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Harbour seal movements and haul-out patterns: implications for monitoring and management

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ABSTRACT

1. Compliance with conservation legislation requires knowledge on the behaviour, abundance and distribution of protected species. Seal life history is characterized by a combination of marine foraging and a requirement to haul out on a solid substrate for reproduction and moulting. Thus understanding the use of haul out sites, where seals are counted, as well as their at-sea movements is crucial for designing effective monitoring and management plans.
2. This study used satellite transmitters deployed on 24 harbour seals in western Scotland to examine movements and haul-out patterns.
3. The proportion of time harbour seals spent hauled out (daily means of between 11 and 27%) varied spatially, temporally and according to sex. The mean haul-out duration was 5 h, with a maximum of over 24 h.
4. Patterns of movement were observed at two geographical scales; while some seals travelled over 100 km, 50% of trips were within 25 km of a haul-out site. These patterns are important for the identification of a marine component to designated protected areas for the species.
5. On average seals returned to the haul-out sites they last used during 40% of trips, indicating a degree of site fidelity, though there was wide variation between different haul-out sites (range 0% to > 75%).
6. Low fidelity haul-out sites could form a network of land-based protected areas, while high fidelity sites might form appropriate management units.

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KEY WORDS: *Phoca vitulina*; harbour seal; Scotland; SRDLs; site-fidelity; conservation; protected areas; satellite telemetry; critical habitat

INTRODUCTION

Knowledge of both absolute abundance and trends in population size are important for the effective management of a species. There are also often legal requirements on species protection, and it is important to determine how to comply with legislative demands at a species-specific and biologically appropriate scale. Like most other pinnipeds, harbour seals (*Phoca vitulina*) spend a significant amount of time hauled out on beaches, sandbanks and rocks (Stevick *et al*., 2002), especially during the breeding (June) and moulting (August) seasons. Consequently, most information on the abundance and distribution of harbour seals is based on observations at terrestrial haul-out sites (Bonner, 1972; Boveng *et al*., 2003) and these sites are often the focus of legislative protection (e.g. the European Commission Habitats Directive, Council Directive 92/43/EEC). However, seals also spend a large proportion of their time at sea thus complicating monitoring methods and management plans. Hence the relationship between where harbour seals are counted on land and

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where they spend most of their time at-sea is important for (a) defining the spatial extent of monitoring studies and (b) designing appropriate protected areas.

Harbour seal surveys are designed to coincide with periods when the highest number of seals are hauled out, yet little is known about the extent to which hauled out seals are representative of the population within any specified region (Härkönen *et al*., 1999). To assess trends in abundance, which is a requirement for monitoring the conservation status of the population, it is necessary to either estimate the proportion of seals that are in the water at the time of survey, or to assume that this proportion does not vary temporally or spatially (Thompson and Harwood, 1990). Harbour seal haul-out behaviour varies according to life history; i.e. the timing of reproduction and moulting according to the sex- and age-class of the population (Thompson and Rothery, 1987; Härkönen *et al*., 1999; Daniel *et al*., 2003), and according to environmental states, which include tidal cycles (Schneider and Payne, 1983; Watts, 1996; Simpkins *et al*., 2003), time of day (Thompson, 1989; Frost *et al*., 1999; Boveng *et al*., 2003), season (Thompson, 1989) and weather conditions (Godsell, 1988; Kovacs *et al*., 1990; Grellier *et al*., 1996). These factors are therefore also important for assessing the significance of observed changes in counts.

Increasingly studies have used telemetry to estimate absolute abundance (Yochem *et al*., 1987; Thompson and Harwood, 1990; Huber *et al*., 2001) and to investigate the movements, physiology and behaviour of seals at sea (Stewart *et al*., 1989; Thompson *et al*., 1991; McConnell *et al*., 1992). Satellite telemetry provides information on animals over relatively long periods, which is useful for the management of harbour seal populations. The use of haul-out sites, both within and outwith protected areas, and the duration and extent of foraging trips were examined, using satellite telemetry, to determine the appropriateness of currently designated terrestrial protected areas for harbour seals. The effects of temporal, spatial and endogenous factors on the proportion of time harbour seals were hauled out were also investigated. This study considers how to interpret policy requirements for protecting harbour seals using approaches involving site-based management.

MATERIALS AND METHODS

Satellite relay data loggers (SRDLs, Sea Mammal Research Unit: http://smru-inst.st-andrews.ac.uk/) were deployed on 24 harbour seals in north-west and south-west Scotland in September 2003, April 2004, September 2004 and March 2005. To maximize seasonal coverage, approximately half the deployments were after the annual moult (September) and the rest in the spring (March or April). Seals were captured either on land or in the water near haul-out sites. Adult seals were selected for tagging according to their sex and were weighed and measured before being anaesthetized with Zoletil (Virbac, France). The seal fur at the dorsal base of the skull was de-greased and dried prior to attaching the SRDL to the fur, with two-part rapid setting epoxy resin (Fedak *et al*., 1983), in a way that allowed the antenna to emerge from the water when the seal surfaced.

McConnell *et al*. (1999) provide details of the SRDL telemetry system, which consisted of a data logger interfaced to an ARGOS transmitter unit. Data from a depth sensor and a wet-dry sensor were used to classify the 'activity' of the seal into one of three categories: 'diving', when deeper than 2 m for at least 16 s, 'hauled out', or 'at surface'. A 'haul-out event' was defined as beginning when the wet/dry sensor remained continuously dry for a 10 min period and ending when the sensor was wet for a 40 s period. Daily and monthly mean proportions of time hauled out were derived from 6 h summary activity data transmitted by the SRDLs (Fedak *et al*., 2002). Seasonal (monthly) variation in the proportion of time hauled out and the relationship between this proportion and body mass or sex were examined.

The ARGOS system provides estimates of the animal's position and reports these with a Location Quality (LQ) to indicate their accuracy. Locations with a large degree of error were excluded using an iterative forward/backward averaging filter (speed threshold of $2\,m\,s^{-1}$) that rejected locations that required unrealistic rates of travel (McConnell *et al*., 1992). The data were smoothed by weighting each point according to its LQ, fitting separate cubic splines to longitude and latitude, and using generalized cross validation to optimize the complexity of the resulting path (M. Lonergan, unpublished). The resulting locations were not equally distributed through time. To avoid bias in the temporal and spatial distribution of seal activity, locations were estimated at hourly intervals by interpolation. Using the date and time records, haul-out events were assigned a location from the filtered and smoothed tracks. Haul-out events separated by 15 min or less were concatenated.

'Haul-out sites' and 'haul-out clusters'

Every location on the west coast of Scotland where a harbour seal was observed hauled out during breeding and moult aerial surveys, carried out between 1988 and 2005 (SCOS, 2006), was considered a 'haul-out site'. Harbour seals appear to use the same haul-out sites consistently from year to year (Anderson, 1981; Thompson, 1989) and, although there may be seasonal differences in haul-out site usage, it was assumed that these sites were representative of the actual haul-out sites available during the study period.

The precision of the SRDL locations was less than the distance between individual haul-out sites identified during aerial surveys, so nearby haul-out sites observed during aerial surveys were grouped into 'haul-out clusters'. Each haul-out cluster contained all the haul-out sites occurring within a cell of a 5 km grid and was located at the mean of their locations. Haul-out cluster locations were checked visually to ensure that none were far inland as a result of the clustering process.

The locations of haul-out events provided by the telemetry data were not always on land, due to ARGOS location error. Locations were therefore 'snapped' to the nearest haul-out cluster, provided this was within 15 km. A maximum snapping distance of 15 km was chosen, on the basis that snapping beyond this threshold implied too much uncertainty about the actual location of the haul-out event. A Spearman's rank order correlation coefficient was used to investigate the presence of a correlation between the number of haul-out clusters used by individual seals and the tracking duration.

'Travel trips' and 'return trips'

The frequency and duration of all trips made by tagged harbour seals were recorded. The start and end of a trip was determined when the seal was a pre-specified distance from a haul-out cluster and when the seal was not classified as being hauled out. This was to avoid inflating the number of trips by including occasions when animals entered the water following disturbance events. Trips specified by distances of 1 and 10 km from haul-out clusters had almost identical durations, and so for the purpose of this study, trips were defined as movements of greater than 1 h in duration that were more than 1 km from a haul-out cluster. Note that the distinction between travel-trips and return-trips depends on the 5 km grid used in the creation of the haul-out clusters.

Trip extent (measured to the nearest 1 km) was defined as the distance from the centre of a haul-out cluster to the furthest at-sea location. For travel-trips it is therefore the longer of two possible trip extents. Trips were investigated to describe the spatial link between haul-out sites (i.e. where seals were counted) and foraging areas.

RESULTS

In total, 1195 days of data were collected from 10 harbour seals (five females, five males) captured in south-west Scotland in September 2003 and April 2004. In north-west Scotland, 1854 days of data were collected from 14 harbour seals (five females, nine males) tagged in September 2004 and March 2005. The mean tag longevity was 126 days (range = 31 to 243 days); the data coverage was not equal for all months (Figure 1) but every month of the year, except August (when the seals were moulting), was covered. Although it was not possible to ascertain if they were actively breeding, all seals in this study were over 40 kg and thus deemed to be physically mature. Males weighed between 56 and 103 kg (mean = 84, SE = 4); females between 40 and 87 kg (mean = 66, SE = 6).

After filtering, 6868 locations (60% of all locations) were extracted from seals tagged in south-west Scotland and 11 306 (70%) from seals in north-west Scotland (overall mean = 5.96 locations/day). Of these, 4.7% were assigned the highest location quality index (LQ = 3, where 68% of locations will be 226 m from the true location (Vincent *et al*., 2002)).

Seal movements

Trip extent and duration

The mean travel-trip extent was 10.5 km (95% CI = 9.91–11.04), while the maximum was 144 km. The maximum extent of a return trip was 46.2 km (mean = 7.25, 95% CI = 6.73–7.78). Neither travel-trip nor return-trip distances were correlated with individual body mass (Spearman's rank correlation for travel-trips: $r_s = 0.231$, $P = 0.29$ and return-trips $r_s = -0.187$, $P = 0.40$).

About half (48%) the travel-trips in this study lasted between 12 and 24 h. However, some travel-trips lasted several days, with the longest being greater than 9 days (mean = 31.1 h, 95% CI = 29.5–32.5). A similar pattern was seen in the duration of return-trips, with the longest lasting 7.7 days (mean = 28.1 h, 95% CI = 26.05–30.23). The longer trips were associated with longer distance movements (Spearman's rank order correlation for travel-trips: $r_s = 0.397$, $P < 0.001$, return-trips: $r_s = 0.368$, $P < 0.001$).

Spatial, seasonal and sexual variation

Overall mean travel-trip duration was 25 h (95% CI = 23–27 h) in south-west Scotland and 35 h (95% CI = 33–37 h) in north-west Scotland. There was a gradual increase in travel-trip duration in south-west Scotland from September until May and a decrease in north-west Scotland, although these were not significant at the 0.05 level. Mean travel-trips were longer in north-west Scotland until March, after which they were shorter than travel-trips in south-west Scotland (Figure 2). The mean maximum travel-trip extent was 10.9 km (SE = 10.1) in south-west Scotland and 10.2 km (SE = 10.3) in north-west Scotland. There was no apparent seasonal pattern in mean trip extent in either north-west or south-west Scotland (Figure 3, NW: $\chi^2 = 2.60$, $P = 0.995$; SW: $\chi^2 = 1.72$, $P = 0.996$). The duration and extent of trips

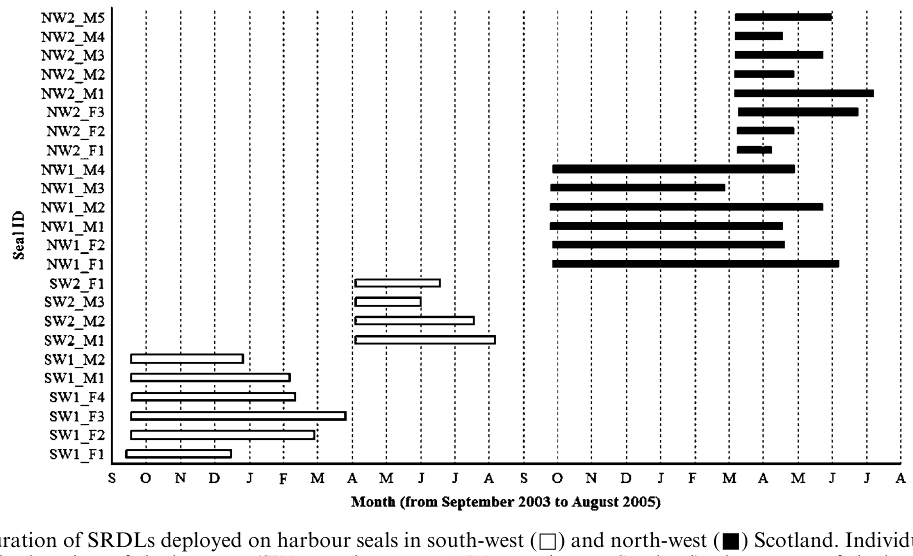

Figure 1. Operating duration of SRDLs deployed on harbour seals in south-west (□) and north-west (■) Scotland. Individual seals are represented by a code indicating the location of deployment (SW = south-west or NW = north-west Scotland), the season of deployment (1 = September or 2 = March/April) and the sex (F = female, M = male).

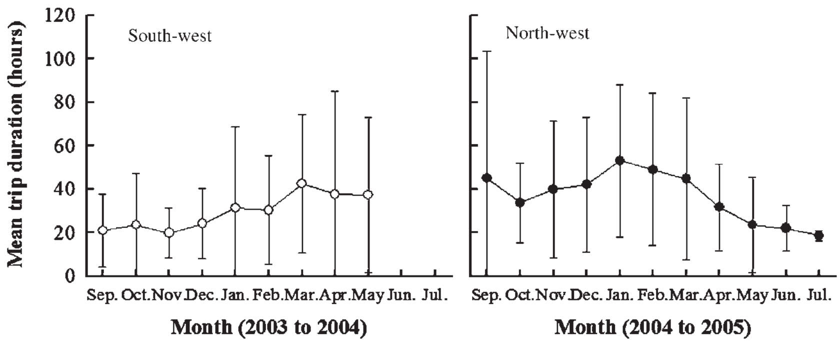

Figure 2. Mean travel-trip duration (with standard errors) in hours for 10 harbour seals tagged in south-west Scotland in 2003/2004 (○) and 14 seals in north-west Scotland in 2004/2005 (●).

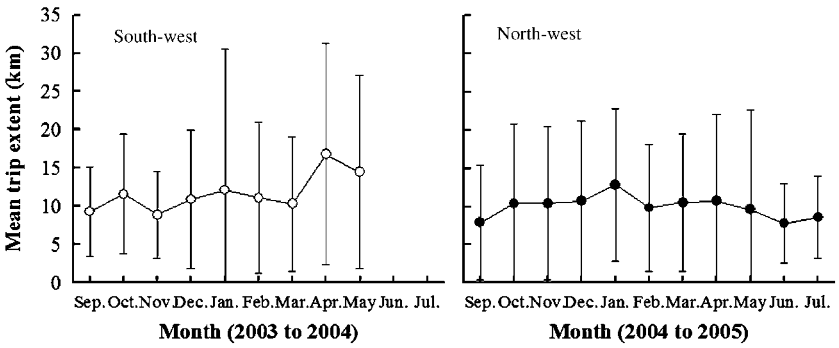

Figure 3. Mean maximum travel-trip extent in kilometres (with standard errors) of 10 harbour seals tagged in south-west Scotland in 2003/2004 (○) and 14 seals in northwest Scotland in 2004/2005 (●).

differed between seals tagged in south-west Scotland and those in north-west Scotland (Mann Whitney U, $z=-7.823$, $P<0.001$; $z=-3.251$, $P=0.001$ respectively), with shorter trip extents in north-west Scotland and increasing trip durations from autumn to spring (compared with decreasing durations in south-west Scotland). There was no statistically significant difference in trip duration between the sexes, but females travelled further from haul-out sites than males (Mann Whitney U: $z=-5.180$, $P<0.001$, pooled data from both areas).

Usage of haul-out clusters

In total, 1254 trips were identified from the movement data, of which 39% were return trips. Although haul-out clusters around the SRDL deployment locations were frequently used, some individuals also used more distant haul-out clusters (Figure 4). Most individuals switched between two main haul-out clusters and occasionally used other haul-out clusters briefly when travelling between these.

Visual inspection of haul-out clusters used by individual seals gave no evidence for seasonal changes in north-west Scotland. However, in south-west Scotland different haul-out clusters were used in the autumn/winter (October to February) compared with in the spring/summer (March to July). These seasonally used clusters were separated by between 40 and 130 km, with spring/summer haul-out sites located north-east of autumn/winter sites.

In total, harbour seals used 50 haul-out clusters in south-west Scotland and 60 in north-west Scotland during the study periods. Individual seals used a mean of 13 haul-out clusters (range = 6 to 29, SE = 6), although the number of haul-out clusters used increased with tracking duration (Spearman's rank order correlation: $r_s=0.435$, $P=0.038$). Fifty-one haul-out clusters (48% of total used) were never used for return trips and so could be considered as transient sites. Other clusters showed a high level of return trips (only five clusters used for $>75\%$ return trips). Two seals left the deployment location soon after tagging, travelling up to 250 km away (Figure 5).

Haul-out patterns

In north-west Scotland females spent less time hauled out than males between October and May, but more time in June and September (Figure 6). The pattern was less clear in south-west Scotland. In both areas a higher proportion of time was spent hauled out during the late winter to early summer period (February to June: mean = 25.1, CI = 21.6–28.6) than in the autumn/winter months (October to January: mean = 13.4, CI = 11.3–15.4; Mann Whitney U: $z=-6.654$, $P<0.001$).

The observed haul-out patterns showed considerable individual variation. Seals spent between 11 and 27% of their time hauled out. Individual daily mean time hauled out (mean = 4.39 h, 95% CI = 4.13–4.52) varied by location (Mann Whitney U: $z=-4.13$, $P=0.04$) and season (Kruskal–Wallis: $\chi^2=121.75$, df = 10, $P<0.001$), with a strong seasonal pattern apparent in north-west, but not south-west, Scotland. Between February and May males hauled out for a larger proportion of the day than females, whereas the opposite was true between June and September (Mann Whitney U for sex: $z=-2.02$, $P<0.001$). The proportion of time hauled out was not correlated with individual body mass (Spearman's rank order correlation: $r_s=0.275$, $P=0.194$).

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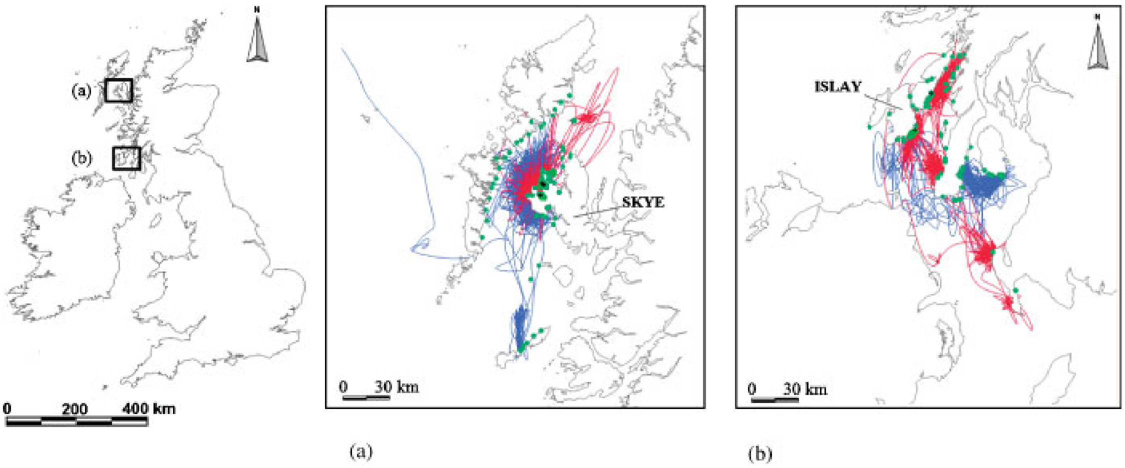

Figure 4. Individual tracks of male (blue) and female (red) harbour seals tagged in northwest Scotland, off the Isles of Skye (a), and south-west Scotland off Islay and Jura (b). ● = SRDL deployment locations. Locations of haul-out events interpolated from smoothed track data and 'snapped' to the nearest known haul-out clusters (shown in green).

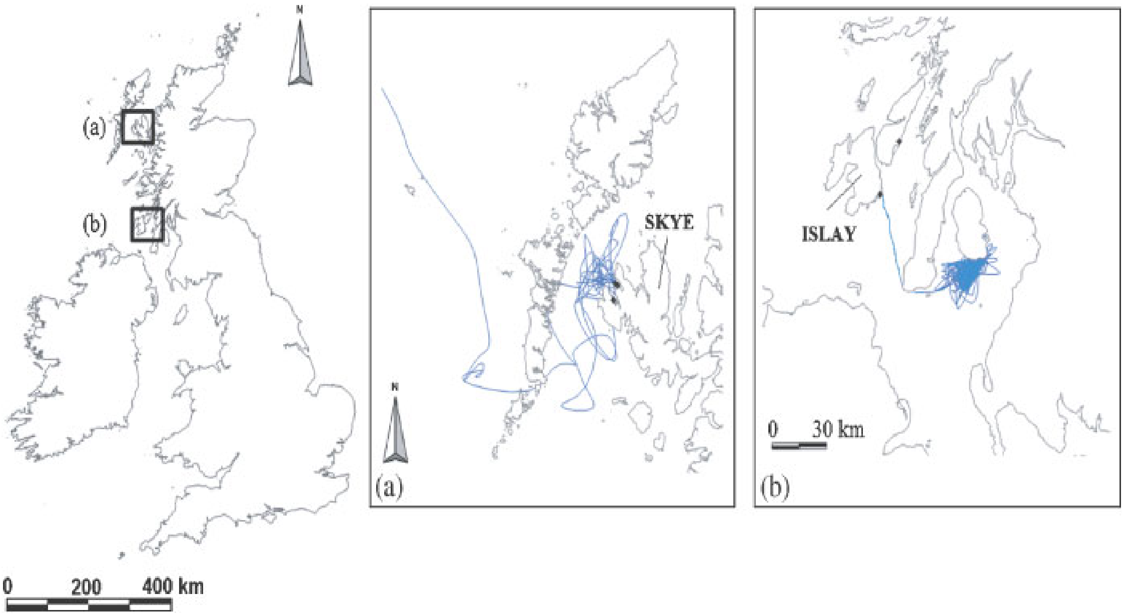

Figure 5. Smoothed tracks of dispersal movements of males NW2_M4, caught on Skye in March 2005 (a) and SW1_M2, caught on Islay in September 2003 (b). ● = SRDL deployment locations.

The probability of a seal being hauled out around midday, when aerial surveys are often conducted, showed strong seasonal patterns, particularly in north-west Scotland (Figure 7a and 7b). Between March and July, the highest probability of hauling out occurred at midday, but between September and February the probability of being hauled out around midday was either the same as, or lower than, that at other times of day. This diurnal pattern was particularly strong between May and July when there was an 80% chance that a seal would be hauled out around midday and less than 10% chance that it would haul out between 18:00 and 08.00. However, harbour seals did not haul out every day, spending less than 1 h hauled out on over 66% of days in this study. The mean duration of a haulout event was 4.77 h (SE = 3.6), with about 30% of all haulout events longer than 6 h. Occasionally haul-out events lasted over 20 h, with a maximum haul-out duration of 24.6 h, approximating a full tidal cycle.

DISCUSSION

The highest proportions of seals hauled out coincide with important life-cycle events, such as pupping, breeding and moulting (Thompson *et al*., 1998). Harbour seal aerial surveys conducted during these periods only provide a minimum estimate of the population because they do not account for seals in the water at the time of survey. Thus it is necessary either to assume that this proportion does not vary temporally or spatially, or to estimate the proportion of seals that are in the water at the time of survey in order to assess long-term trends in abundance. The estimate, related to a particular survey, allows a total estimate of the population to be derived; the assumption permits comparisons to be made between trends in minimum abundance, even if they do not give absolute numbers. These alternatives offer different opportunities and are considered below.

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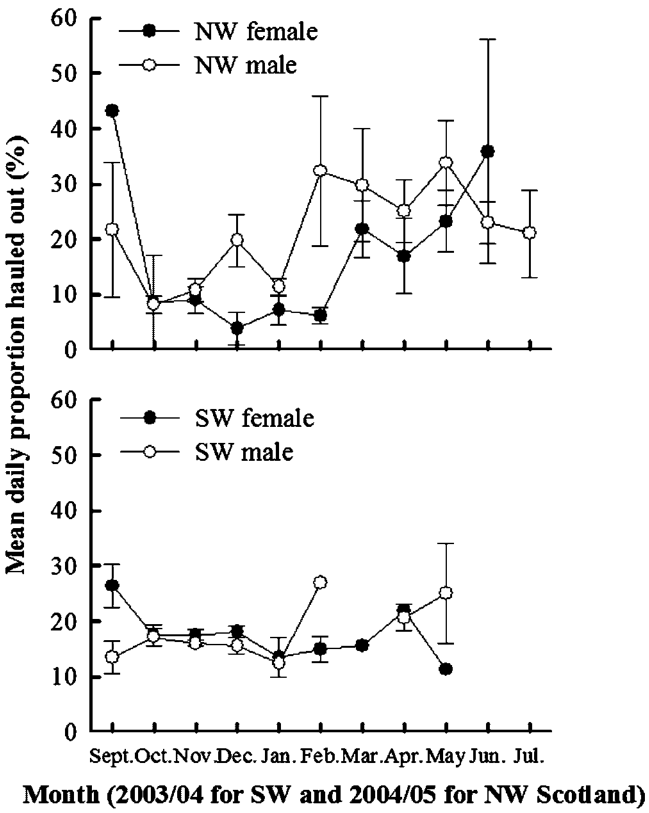

Figure 6. Individual daily percentage of time hauled out by month (with standard errors) for 10 seals in south-west Scotland in 2003/2004 (-○-) and 14 seals in north-west Scotland in 2004/2005 (-●-).

This study suggests that the time of day at which surveys are conducted should be a primary criterion for optimizing monitoring conditions. Previous estimates of the number of harbour seals ashore during peak haul-out times vary from 42–70% (Yochem *et al.*, 1987; Härkönen and Heide-Jørgensen, 1990; Thompson and Harwood, 1990; Thompson *et al.*, 1997; Ries *et al.*, 1998; Huber *et al.*, 2001; Gilbert *et al.*, 2005) to 79–88% (Olesiuk *et al.*, 1990). However, there is a gap in the telemetry data during the moult as tags, attached to the fur, are lost at this time. In this study the peaks in the daily proportion of time individuals spent hauled out were 36% in June, when animals were pupping, and 43% in September, towards the end of the moult. The mean daily time an individual was hauled out ranged from 10–30% during the study (September to July). In the months prior to the current aerial surveys (i.e. May to July, surveys occur in August) there was a strong diurnal influence on the probability of a seal being hauled out, such that there was an 80% chance that a seal would be hauled out around midday (which was therefore consistent with previous studies), but a mean of 10% at night (18.00–08.00). In contrast there was no clear diurnal pattern in September, with the probability of being hauled out fluctuating around 20%. During the autumn and winter haul-out events were more likely at night than during the day, whereas the opposite was true in the spring/summer. This may be a result of the need to spend time ashore when pupping, suckling and moulting in the summer (July–August).

It is essential to ensure that the timing of the monitoring period coincides with a peak in the probability of a seal being hauled out. While the timing of aerial surveys has previously

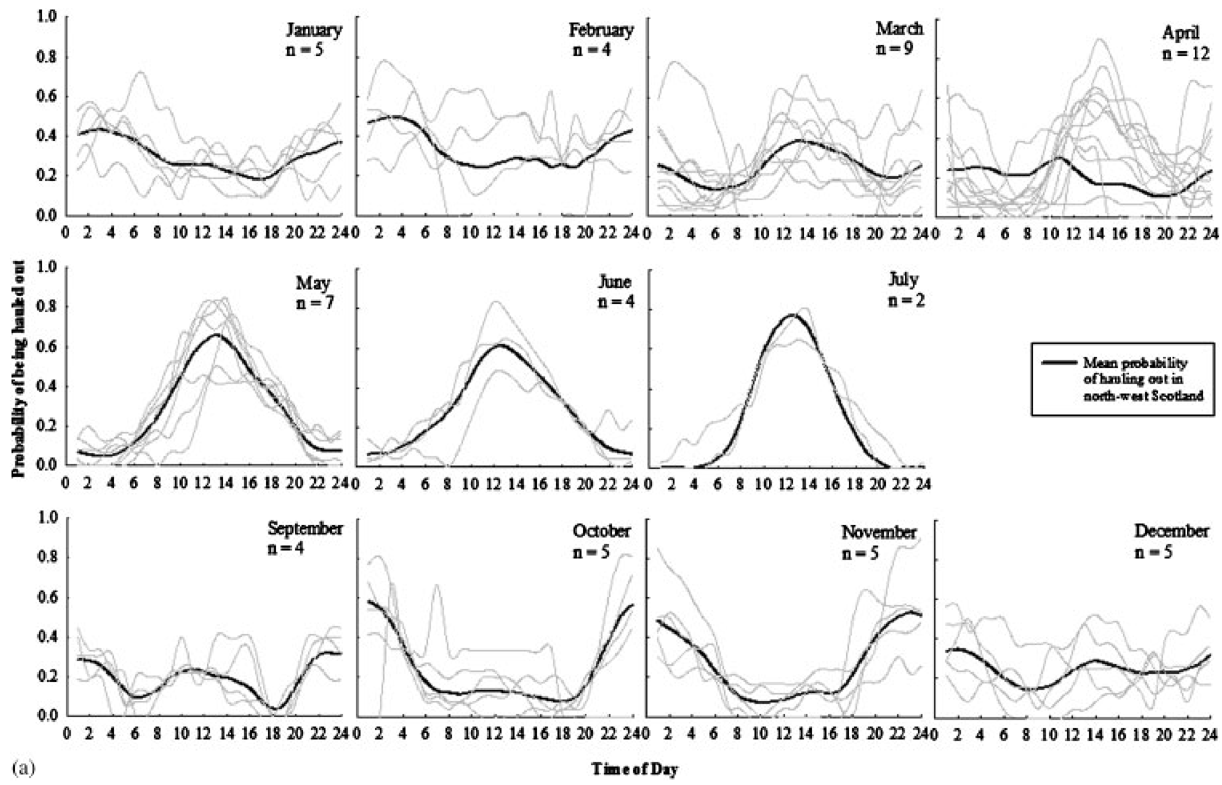

Figure 7. Diurnal and seasonal variation in the probability of a seal being hauled out in north-west (a) and south-west (b) Scotland. A running mean with a 3 h window was plotted for each month. n = total sample size of animals with haul-out records, plotted individually to show variation. A formal confidence interval requires strong assumptions that were deemed inappropriate for a small sample size.

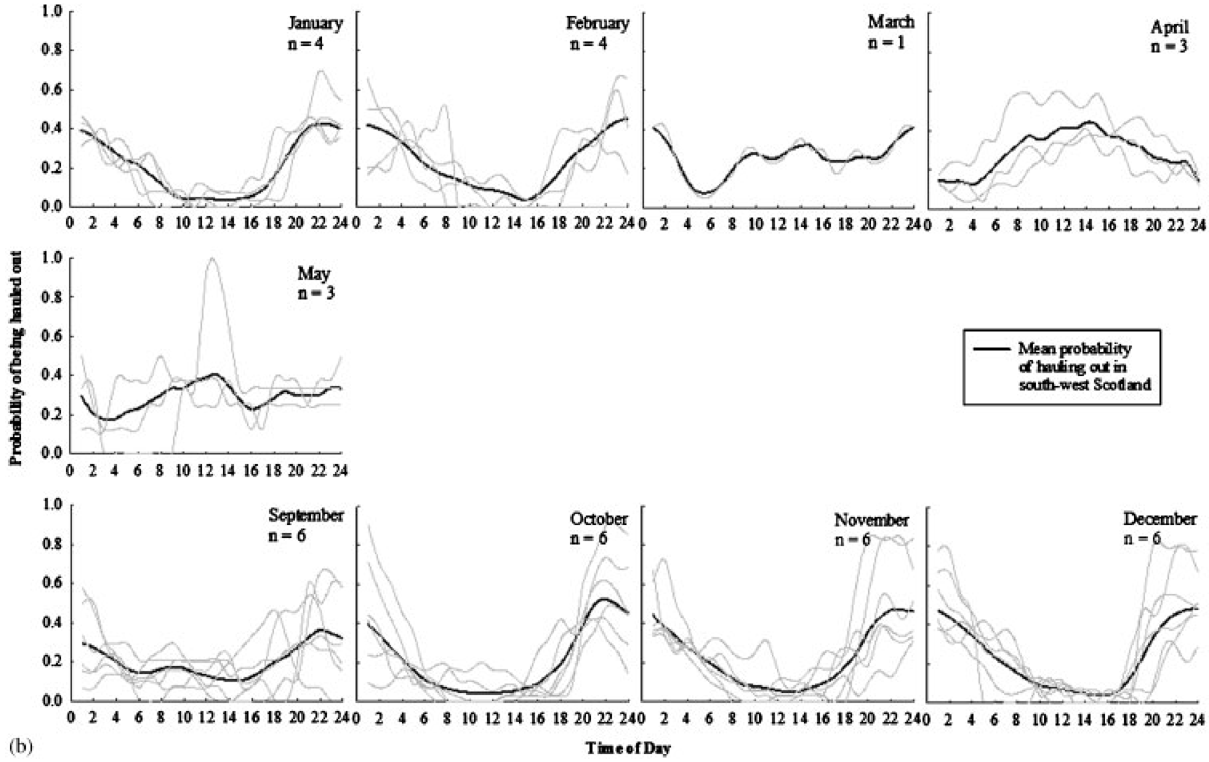

Figure 7. Continued.

been determined to coincide with the state of the tide (2 h either side of low tide — SCOS, 2006), the effect of temporal variations should also be taken into consideration. The seasonal change in diurnal haul-out behaviour showed no spatial variation between north-west and south-west Scotland, which consist of similar rocky habitats. However, there may be regional variations in haul-out behaviour over larger distances; for example seals may haul out less frequently in areas of low food abundance or high disturbance (Huber *et al*., 2001).

In the absence of data from August, when seals are typically surveyed, the proportion of time harbour seals are in the water, and consequently not counted, remains unknown. It is essential that haul-out patterns for this time are measured if true seal population size is to be estimated accurately from aerial survey data. Thus alternative attachment methods that collect information during this period must be considered, e.g. attaching telemetry devices to the flipper (Huber *et al*., 2001; Simpkins *et al*., 2003) or by means of an implantable tag (Horning and Hill, 2005; Lander *et al*., 2005).

Female harbour seals are thought to moult before males (Thompson *et al*., 1989), yet in this study the mean proportion of time hauled out in September, towards the end of the moulting period, was higher in females than in males. This either suggests that there are regional differences in the order in which the sexes moult, that females take longer than males to complete their moult, that females may rest for longer due to hard post-moult foraging, or may be a sampling anomaly, the result of a relatively small sample size. Mating is thought to occur in the water (Van Parijs *et al*., 1997) towards the end of lactation (Thompson, 1988) and hence the decrease in the proportion of time hauled out by males in July may be a result of males spending more time in the water to increase their chances of encountering females. However, as the animals tagged in this study were selected as having completed or almost completed the moult, the patterns observed in September may not be representative of the population. Furthermore, although juvenile seals are counted during aerial surveys, in this study only the haul-out behaviour and movements of adults were examined. Haul-out behaviour differs among age and sex classes (Härkönen *et al*., 1999), and harbour seals show age and sex segregation at haul-out sites (Härkönen and Harding, 2001). Consequently, surveys that are biased towards haul-out sites favoured by mature females will overestimate the recruitment rate for the population as a whole. Knowledge of the age structure of the Scottish population of harbour seals is sparse (Mackey, 2004), yet this information is of vital importance because it affects the relationship between counts of seals hauled out and the total population size (Härkönen *et al*., 1999).

Haul-out patterns and site usage

Harbour seals show a degree of site fidelity (Yochem *et al*., 1987; Thompson, 1989; Corpe, 1996), while marking studies have shown that seals use different haul-out sites throughout the year (Brown and Mate, 1983; Thompson, 1989; Thompson *et al*., 1996; Simpkins *et al*., 2003). High levels of site fidelity would support the designation of protected areas for harbour seals at haul-out sites.

Both the probability of hauling out and the duration of haul-out events are important for monitoring protocol design. Haul-out duration was longer in the spring compared with the autumn/winter months. The west coast of Scotland contains numerous rocky skerries, which remain available for hauling out throughout the tidal cycle. Nevertheless, most (85%) haul-out events in this study lasted for less than 8 h (mean = 4.77 h).

This is comparable with results from similar studies conducted in the Moray Firth, north-east Scotland (Thompson and Miller, 1990) despite the differences in haul-out habitat (estuarine sandbanks) and availability (strongly influenced by the tide) at this site. Visual inspection of the data showed no correlation with tidal phase and it is therefore possible that haul-out duration is governed by physiological factors and food availability, rather than habitat characteristics, limiting its variability.

On average the harbour seals in this study each used 13 haul-out clusters, though the number of clusters used by an individual was positively correlated with the tracking period. Nevertheless, 40% of consecutive haul-out events occurred at sites separated by less than 2 km. This illustrates that harbour seals show a degree of site-fidelity and consequently could benefit from legislative protection of terrestrial sites. Some haul-out sites were never used for return trips, and so could be considered as transient sites with a high degree of population flux. These sites may be important for maintaining a network of protected areas. Other sites, with high levels of site fidelity, may be more appropriate in areas where haul-out sites are separated by large distances, or for managing the protection of a local population.

Seasonal switches in haul-out site usage have been reported in harbour seals in other areas (Brown and Mate, 1983; Thompson *et al*., 1994; Lowry *et al*., 2001). Some seasonality was apparent in movements from one haul-out cluster to another in this study, but this did not appear to be sufficient to explain the observed patterns. Site-switching may be related to prey availability, with seals changing haul-out site to minimize the distance to prime foraging areas (Thompson, 1988). The timing of a change in haul-out site could be influenced by a range of factors including prey preferences and availability, or the movements of other seals.

Seal movements

This study showed that harbour seals generally remained within a 25 km radius of haul-out sites: only one seal travelled more than 30 km from land. Although some trips were several days in duration (maximum = 9 days) almost half of the trips made by harbour seals in this study lasted between 12 and 24 h (mean of all trips = 31 h). Previous studies have also suggested that harbour seals haul out and feed locally (Brown and Mate, 1983; Thompson *et al*., 1996; Suryan and Harvey, 1998; Lowry *et al*., 2001). Most of these studies either relied on VHF telemetry, which could potentially have missed longer distance movements, or were of harbour seals that utilize a different habitat from that considered in the present study (sandbanks or estuaries). The satellite telemetry data confirms that the majority of harbour seal trips were to coastal waters and that animals usually remained within fairly restricted areas, presumably because sufficient prey were available in these areas. This supports the suggestion that these marine high-use areas could be considered as 'management units' for harbour seals (Thompson *et al*., 1996).

Not all movements in this study were short, small-scale return-trips to sea. Although the seals in this study did not travel as widely as grey seals (Thompson *et al*., 1996; McConnell *et al*., 1999), this study suggests that adult harbour seals, which occasionally travelled over 100 km, have the opportunity to mix with seals elsewhere and consequently are not ecologically isolated from other harbour seal 'populations'. Pacific harbour seals have also been reported to show inter-annual or inter-seasonal use of haul-out sites that were over 200 km apart (Brown and Mate, 1983; Yochem *et al*., 1987). The relatively low proportion of return trips (40%) further suggests that there is a degree of mixing between local harbour seal populations on the west coast of Scotland. This could be a consequence of the arbitrary definition of haul-out clusters and trips, and the error associated with ARGOS locations. However, increasing the scale of the grid used to cluster haul-outs to 10 km decreased the number of return-trips, as did increasing the minimum duration of a trip to 10 hours. Hence even if these definitions are changed, large-scale harbour seal movement was still observed and so monitoring methods that assume a closed population, e.g. some capture–recapture models, should be used with caution.

Some previous work suggests that the duration and extent of trips varies with body size, sex (Thompson *et al*., 1998) and season (Lowry *et al*., 2001). These relationships were not apparent in this study, potentially due to food availability meaning that the requirements for all individuals, regardless of sex or size, were accessible within easy range of the haul-out cluster throughout the year. The observed spatial variation in the duration and extent of trips between harbour seals in north-west and south-west Scotland, possibly as a result of the distance from haul-out sites to prime foraging areas, provides weight to the suggestion that the patterns in this study probably show at least some regional specificity.

Although harbour seals spend a large proportion of their time in the water, conservation legislation usually only protects them at designated terrestrial haul-out sites. In this study the majority of harbour seal movements remained within 25 km of the coast, thus providing the potential for designating a marine component to protected areas. Furthermore, individual seals used multiple haul-out sites, providing support to the concept of a network of protected sites with the potential for interaction between 'populations'. Individual seals frequently returned to some specific haul-out sites, suggesting that these sites may be particularly appropriate as management units to ensure the effective conservation of the harbour seal population.

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