, although normal searching mode ceased when a school of dolphins was encountered, other sightings were sometimes made and recorded while individuals were being photographed. The effect of this would be to increase slightly the probability of seeing animals in areas where they had already been seen and, therefore, increase the clumped nature of our results. But it could not artificially create concentrations of sightings. Secondly, systematic variations along the survey track in the width of the strip searched could have led to an uneven distribution of searching effort. In fact, the concentrations of sightings that were detected were along those parts of the survey track which were most restricted in width, and thus the opposite effect was found to that expected if any bias had occurred. Finally, because of the inclusion of the Three Kings area, the survey route effectively passed through the Sutors area twice. In recognition of this, the northward and southward legs through this area were kept as far apart as possible and so the narrows and main body of the area were only searched once. The concentration that was found in this area encompassed parts where there was no possibility of double searching. Overall therefore, we are confident that the concentrations found during full surveys, were a real reflection of a clumped distribution of dolphins in the inner Moray Firth study area and were not a product of the survey technique.

Because the sightings occurred at narrow points in the Firth, it is possible that they acted as bottlenecks and simply concentrated animals which were moving through the inner Moray Firth. However, observations in the Kessock zone (Fig. 2) suggest that this was not the case, as animals were observed only in waters on one side of the narrows. Additional characteristics must therefore be responsible for these concentrations of sightings. Unlike other parts of the inner Moray Firth, all three favoured areas have deep water, rapid changes in bottom relief and strong tidal currents. Preferential use of narrow channels with strong currents have also been observed in other odontocetes, including bottlenose dolphins (Leatherwood & Reeves 1983b; Lockyer & Morris 1986; Leatherwood, Kastelein & Hammond 1988; Felleman, Heimlich-Boran & Osborne 1991; Liret *et al.* 1994). Features such as steep slopes, uneven bottom substrates and tidal eddies are known to attract fish (Glass *et al.* 1992), and the bottleneck characteristics of these areas may concentrate those prey that do use them as a thoroughfare. Alternatively, the characteristics of these areas may facilitate prey capture by providing obstructions on which to herd or ambush fish (Rae 1960) or by producing favourable currents to reduce the energetic costs of foraging (Williams, Shippee & Rothe 1996).

SEASONAL MOVEMENT PATTERNS

In their review of the behaviour and ecology of bottlenose dolphins, Shane, Wells & Würsig (1986) suggested that inshore populations off the NE coasts of North America exhibited a trend for increased migratory behaviour at higher latitudes. The Moray Firth contains the World's highest latitude population of bottlenose dolphins yet studied, so one might predict them to be migratory and for their occurrence in the inner Moray Firth to be highly seasonal. However this was not the case. Despite seasonal fluctuations in the numbers of individuals present (Fig. 3) dolphins were observed in the survey area at all times of year.

Although dolphins were never absent from the inner Moray Firth, the number of individuals increased markedly in the summer (Fig. 3). Similar seasonal influxes have been reported from several studies in tropical regions. (Shane 1980; Weigle 1990; Ballance 1990). Such changes have been attributed to spatial variations in local conditions, resulting in certain areas being more suitable for: predator avoidance (Ross 1977; Wells, Irvine & Scott 1980); the rearing of offspring (Scott, Wells & Irvine 1990); mating (Wells, Irvine & Scott 1980); or foraging (Irvine *et al.* 1981). There is no evidence of predation (from either sharks or killer whales) in waters anywhere around northern Scotland (Wilson 1995). On the other hand, shelter from prevailing south-westerly winds (H.M.S.O. 1991) and relatively high inshore water temperatures during the summer calving season (Adams & Martin 1986; Wilson 1995) may make the inner Moray Firth a preferred area for females with young calves. An assessment of the relationship between foraging activity and distribution is constrained by limited information on the diet of bottlenose dolphins in this area. However, dolphins were regularly seen taking large salmonids (salmon *Salmo salar* and sea trout *Salmo trutta*) during the study, which were also identified as prey species from the stomach contents of stranded dolphins (Santos *et al.* 1994). Little is known about the behaviour and migration patterns of salmonids in Scottish coastal waters (Clarke & Gee 1992). But, as 99 tonnes of adult salmon (17% of the entire Scottish catch) are caught annually in the rivers leading off the inner Moray Firth (Anon. 1996), large numbers of these anadromous fish must migrate through this area in spring and summer to spawn. This seasonal increase in food availability could influence the movement of dolphins into inshore areas. Consequently, both calving and feeding preferences provide plausible explanations for the observed summer increase in dolphin abundance in the inner Moray Firth.

Using information from identifiable individual dolphins, it is clear that the summer influx did not result in random mixing of individuals, but that there was a horizontal stratification in the use of the survey area throughout the year. For example, the animals seen most frequently, the common category, used the Eathie zone in winter and spring and used areas progressively closer to Inverness in summer (Fig. 6). Meanwhile, animals categorized as occasional, moved from outside the survey area to use the Eathie zone in summer. Spatial stratification in other vertebrate populations is common (Baker 1978), and may result from territoriality (Begon, Harper & Townsend 1990) or dietary specialization (Holbrook & Schmitt 1992). What was unusual in this case was that stratification of individuals persisted while the population exhibited seasonal movements in and out of the inner Moray Firth. In migratory populations, such spatial stratification may result from differences in departure times (Dawbin 1966). However, the dolphins are capable of moving through the whole area in only a few hours, whereas the seasonal inshore movement took several months. Similarly, differences in prey selection between dolphins would seem unlikely to produce such a regular pattern of area use.

Instead, we suggest that the observed pattern was more likely to have resulted from social factors. Bottlenose dolphins exhibit a hierarchy of relationships between different individuals (Wells, Scott & Irvine 1987; Smolker *et al.* 1992; Wilson 1995), and close associates often appear to co-operate when foraging, competing against other dolphins or avoiding predators (Connor, Smolker & Richards 1992). Area defence by individuals or social groupings could thus explain the patterns of stratification observed in this study. Similarly, it could go some way to explain the intra-specific and unusual inter-specific aggressive interactions observed in the inner Moray Firth (B. Wilson, unpublished data; Ross & Wilson 1996). The observed pattern of stratification also implies that not all individuals within the population have equal access to all parts of the inner Moray Firth.

The observed movements of individuals between the outer Moray Firth (and beyond) and the inner Moray Firth were comparatively rapid with 190 and 65 km movements taking 5 and 2 days, respectively. These were similar to the apparent migratory rates recorded for dolphins tracked by satellite off Japan (compare minima of 1·6 and 2·9 km h^{-1} in this study with 2·0 and 2·7 km h^{-1} for prolonged active swimming, Tanaka 1987).

IMPLICATIONS FOR CONSERVATION MANAGEMENT

The results of this study have shown that the inner Moray Firth is used heavily by the only known population of bottlenose dolphins in the North Sea. For example, in a single year, 85% of the estimated 130 individuals in the population (Wilson 1995) were identified in this area, whilst up to 50% were seen on any one full survey in summer. In terms of conservation effort, this area clearly deserves protection, especially during the summer months. Furthermore, particular areas were consistently favoured within the inner Moray Firth itself. Although the precise reason(s) for the intensified use is unclear, anthropogenic changes in these areas (through factors such as disturbance, land reclamation or pollution) are likely to have greater impacts on the population than they might in other parts of the inner Moray Firth.

However, it is clear that the survey area did not encompass the whole range of this population. For example, animals were sometimes observed in other parts of the inner Moray Firth (e.g. in the Cromarty Firth) and were seen sporadically in the outer Moray Firth, particularly along its southern shores and along the coast as far south as St. Andrews Bay (Fig. 1). The observed rapid movements of individuals between these areas and the inner Moray Firth survey area confirm that these animals must be considered as belonging to the same population unit. Thus, although the importance of areas outside the inner Moray Firth is unknown and should not be ignored, applying effective conservation action to the inner Moray Firth should serve to improve the status of the whole population.

The observed patterns of stratification in the inner Moray Firth also have implications for conservation management. First, impacts, whether positive or negative, occurring in limited parts of the inner Moray Firth will affect different fractions of the population. The fraction would become smaller with increasing proximity to the Inverness area, because fewer animals use these areas. Thus, the severity of an impact on the population as a whole would vary depending, not only upon its intensity but also upon its location. Secondly, the stratification would mean that anthropogenic impacts on the population may not be expressed as changes in the range of the individuals. For example, it has been argued that, if dolphins around the Kessock zone were disturbed by tourist boats, the animals would simply move to a different area. However, results from this study indicate that if animals were to move out of the Kessock zone in summer they would either have to compete with other animals or use a vacant and presumably less suitable area. The view that animals could simply move if disturbed, reflects a common misperception of the marine environment as a uniform space. This may be because, unlike terrestrial environments, the distribution of resources, barriers and competitors are hidden from view. Results from this study have clearly indicated that, for bottlenose dolphins, the inner Moray Firth is far from a uniform area. Effective conservation of this and other similar cetacean populations must take this into account.

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