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Estimating harbour seal abundance and status in an estuarine habitat in north-east Scotland

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Summary

1. Harbour seals are the most widespread of pinniped species, coming ashore onto a variety of different habitats to rest, moult and breed. Estimates of their abundance and status rely on counts of animals in terrestrial haul-out groups but it is not clear to what extent current techniques are appropriate for all habitats.

2. This study aimed to determine the most appropriate methods for estimating the abundance and status of harbour seals in an estuarine habitat in north-east Scotland. Regular low-tide counts were conducted to identify the best time for annual counts. Survey data for 1993 were then combined with telemetry data on seal activity to produce an estimate of abundance. Finally, simulations using data on the variability of counts within a single year were used to determine the power of these techniques to detect trends in abundance.

3. The results suggest that annual counts conducted during the pupping season (mid-June to mid-July) provide the best estimates of abundance in this habitat. These results contrast with those from studies in rocky-shore habitats where counts made during the August moult provided more reliable abundance estimates.

4. In 1993, an average of 1007 seals were hauled out at low tides during the period 15 June–15 July. There were significant differences in haul-out frequency for males (0·521 of low tides) and females (0·698 of low tides) but no within-sex variation was detected during this period. Combining the telemetry data with the results of counts from the Moray Firth produced an abundance estimate of 1653 (95% confidence limits 1471–1836).

5. The potential effects of within and between-year variation in haul-out behaviour are discussed in relation to identifying suitable indices of abundance for trend analysis. In view of likely seasonal changes in the sex structure of haul-out groups, we recommend that programmes to monitor trends in harbour seal abundance should conduct annual counts at two different points in the annual cycle.

Key-words: abundance trends, activity budgets, pinnipeds, telemetry.

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Introduction

Harbour seals *Phoca vitulina* L. are widely distributed around the coasts of the North Atlantic and North Pacific, where they use a variety of habitats to haul out and breed, moult or rest. In many areas numbers are believed to be increasing and the species is considered a threat to local fisheries (Beddington, Beverton & Lavigne 1985; Harwood & Croxall 1988; Olesiuk, Bigg & Ellis 1990). In other cases, declines in abundance at haul-out sites have been observed and concern has been expressed over the status of the seals in certain areas (Pitcher 1990; Simmonds 1991). Counts on land can provide an index of abundance. However, the number of harbour seals present on land may vary according to a variety of factors such as season (Slater & Markowitz 1983; Thompson 1989), time of day (Stewart 1984; Thompson *et al.* 1989; Watts 1992), tidal cycles (Schneider & Payne 1983; Thompson & Miller 1990) and weather conditions (Kreiber & Barrette 1984; Watts 1992). Assessments of the significance of abundance trends therefore require a systematic time-series of counts, which take account of these sources of variability. In addition, if either the effect of seals upon fish stocks (e.g. Lavigne *et al.* 1982; Olesiuk 1993) or the stability of small populations (e.g. Durant & Harwood 1992) is to be modelled, it must be possible to relate this index of abundance to absolute abundance.

In Britain, harbour seals are found both at rocky-shore haul-out sites (e.g. Orkney, Shetland, Outer Hebrides) and at sites on inter-tidal sandbanks in the east coast estuaries (e.g. Moray Firth, Tay Estuary, The Wash). These haul-out areas, particularly on the east coast of Britain, appear to form relatively discrete populations (Bonner & Thompson 1990) with only limited dispersal of individuals between them (Bonner & Witthames 1974; Thompson 1993; Thompson, Kovacs & McConnell 1994). Previous estimates of harbour seal abundance in all these areas were based on counts made from boats during the breeding season (e.g. Summers *et al.* 1980; Anderson 1981). However, these studies provided only minimum estimates of abundance because there is no point in their annual cycle when all animals, even mothers and their pups, are ashore. Subsequently, observational and radio-tracking studies in Orkney suggested that higher and more consistent counts could be made later in the summer, primarily due to behavioural changes during the moult (Thompson 1989; Thompson *et al.* 1989). Furthermore, it was shown that counts could be carried out more efficiently using aerial photography (Thompson & Harwood 1990). Since 1988, this methodology has been used extensively by the NERC Sea Mammal Research Unit around the British coast, and efficiency has been improved through the use of thermal imaging equipment instead of conventional photography (Hiby *et al.* 1996). Similar peaks in abundance have been observed during the moult in other European and North American areas and many other counts are conducted at this time (e.g. Everitt & Braham 1980; Heide-Jørgensen & Härkönen 1988). Nevertheless, these counts still represent only estimates of minimum abundance.

Such counts can, however, be used to estimate absolute abundance if information is also available on the seals' activity patterns (Eberhardt, Chapman & Gilbert 1979). In Orkney, for example, studies of individual behaviour patterns were used to extrapolate from haul-out counts to provide an estimate of total population size (Thompson & Harwood 1990). In carrying out this exercise, however, it was recognized that harbour seal behaviour may differ geographically due to the wide variety of habitats and climatic regions which they inhabit. Consequently, the recommendations made for study design and abundance estimation on Orkney's rocky shores may not apply in other areas. In particular, Orkney's flat rocky-shore sites are often used by seals throughout the tidal cycle (Thompson *et al.* 1989). In contrast, harbour seals at many estuarine sites haul out onto inter-tidal sandbanks that may be available for only a few hours at each low tide (Vaughan 1978; Reijnders 1978). Thus, haul-out patterns observed in Orkney and at other rocky-shore sites tend to be dominated by diurnal cycles (Stewart 1984; Yochem *et al.* 1987; Thompson *et al.* 1989), whereas the activity of seals in estuarine areas is strongly influenced by tidal cycles (Thompson & Miller 1990). The methodology used to estimate absolute abundance is therefore likely to need adapting for use in different habitats.

This study aimed to determine the most appropriate and cost-effective methods for estimating absolute abundance and for assessing status by identifying trends in abundance as part of a wider study of the foraging and population ecology of Moray Firth harbour seals. These animals almost exclusively use inter-tidal sandbank haul-out sites. As such, the Moray Firth and Orkney provide good examples of two ends of the spectrum of haul-out habitats that are used by British harbour seals. Because of their close proximity (125 km) and relatively similar climatic conditions, these populations offer the opportunity to explore the extent to which haul-out site habitat should be taken into consideration when designing studies to assess the abundance and status of this species.

Initially, we used information on seasonal, diurnal and tidal patterns of abundance to identify the most suitable time to make annual counts. VHF radio-tracking data on individual behaviour patterns were then combined with counts to provide an estimate of the abundance of seals in the Moray Firth area in 1993. Finally, simulations were conducted to determine how sampling rate influenced the length of the time-series of counts required to detect different rates of annual change in abundance.

Methods

STUDY AREA

In the inner Moray Firth (57°41′N, 4°0′W), breeding groups of harbour seals are found in three sheltered estuaries; the Beauly, Cromarty and Dornoch Firths (Fig. 1). Each of these areas contains several inter-tidal

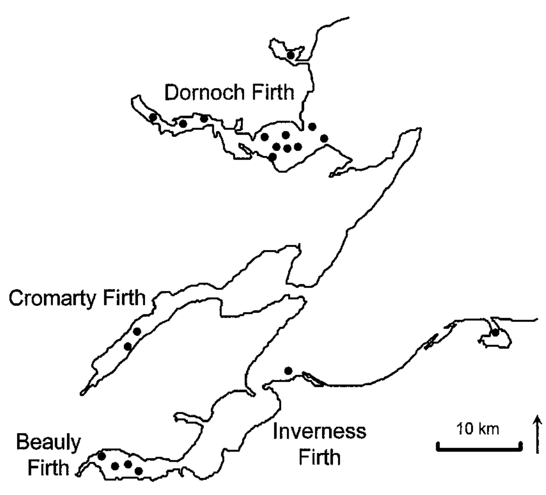

Fig. 1. A map of the Moray Firth study area showing the five sub-areas and major haul-out sites mentioned in the text.

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sandbank or muddy-shore haul-out sites. Seaward of the Beauly Firth is another relatively enclosed area of water, the Inverness Firth. Large groups of seals are found at a single site near the mouth of this firth and small groups are seen at sites along the coast of the outer part of the Moray Firth to the north and east (Fig. 1).

NUMBERS OF SEALS AT HAUL-OUT SITES

Haul-out sites were identified from previous studies in the area (McConnell *et al.* 1985) and from complete aerial surveys in the summers of 1987 and 1989 (P. Thompson, unpublished data). Changes in the number of seals at all sites in the inner Moray Firth were investigated by making regular counts throughout the year from January 1988 to August 1990 and during June–August of 1991–93. In the Beauly, Cromarty and Inverness Firths, counts were made at least once each week, and in the Dornoch Firth and Loch Fleet at least twice each month.

Seals were observed from the shore at distances of 0·5–4·0 km using a 30 × 70 telescope. All counts were made within ±2 h of low tide in good visibility.

INDIVIDUAL HAUL-OUT PATTERNS

Haul-out patterns were studied using VHF radio-telemetry (Thompson *et al.* 1989). A total of 26 seals was captured at sites in the Dornoch, Inverness and Cromarty Firths in April or May of 1988, 1989, 1991, 1992 and 1993. Details of techniques for capture, handling and the collection of morphometric data are given in Thompson *et al.* (1992). The sample of seals was biased towards adult females but included both immature and mature individuals of both sexes. Data were collected using automatic recording stations (Nicholas *et al.* 1992) that were sited to overlook the principal haul-out areas used by radio-tagged seals in each year of the study. These stations recorded signals from each individual for at least 6 min h^{-1} and the nature of the signal allowed us to determine whether seals were hauled out, diving or absent from the study area (Thompson *et al.* 1989). Observations at haul-out sites indicated that, once hauled out, seals generally remained settled for most of the low-tide period unless disturbed (P. Thompson, unpublished data). Individual activity budgets were therefore constructed by assuming that a seal's behaviour during a sample period was representative of its behaviour for that hour of the day. Activity budgets were then sampled to determine the extent of variation in individual haul-out frequency with relation to factors such as tidal state, time of day and stage of season.

ESTIMATE OF TOTAL NUMBER OF SEALS

Preliminary examination of the telemetry data indicated a difference between male and female behaviour, so absolute abundance was estimated from the equation:

$$n = h_1(N/2) + h_2(N/2) \qquad \text{eqn 1}$$

where N is the total abundance of seals (> 1 year old) in the study area assuming a sex ratio of 1:1; h_1 and h_2 are the proportion of low tides on which male and female seals were hauled out during the sampling period; and n is the mean low-tide count during this same period. Thus:

$$N = 2n/(h_1 + h_2) \qquad \text{eqn 2}$$

with variance estimated by the 'delta' method from:

$$CV^2N = CV^2n + CV^2(h_1 + h_2) \qquad \text{eqn 3}$$

so that:

$$var(N) = N^2[(var(n)/n^2) + (var(h_1) + var(h_2))/(h_1 + h_2)^2] \qquad \text{eqn 4}$$

assuming n, h_1 and h_2 are independent.

Estimates of n were based on counts made between 15 June and 15 July 1993 (see the Results). At least eight counts were carried out in each of the five sub-areas (Beauly Firth, Inverness Firth, Cromarty Firth, Dornoch Firth and Loch Fleet) during this period, and mean counts for each sub-area were combined to provide a total mean count. These counts did not include pups of the year, primarily because pups were being born throughout this period.

Telemetry data from the period 15 June–15 July were used to estimate h_1 and h_2. Because the number of seals tracked in any one year was low, activity data from all years were combined. Thus, we assume that activity did not vary among years. In addition, we assume that any age-related differences in behaviour were accounted for by our sample being representative of seals aged 1 and older.

In order to compare this estimate of abundance with that used in a previous study where no telemetry data were available, we made a second estimate of abundance using Olesiuk *et al.*'s (1990) bounded count method. This method used the variability of replicated counts obtained during the period 15 June–15 July to estimate the average proportion of seals that were ashore during the survey period:

$$P_{it} = C_{it}/[C_{max} + (C_{max} - C_{max-1})] \qquad \text{eqn 5}$$

where P_{it} is the proportion of seals that were ashore and C_{it}, C_{max} and C_{max-1} are the mean, the highest and the second highest of the replicate counts, respectively.

SAMPLING STRATEGY FOR DETERMINING TRENDS

A key aim of this study was to develop cost-effective methods for detecting changes in the abundance of seals in this study area. A simple way to estimate how long it will take to detect a trend in abundance is known as power analysis (Gerrodette 1987). In power analysis, there are a number of complicating factors such as whether abundance is assumed to change linearly or exponentially, the way in which the precision of estimates depends on the method of estimating abundance, and the level of statistical significance accepted. But if we accept the usual 5% level of statistical significance, a useful approximation that avoids the need to consider the other factors is represented by the inequality:

$$r^2 n^3 = 156\,CV^2 \qquad \text{eqn 6}$$

where r is the annual rate of change in abundance, n is the number of annual surveys, and CV is the coefficient of variation (an estimate of relative precision) of the abundance estimates, assumed to be the same for all surveys (Gerrodette 1987). Here we used a power analysis to explore the effects of varying the number of counts made in a year in each sub-area (Fig. 1) on the probability of detecting trends at different annual rates of change in abundance.

Data collected during the period 15 June–15 July 1993 were first used to estimate parameters for the mean and standard deviation of haul-out counts in each of the five sub-areas (see above). We then used these parameters in a Monte-Carlo simulation to predict mean counts for each sub-area at sampling rates that varied between two and nine counts per year. Mean counts were estimated from 50 replicates in each case.

The relationship between the variability of the total mean count and the number of counts made in a year was determined by fitting a geometric regression to the CV of the sum of the simulated mean counts from each sub-area, over the range of sampling rates. Estimated CV from the fitted relationship were then used to predict how the number of counts made each year affected the number of years required to detect a trend in abundance for a range of assumed annual rates of change in abundance.

Results

VARIATIONS IN ABUNDANCE AT HAUL-OUT SITES

Data from year-round counts made between 1988 and 1990 showed that haul-out counts were highest between June and August (Fig. 2). Maximum counts for each year between 1988 and 1992 varied by less than 20%, and data were therefore pooled to explore changes in abundance during this period in more detail. These data indicated that seasonal trends in abundance varied between sites (Fig. 3). In the Dornoch Firth, mean weekly counts were similar throughout the summer, whereas those in the Cromarty and Beauly Firths increased during early June and decreased again in late-July and August. There was a significant positive correlation between the trends in the Cromarty and Beauly Firths, and mean weekly counts at both sites were significantly and inversely related to those in the Inverness Firth (Table 1). Overall, combined counts for the four areas showed no evidence of an increase between the June/July pupping season and the August moult (Fig. 3).

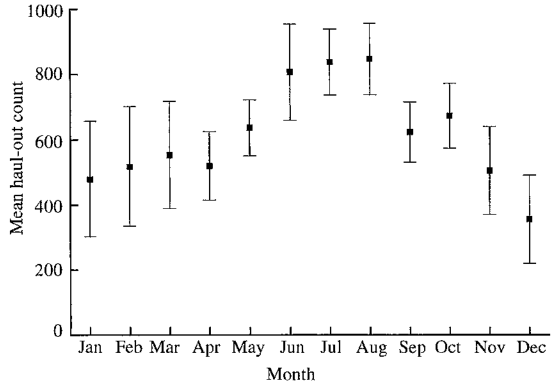

Fig. 2. Seasonal changes in the mean (±1 SE) number of harbour seals present at haul-out sites in the Moray Firth, 1988–90.

INDIVIDUAL HAUL-OUT PATTERNS

Radio-tags remained attached for up to 14 weeks before they were lost during the seals' annual moult. On average, tags were lost on 23 July (SE = 2·7 days). Consequently, the most complete data on individual behaviour patterns were those from the early part of the summer. Given the lack of any overall trend in abundance that dictated that counts should be conducted during a particular time period (Fig. 3), estimates of population size were based on telemetry and counting data collected during the period 15 June–15 July.

During this part of the summer, the behaviour of all radio-tagged seals was strongly related to the tidal

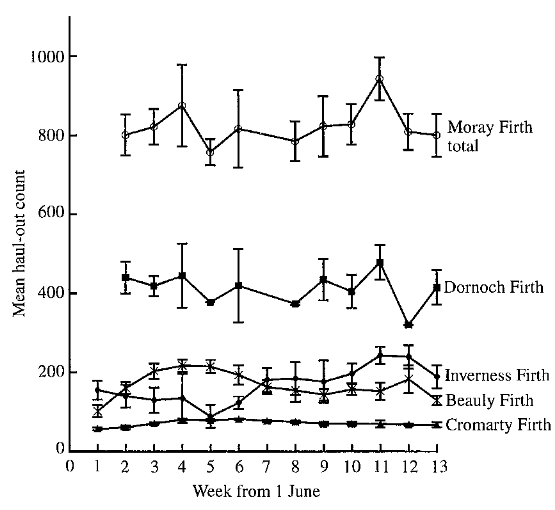

Fig. 3. Changes in the abundance of harbour seals at haul-out sites during the summer. Data are weekly means (±1 SE) for the whole Moray Firth and for major sub-areas, and are based upon counts made between 1988 and 1992.

Table 1. Results of the Spearman's rank correlation used to determine the relationship between observed seasonal trends in the abundance of harbour seals in the four different haul-out areas

Haul-out area	Spearman's rank correlation	d.f.	*P*-value
Inverness vs. Beauly	−0·566	11	0·022
Inverness vs. Cromarty	−0·512	11	0·037
Inverness vs. Dornoch	−0·064	9	0·43
Beauly vs. Cromarty	0·674	11	0·006
Beauly vs. Dornoch	−0·027	9	0·47
Cromarty vs. Dornoch	0·18	9	0·48

cycle. The probability of animals being ashore varied little over the period 2 h either side of high tide, but decreased sharply at other tidal states (Fig. 4). In contrast, the time of day at which the low tide occurred had no effect on the probability of radio-tagged seals being hauled out (Fig. 5).

Comparisons of the behaviour of small (<60 kg) and large (>70 kg) males, and of females that were seen with and without pups, showed that there were no significant within-sex differences in haul-out behaviour during the study period (Table 2). Data for each sex were therefore combined for further analyses, which showed that, on average, females hauled out on 0·698 (SE = 0·0357) of low tides between 15 June and 15 July, significantly more often than males, who were ashore on only 0·521 (SE = 0·0441) of low tides during this period (Table 2).

ESTIMATE OF POPULATION SIZE

Between 15 June and 15 July 1993, at least nine counts were made in each of the four main estuaries in the study area, and eight at the smaller site in Loch Fleet. Mean counts for each of these sub-areas are presented in Table 3. The total mean for the whole Moray Firth was 1007 (SE = 31·8, 95% confidence interval = 945–1069).

From equation 2, and using values of h_1 and h_2 from Table 3, the abundance of Moray Firth harbour seals, not including pups of the year, was estimated to be 1653 (SE = 93·1, 95% confidence interval = 1471–1836). The use of the bounded count method produced a higher estimate of the proportion of seals ashore (Table 4) and thus a lower estimate of abundance of only 1398.

POWER TO DETECT TRENDS IN ABUNDANCE

Figure 6 shows how the *CV* of the total mean count changes with the number of counts made each year, as estimated from the simulations for each sub-area. The *CV* improves from about 0·11 to about 0·06 when count frequency is increased from two to five per year, but little further gain in precision is achieved if count frequency is increased to nine per year. Using the estimated *CV* from the fitted relationship in equation 6, Fig. 7 shows how the number of counts made each year affects the number of years required to detect a trend in abundance for a range of annual rates of change. The number of years required to detect a trend increases markedly as annual rate of change decreases below about 0·05. Similarly, as annual rates of change decrease below 0·05, the number of counts per year has an increasing effect on the number of years required to detect a trend.

A total of nine counts per year was the maximum possible during the 1-month counting period because of logistic and weather constraints. To show the effect of reducing this, the number of additional years required to detect a trend was plotted against annual

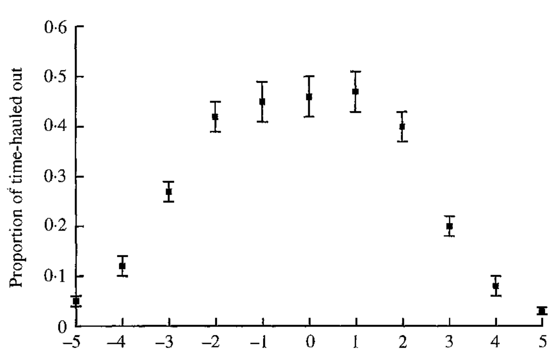

Fig. 4. Changes in the proportion of time that radio-tagged harbour seals spent hauled out at different stages of the tidal cycle.

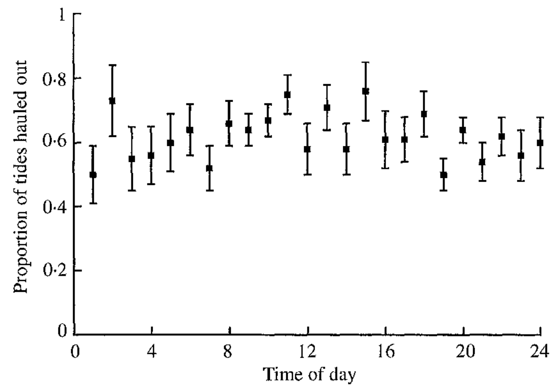

Fig. 5. Variations in the proportion of low tides on which radio-tagged harbour seals were hauled out with respect to time of day.

Table 2. Results of Mann–Whitney U tests to compare the proportion of low tides on which harbour seals of different sex and reproductive status hauled out

Seal status	Number of seals	Proportion tides used	SE	Mann–Whitney P-values
Female with pup	10	0·724	0·032	0·396
Female without pup	4	0·632	0·098	
Male >60 kg	6	0·502	0·076	1·00
Male <60 lg	6	0·540	0·076	
All females	14	0·698	0·036	<0·01
All males	12	0·521	0·044	

Table 3. Mean low-tide haul-out counts of harbour seals for each of the sub-areas and for the whole Moray Firth, 15 June–15 July 1993

Area	Number of counts	Mean	SE
Beauly Firth	10	247·4	6·55
Cromarty Firth	29	86·7	3·12
Inverness Firth	10	125·9	26·51
Dornoch Firth	9	540·3	15·94
Loch Fleet	8	6·6	1·85
Moray Firth Total		1006·9	31·83

Table 4. Estimates of the proportion of seals hauled out (P) and the resulting abundance estimates for each sub-area based on the bounded count method (eqn 5)

Area	Mean	C_{max}	C_{max-1}	P	Estimated abundance
Beauly Firth	247·4	281	270	0·85	292
Cromarty Firth	86·7	106	104	0·8	108
Inverness Firth	125·9	235	199	0·46	271
Dornoch Firth	540·3	642	573	0·76	711
Loch Fleet	6·6	24	12	0·4	16

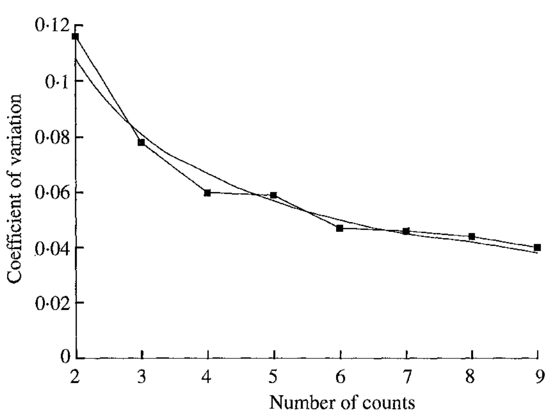

Fig. 6. The effect of changes in the number of replicate counts per year on the CV of estimated total mean haul-out count. Results from simulations are plotted with the fitted geometric regression.

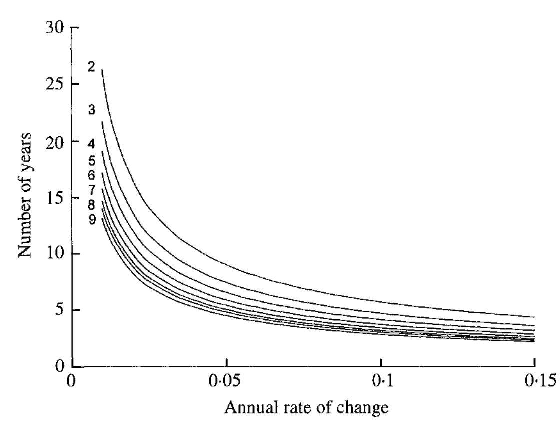

Fig. 7. Results of simulations to determine the number of years required to detect different magnitudes of annual rates of change (r) in abundance of Moray Firth harbour seals. Plotted lines are for 2–9 replicate counts per year.

rate of change for a range of number of counts per year (Fig. 8). Figure 8 shows that, if the annual rate of change is greater than about 0·10, reducing the number of counts from nine to five per year would result in only one more year being required to detect a trend. At this sampling rate of five counts per year, only two more years are required to detect a trend for annual rates of change down to 0·03. If the number of counts is increased to six, a trend with an annual rate of change as low as 0·05 could be detected in only one additional year.

Discussion

TIMING OF COUNTS

These results indicate how habitat differences can strongly influence the behaviour of harbour seals, and highlight that this requires counting techniques to be adapted for different areas. In contrast with studies of harbour seals in both nearby (Orkney: Thompson & Harwood 1990) and more distant (Washington State: Jeffries 1986; Kattegat: Heide-Jørgensen & Härkönen 1988) areas, there was no evidence of a seasonal increase in the abundance of Moray Firth seals during August (Fig. 4). Changes in the number of pups in the Cromarty Firth (P. Thompson, unpublished data) and in Orkney (Thompson & Harwood 1990) indicated that most pups were born during June in both areas. The timing of the annual cycle was therefore similar in both areas, and there appeared to be genuine geographical differences in the relative proportion of the population that was ashore at different stages of the annual cycle. In Orkney, approximately twice the number of seals were seen at haul-out sites during the moult compared with counts during the pupping season (Thompson & Harwood 1990) and the increase was a result of a marked increase in the synchronicity of adult male haul-out behaviour (Thompson *et al.* 1989).

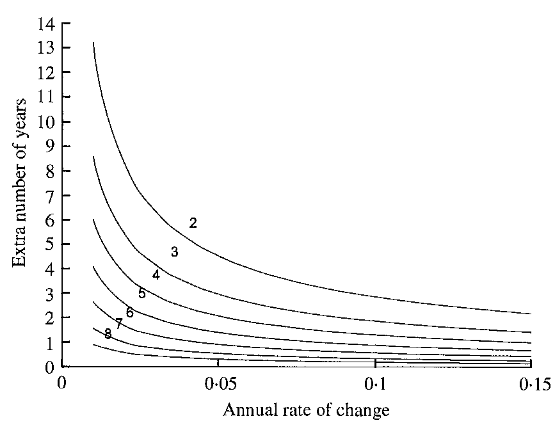

Fig. 8. Estimates of the additional number of years required to detect different annual rates of change in the abundance of Moray Firth harbour seals, using 2–8 replicate counts per year instead of the nine counts used in 1993.

Within many estuarine environments, suitable haul-out sites are available only at low tide; restricted site availability may therefore result in more synchronous haul-out behaviour throughout the summer. Consequently, observed differences between the Moray Firth and Orkney seals may have occurred because a higher proportion of Moray Firth seals hauled out on low tides during the pupping season rather than because of a reduction in their tendency to haul out during the moult. Alternatively, because of the strong effect that adult male behaviour had on seasonal abundance trends at Orkney sites, relative differences in haul-out numbers could have been affected by between-area differences in sex ratio or age structure.

In the absence of more consistent or higher counts during the moult, we suggest that three factors made it more appropriate to base our abundance estimate on counts made during the pupping season. First, although trends in counts (Fig. 2) and data on individual movements (Thompson *et al.*, 1996) indicated that there was some exchange between different sub-areas, relative abundance in each sub-area remained fairly stable during the peak of the pupping season (Fig. 3). Restricting counts to the period 15 June–15 July therefore minimized the probability of double counting individuals at different sites. Secondly, there were more telemetry data available from the period 15 June–15 July, primarily because seals lost their radio-tags early in the moult. Thus, these greater sample sizes provided more precise estimates of h_1 and h_2. Finally, it was relatively easy to distinguish pups of the year at this time, on the basis of size and pelage characteristics or from the presence of their mothers. Later in the season, there was more potential for confusion with moulted yearlings (Thompson & Harwood 1990). While total counts could be made of all seals, excluding pups provided a more robust estimate of abundance that should have been less dependent on short-term changes in reproductive success. In future, parallel methods could be developed to use changes in the number of pups to provide an independent index of reproductive success.

ESTIMATION OF POPULATION SIZE

The use of telemetry data to extrapolate from our mean count of 1007 produced an abundance estimate of 1653 with a SE of 93. To assess the relative contribution to the overall variance of the counts and the telemetry data, it is necessary to compare the CV^2 of the total mean count and the sum of the proportions hauled out (equation 3). This shows that 68·5% of the variance is due to the telemetry data and 31·5% to the count data. Clearly, investment of resources in more telemetry data is most needed to improve precision of the abundance estimate. We found no significant differences in the behaviour of reproductive and nonreproductive females or different sized males, and therefore pooled data for each sex. Larger sample sizes would clearly increase the likelihood of detecting differences. However, we would argue against further stratification for age or body size unless there are major advances in our ability to obtain representative data on the age structure of harbour seal populations. Currently, data are available only for populations subjected to exploitation (Bigg 1969; Boulva & McLaren 1979) or mass mortality (Härkönen & Heide-Jørgensen 1990a), and probable temporal and spatial differences in the age structure (Harwood & Hall 1990; Trillmich 1993) will limit the applicability of these data to other areas. We suggest, therefore, that it is more important to increase the number of seals fitted with transmitters in order to investigate variability in activity patterns over time, as these data are also important for interpreting trends in abundance.

Previous estimates of the proportion of harbour seals that are ashore during peak haul-out times have been made using a variety of techniques. These have included behavioural observations of recognizable individuals (Sullivan 1982), telemetric studies (Pitcher & McAllister 1981; Yochem *et al.* 1987; Harvey 1987; Thompson *et al.* 1989), the bounded count method (Olesiuk *et al.* 1990) and an estimate based on changes in haul-out numbers following the death of a reported number of seals during a mass mortality (Härkönen & Heide-Jørgensen 1990b). In most cases, the average proportion of seals hauled out has been estimated to lie between 0·5 and 0·75, a range which straddles our own estimates of 0·52 for males and 0·70 for females. On the other hand, higher estimates of 0·79–0·88 were produced by Olesiuk *et al.* (1990) using the bounded count method. They noted the difference between their estimate and previous studies, but suggested that the higher values resulted from the fact that counts were only made under optimal conditions (Olesiuk *et al.* 1990). However, our bounded count estimates of the proportion of time that seals spent ashore (Table 4) were also higher than those obtained from our telemetric studies (Table 2), even when counts were made under a wider range of conditions than those accepted for Olesiuk *et al.*'s (1990) study. This resulted in a 15% underestimate of abundance compared with our estimate based on equation 1. The bounded count method may be attractive because it does not require independent data on seal activity. However, its consistent over-estimation of the proportion of time that seals spend hauled out, and the lack of a variance estimate around this figure, suggest that it provides a poor estimate of abundance.

DETECTING POPULATION TRENDS

If the mean number of seals counted at haul-out sites during a survey period is to be used as a basis for detecting trends in abundance, it is essential that these counts provide a reliable index of the number of animals in the area. To achieve this, counting methods must first be designed to minimize within-year variation due to factors such as diurnal and tidal cycles. In Orkney, because numbers at haul-out sites showed a strong peak in the late afternoon, counts made at haul-out sites were corrected to account for time of day (Thompson & Harwood 1990). Studies in other regions have also taken account of daily peaks in abundance (e.g. Olesiuk *et al.* 1990), although the timing of such peaks has differed between populations. In this study, however, radio-tagged seals showed no tendency to spend more time ashore on low tides at particular times of day (Fig. 4), even though seals from Moray Firth sites have shown diurnal trends in abundance at other times of year (Thompson *et al.* 1991). Instead, the behaviour of tagged seals was more strongly influenced by the tidal cycle. However, there was little variation in the amount of time which seals spent hauled out during the period 2 h either side of low tide (Fig. 5) and no additional corrections were required because all counts were made during this 4-h period. Other studies have also found wide variations in the importance of the tidal cycle as an influence on haul-out behaviour, and these results again highlight the extreme variability of harbour seal behaviour patterns. Consequently, if annual counts in a particular area are to provide a consistent index of abundance, it is essential that local studies assess the extent of seasonal, tidal and diurnal variations in behaviour prior to the start of a monitoring programme.

Once variation due to diurnal and tidal cycles has been controlled for, the power of these counts to detect trends in abundance depends upon the extent of the remaining within- and between-year variation in the number of seals hauled-out. We used data from our intensive work in 1993 to assess how within-year variation might affect the power of these techniques to detect trends. Several long-term studies in areas where harbour seals have increased in abundance have reported annual rates of change in the range of 0·1–0·15 (Payne & Schneider 1984; Jeffries 1986; Heide-Jørgensen & Härkönen 1988; Olesiuk *et al.* 1990), and chronic and sudden declines have occurred at even greater rates (Pitcher 1990; Dietz *et al.* 1989). Our results suggest that annual rates of change similar to those reported in the literature should be detected after 4–6 years, even where annual counts are based on only two or three counts per year. These data also indicate that it would be inefficient to make more than five or six counts per year, because increases in effort above this level make little difference to the time taken to detect trends.

While these results appear reassuring, it must be stressed that no study of pinnipeds has yet been able to assess the extent to which between-year differences in haul-out behaviour might occur, for example as a result of changes in food availability. Sample sizes from the telemetry studies currently remain too small to address this question and we have assumed that behaviour is constant between years. On the other hand, our results do suggest that haul-out behaviour differs during the two most commonly used counting periods.

The proportion of animals that were ashore during counts in the Moray Firth was similar to that estimated in previous studies in Orkney (0·71; Thompson & Harwood 1990), but our results suggest that there were differences in the sex structure of groups. In the present study, females hauled out most frequently during the June–July period (Table 2), whereas data from Orkney indicated that males hauled out more frequently during August (Thompson *et al.* 1989). Therefore, while the present study found no seasonal trend in haul-out counts (Figs 2 and 3), the sex structure of haul-out groups in the Moray Firth may have changed over this period. Consequently, counts carried out at different points in the season may vary in their sensitivity to changes in haul-out behaviour of particular groups of animals. Counts during the pupping season are biased towards females and will be most sensitive to changes in female numbers and haul-out frequency. In contrast, counts made during the moult could be more sensitive to changes in male numbers and behaviour. Future studies of the status of harbour seals may therefore benefit from conducting annual counts at two points in the annual cycle in order to obtain a more complete picture of their population dynamics.

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