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METHODS FOR ESTIMATING THE POPULATION SIZE OF COMMON SEALS, *PHOCA VITULINA*

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SUMMARY

(1) This study evaluates the use of two different survey techniques for providing an estimate of the size of the common seal population in Orkney, U.K.

(2) In August 1985, an aerial survey was made over the coast of Orkney during the seals' moult. These results were compared with those from a series of boat surveys made over a sample of this area during the pupping season, in June and July.

(3) Over twice as many seals were found hauled-out on the survey made during the moult, and it is recommended that future estimates of population size should be based on surveys made at this time of year.

(4) Time-lapse photography was used to look at changes in the number of common seals hauled-out in relation to the tidal cycle and the time of day. These data, together with data collected on the activity patterns of radio-tagged individuals, were used to provide correction factors to compensate for seals which were in the water at the time of the survey.

(5) The application of these correction factors to the survey total of 6616 produced a provisional estimate of 9331 (95% C.L.s 8147–10515) for the size of the Orkney common seal population. This estimate is discussed in relation to previous estimates of the size of both the Orkney and the total British common seal population.

INTRODUCTION

Current estimates of common seal (*Phoca vitulina* L.) population size are based on counts of the individuals present at terrestrial haul-out sites (Eberhardt, Chapman & Gilbert 1979). Throughout Great Britain and Ireland, most counts have been made from boats (e.g. Summers *et al.* 1980; Anderson 1981), while other areas have been covered using aerial photographic surveys (e.g. Vaughan 1971, 1978; Reijnders 1976; Drescher 1979; Everitt & Braham 1980) or observations from land (e.g. Newby 1973; Payne & Schneider 1984). Although the timing and methodology of surveys differ considerably between studies, they all share one problem: common seals spend an unknown proportion of their time in the water, even as pups, and these counts can therefore be regarded only as minimum population estimates. Consequently, if such counts are to be used to assess long-term trends, it is necessary either to estimate the proportion of seals which were in the water at the time of the survey, or to assume that this proportion does not vary from year to year or from site to site.

Although the results of common seal surveys are normally presented as minimum population estimates, estimates of total size have been made in a few studies. Bonner, Vaughan & Johnston (1973) used arbitrary correction factors, often based on local information from seal hunters, to produce an estimate for the common seal population in Shetland. On the Dutch Wadden Sea, it was assumed that each seal came ashore every day and that the whole population was therefore on land during the daily peak in numbers

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(Van Bemmel 1956; Reijnders 1976). However, data on individual activity patterns (Yochem *et al.* 1987; Thompson *et al.* 1989) suggest that this is unlikely and that these counts should also be considered as minimum population estimates.

In other studies, annual pup production figures have been used to model total population size (Summers & Mountford 1975; Jeffries 1986). Although this method has been used successfully for species whose pups remain ashore throughout the lactation period (e.g. grey seals *Halichoerus grypus* Fabricus: Harwood & Prime 1978; Summers 1978), the problems involved in estimating common seal pup production (Summers 1979; Slater & Markowitz 1983) make it less suitable for use with this species. Mark–recapture studies, based on tag-returns from pup hunters, have shown that the number of common seal pups produced each year is considerably larger than the maximum number seen ashore (Summers & Mountford 1975). The use of maximum pup counts in these models (Jeffries 1986) is therefore likely to underestimate population size. The development of suitable models is also restricted by the lack of data on population structure. Consequently, the most reliable data of this type (Bigg 1969), collected in western Canada, have sometimes been applied to models for different subspecies (Summers & Mountford 1975). The situation is further complicated because such data are usually only available from heavily exploited populations (e.g. Bigg 1969; Pitcher 1977; Boulva & McLaren 1979) whose age structure may be quite different from that of unexploited or lightly exploited populations. On the other hand, information on trends in population size is often required in areas where this species is now fully protected (Reijnders 1976; Riseborough *et al.* 1980; Anderson 1981). Therefore, as protection of previously exploited populations is itself likely to alter the population structure, other methods for assessing population size are clearly required.

An alternative approach is to use radio-telemetry to collect data on the proportion of time that individual seals spend ashore (Eberhardt *et al.* 1979; Pitcher & McAllister 1981; Harvey 1987; Yochem *et al.* 1987). This information can then be used both to identify the optimum survey period and, subsequently, to produce population estimates by extrapolating from counts made at haul-out sites. In Orkney, the haul-out behaviour of radio-tagged seals varied considerably during the breeding season, the time at which most common seal surveys have taken place. In contrast, their behaviour was more predictable during the moult in August (Thompson *et al.* 1989), when annual peaks have also been noted in other studies (Van Bemmel 1956; Jeffries 1986). Therefore, it seems likely that the moult may be the most suitable time to census the population (Everitt & Braham 1980; Stewart 1981).

This paper evaluates the potential of aerial surveys, made during the moult, to estimate the size of the British common seal population. Results from a trial aerial survey over Orkney, in August 1985, are compared with those from a series of boat surveys made over a sample of this area during June and July 1985. The survey results are then used with telemetric data on individual behaviour collected in a parallel study (Thompson *et al.* 1989), to produce a preliminary estimate of the size of the common seal population in Orkney.

METHODS

Aerial survey

The aerial survey covered the whole of the Orkney coastline, with the exception of areas of exposed cliff where common seals were unlikely to occur in any numbers (Fig. 1).

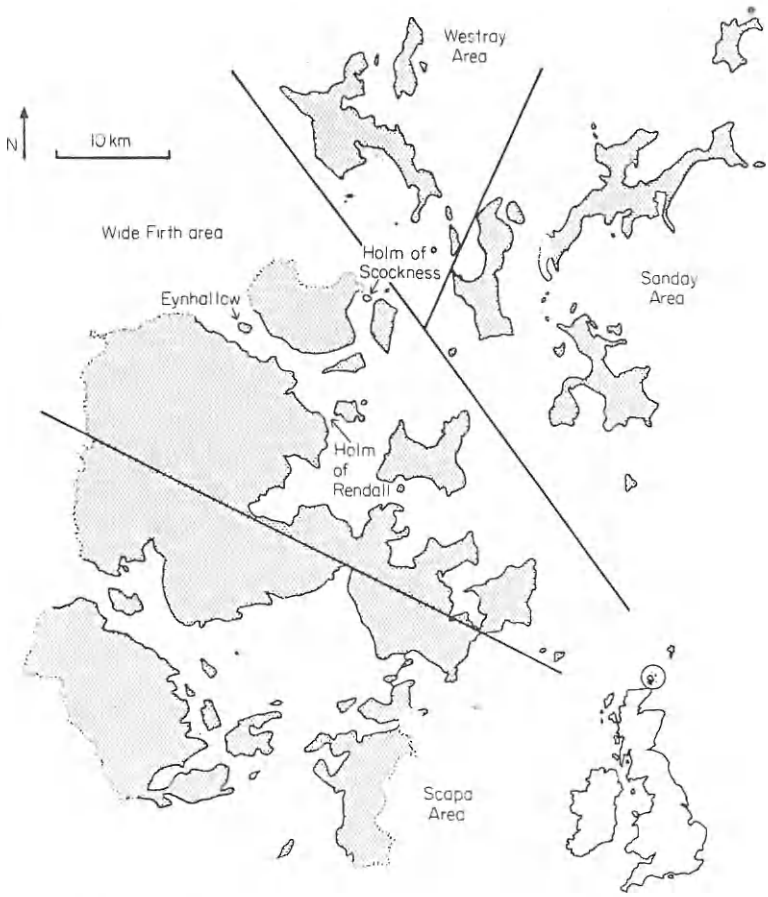

FIG. 1. A map of Orkney, showing the coastline covered during the aerial survey and the areas referred to in Table 2; · · · · · coastline not surveyed.

Surveys were flown on 5, 6 and 7 August 1985, using a Jet Ranger helicopter. The aircraft was flown systematically around the coast of each island, at a height of approximately 100 m. The size of all groups was estimated visually and recorded on 1:50 000 maps. Large groups, and some smaller groups, were photographed using a 35 mm camera with motor drive and 80–210 mm zoom lens. A variety of film types were used: both black and white negative ('XP1', Ilford Ltd, Mobberly, Cheshire) and colour transparency ('Ektachrome 100, 200 and 400', Kodak Ltd, Hemel Hempstead, HP2 7EH). Photographic counts were made directly from the negative or transparency, using a binocular microscope and light table. Each strip of film was viewed underneath an acetate sheet so that overlapping frames, and individual seals, could be marked to avoid duplicate counts.

Boat surveys

Between mid-June and the end of July, surveys were made once a week from an inflatable boat. A standard 35-km route was followed and the size and position of all haul-out groups was noted, together with the number of pups present in each group. If large haul-out groups were encountered, the boat was landed and the seals counted from the

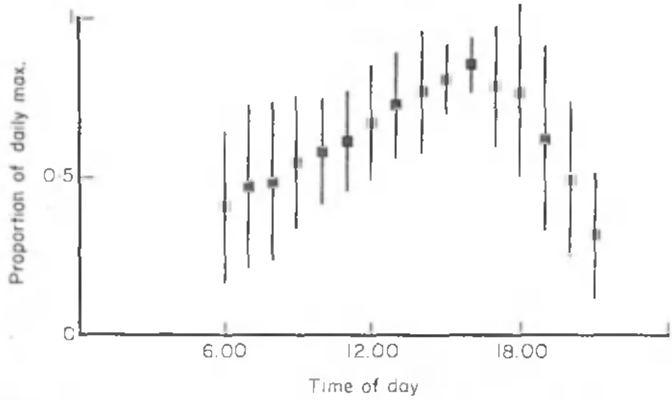

FIG. 2. Changes in the number of common seals hauled-out on the Holm of Scockness through the day. Data shown are mean proportions of the daily maximum count, with 95% confidence intervals ($n = 11$ days).

shore using a telescope. Each survey took 2–4 h to complete and, whilst avoiding high-tide periods, was made as close to midday as possible.

Time-lapse photography

In order to formulate correction factors for haul-out counts (Eberhardt *et al.* 1979), time-lapse photography was used to assess the amount of variation in the number of seals hauled-out in relation to the time of day and tide-state.

A 35 mm camera with a 300 mm lens and data back was housed in a purpose-built waterproof case. This was set in a dry stone dyke on Egilsay, overlooking a haul-out site on the Holm of Scockness (Fig. 1), and left running from 8 to 26 August 1985. The camera was programmed to take one photograph each hour and the film ('Ektachrome 100', Kodak Ltd) was changed every 24–36 h. Counts were made from the transparencies using a binocular microscope and a light table.

Data were analysed by finding the maximum daily count, and considering the numbers present in other frames taken that day as a proportion of the daily maximum (Stewart 1984). This reduces problems caused by the fact that the camera's field of view included a variable, and unknown, proportion of the haul-out group, but assumes that the behaviour of this sample of animals was representative of the whole group.

RESULTS

Time-lapse photography

Photographs could be analysed only when a complete day's data were available, as the time of the daily maximum count had to be identified. This was possible on 11 days, when the maximum number of seals in the field of view ranged from 48 to 158. There was a marked diurnal trend in the number of seals present at this site, with the peak at around 16.00 h (Fig. 2). Analysis of the changes in numbers in relation to the tidal cycle showed a tendency for the proportion of the daily maximum to be lower on an ebb tide (Mann–Whitney $U(2)$ 83,83 = 4763, $P < 0{\cdot}001$). However, when the effect of the time of day was also taken into account, it appeared that this relationship was significant only between 06.00 and 09.00 h (Mann–Whitney $U(2)$ 20,18 = 345, $P < 0{\cdot}001$). During the rest of the day

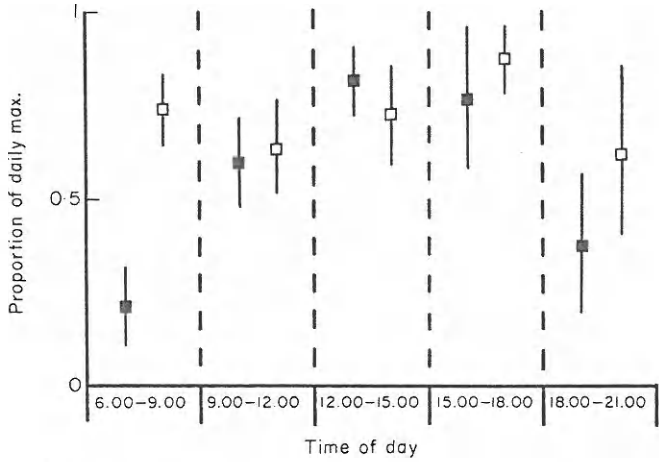

FIG. 3. Comparison between the number of seals hauled-out on rising (■) and falling (□) tides, for different periods of the day. Data are mean proportions of the daily maximum, with 95% confidence intervals ($n = 11$ days).

the stage of the tide had no significant effect, although there was a slight, but not significant, trend towards a tidal relationship again in the evening (Fig. 3).

The aerial counts all took place between 08.30 and 18.30 h and the effect of the tidal state on the number of seals hauled-out was therefore ignored. Correction factors were, however, produced to allow for variation in the time of day at which counts were made at different sites. Each count from the time-lapse photographs was divided by the maximum count on that day, these values were then used to calculate the mean proportion of animals hauled-out in each hour of the day (Fig. 2). The values were then rescaled so that the mean value was 1·0 for the period 16.00–16.59 h when, on average, the highest proportion of animals was hauled out (Table 1).

TABLE 1. Data used to correct aerial survey counts, to allow for variation due to the time of day at which each site was surveyed

Time of day	Value	*n*	S.E.
08.00–08.59	0·62	10	0·113
09.00–09.59	0·69	11	0·097
10.00–10.59	0·72	10	0·075
11.00–11.59	0·75	11	0·073
12.00–12.59	0·82	10	0·082
13.00–13.59	0·87	11	0·076
14.00–14.59	0·92	10	0·087
15.00–15.59	0·95	11	0·050
16.00–16.59	1·00	11	0·038
17.00–17.59	0·93	11	0·085
18.00–18.59	0·92	10	0·122

TABLE 2. The total number of common seals counted in each area of Orkney (see Fig. 1) during the 1985 aerial survey. Data on the number of adults seen on previous SMRU boat counts (from McConnell 1985) are included for comparison

Area	Boat survey 1972	Boat survey 1979	Aerial survey (1985)
Scapa Area	635	907	2196
Wide Firth Area	659	963	2132
Sanday Area	719	646	1685
Westray Area	133	137	603
Orkney Total	2146	2653	6616

Aerial survey

The aerial survey of the Orkney coastline was completed in approximately 12 h flying time, which included time for repeat counts at three sites.

Black and white film proved unsuitable for distinguishing common seals on rocky shores. All colour transparency films produced good results in good light conditions, but photographs taken with 100 and 200 ASA film in poor light were sometimes too blurred for analysis.

The total number of seals counted on the aerial survey was 6616, with a count of 466 for the sample area covered by the boat surveys. Total counts for each area of Orkney (as defined in Fig. 1) were consistently higher than the minimum estimates made during previous Sea Mammal Research Unit boat surveys in 1972 and 1979 (Table 2).

At twenty-nine sites, both photographic and visual estimates of group size were made (Table 3). Overall, the visual estimates for these sites accounted for only 73% of the total number obtained from the photographic count. Visual estimates and photographic counts of groups of fewer than 100 (on the photographic count) were closer, though visual counts still accounted for only 89% of the photographic count. Errors for these groups were very variable, largely depending on whether seals remained ashore long enough to be counted, or whether an estimate had to be made. Visual estimates of groups larger than 100 were normally gross underestimates and accounted for only 67% of the photographic count. In all cases where photographs were of sufficient quality, the photographic count was considered the more reliable.

Repeat photographic counts were made on different days at three sites: Eynhallow (three counts), Holm of Scockness (three counts) and the Holm of Rendall (two counts). Photographs were too blurred for analysis on one day at Eynhallow and Holm of Scockness, leaving two counts at each of the three sites (Table 4). In producing the total count for Orkney, the first count for each of these three sites was used. This avoided duplicate counts due to movements between local sites, as the surrounding areas were surveyed at the same time. The aerial counts on Eynhallow agreed well with regular ground counts (Fig. 4) which were made in the course of other fieldwork throughout July, August and September 1985 (Thompson & Rothery 1987; Thompson 1989). The ground counts suggest that numbers at this site remain high throughout August.

Although 95% confidence intervals for the repeat counts' corrected totals overlapped at all three sites (Table 4), corrected counts made early in the morning were consistently

TABLE 3. Comparison of visual estimates and photographic counts of common seal groups at twenty-seven sites surveyed during the 1985 serial survey

Site name	Visual estimate	Photographic count
Burray	130	125
Widewall Bay	55	77
Switha	450	604
N. Eynhallow	250	497
S. Eynhallow	75	135
E. Wyre	80	85
Sweyn Holm	100	100
Geostane	40–50	51
Galt Skerry	60	86
Helliar Holm	70	67
Holm of Rendall	100	187
Grimbister	30–50	45
Quanterness	55	52
Toab Skerry	53–60	81
Sebay Skerries	80	105
Roanna Bay	50	51
Auskerry	200	246
Lamb Ness	93	97
Mill Bay	67	79
The Stuin	51	51
Holm of Elsness	65	67
Bay of Sowerdie	40	33
Tor Sker	18	23
Lamaness Firth	55	68
Lamaness Skerry	25	23
Holms of Ire	180	286
N. Ronaldsay	130	235
Wasbist	75	125
Holm of Papa	150	187

TABLE 4. Comparison of repeat counts, together with values, corrected for time of day, for Eynhallow, Holm of Scockness and Holm of Rendall

Site	Date (1985)	Time (h)	Original count	Corrected count (95% C.I.)
Eynhallow	5 Aug	15.01	632	665 (597–733)
Eynhallow	7 Aug	09.03	665	964 (698–1230)
Holm of Scockness	5 Aug	15.15	318	335 (301–369)
Holm of Scockness	6 Aug	09.47	299	433 (313–552)
Holm of Rendall	5 Aug	14.50	187	203 (165–241)
Holm of Rendall	6 Aug	09.19	172	249 (180–317)

higher than those made in the afternoon, particularly when compared with ground counts for Eynhallow (Fig. 4). However, given the small sample sizes involved, it is not possible to assess whether these differences are statistically significant.

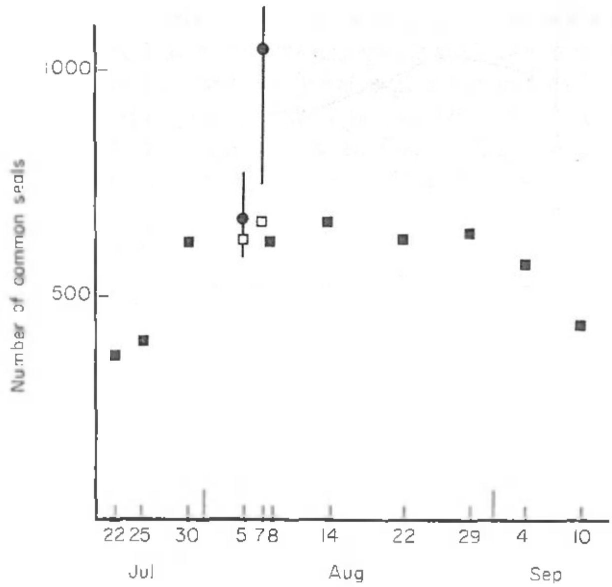

FIG. 4. Maximum daily counts of adult common seals hauled-out on Eynhallow, 1985: (■) ground counts; (□) aerial counts; (●) corrected aerial counts with 95% confidence intervals.

Boat surveys and pup counts

The total number of adults seen on each boat survey was always lower than that observed during the aerial survey (Table 5). Pupping appeared to be highly synchronous. On 8 June, bad weather prevented a full survey. Nevertheless, although the majority of the standard route was covered, only two pups were seen. By the following week, pup numbers had risen to seventy-nine. New-born pups were seen only rarely after the third week in June and the total number of pups seen on each survey declined steadily from the end of June (Fig 5).

TABLE 5. The total number of adult common seals seen hauled-out during each survey made over the sample study area around Rousay, Egilsay and Wyre (Fig. 2)

Date (1985)	Survey method	Number of adults hauled-out
16 Jun	Boat	256
24 Jun	Boat	179
30 Jun	Boat	194
7 Jul	Boat	168
14 Jul	Boat	184
22 Jul	Boat	202
28 Jul	Boat	335
5 Aug	Air	466

surveys (Table 2). Whilst there may have been increases in population size since the last survey in 1979, comparison of survey techniques during 1985, over a sample area, suggests that much of the increase can be explained by a change in the timing of the survey; in 1985, numbers present in the sample area during the period covered by the 1979 survey (5–21 July) were less than half the total counted in the first week of August (Table 5). These results confirm previous suggestions (e.g. Everitt & Braham 1980; Stewart 1981) that surveys made during the moult period produce high minimum population estimates for common seals. Although regular counts on Eynhallow showed that numbers remained high throughout August (Fig. 4), telemetric data on behaviour, needed for total population estimates, are available only from the first 2 weeks of August because the radio-transmitters fell off as the moult progressed. Therefore, the first 2 weeks of August would appear to be the most suitable period for surveys of common seals on rocky shore coasts around Britain. In other areas, however, the timing of the annual cycle may vary considerably (Bigg 1973, 1981) and appropriate dates for surveys during the moult period will also differ.

As well as providing higher minimum population estimates, surveys made during the moult have two other important advantages. Increases in the number of seals ashore at this time appear to be due to changes in male behaviour, directly associated with the moult (Thompson *et al.* 1989). The increased predictability of their behaviour at this time makes it more feasible to extrapolate from haul-out counts to produce total population estimates. Furthermore, because the change in activity appears to be the result of physiological constraints, which each individual undergoes annually, haul-out frequency over this period is likely to remain constant between years. In contrast, haul-out frequency at other times of year may vary in relation to factors such as food availability or breeding success; consequently, year-to-year variation in these factors could complicate the assessment of population trends. Therefore, by making surveys during the moult, between-year variation in behaviour should be minimized and year-to-year changes in the number of seals ashore are more likely to reflect real changes in population size.

To reduce the effect of within-year variation, counts were standardized to allow for variation in the number of seals ashore throughout the day. The diurnal trend in numbers seen on the Holm of Scockness (Fig. 2) was similar to that found in other studies (e.g. Allen, Ainley & Page 1980; Stewart 1984) and it seemed reasonable to use these data to formulate provisional correction factors for counts (Table 1). However, use of these correction factors with the repeat counts at three sites (Table 4), and comparison with ground counts on Eynhallow (Fig. 4), suggest that they may overcompensate for counts made during the early morning. Further work is needed to improve these correction factors and assess whether similar trends are found at other sites, particularly as group structure has been found to differ between sites (Knutson 1977; Slater & Markowitz 1983; Thompson 1989). More intensive studies of this kind should also reduce the confidence intervals on these correction factors.

There was no evidence that the number of seals hauled-out on the Holm of Scockness was affected by the tidal cycle, except during the early morning and possibly also the late evening (Fig. 3). Consequently, no additional corrections were made for tidal state. It may be wise in future to survey in the middle of the day to minimize any effect of tide but trends at other sites should also be assessed to verify that this pattern is widespread. In this respect, the survey methods discussed in this section apply only to areas where haul-out sites are available throughout the tide-cycle: Orkney, Shetland, the Hebrides, and the west coast of Scotland. In estuarine areas on the east side of Britain, inter-tidal sandbanks are generally used as haul-out sites and animals are rarely ashore over the high tide period (Vaughan 1978; McConnell *et al.* 1985). Different survey techniques may therefore be required in these areas.

Although the moult period may be the most appropriate time at which to estimate population size in rocky shore areas, estimates of pup production cannot be made at the same time, as weaned pups cannot easily be distinguished from older animals (Reijnders 1978; Thompson & Rothery 1987). In the past, common seal surveys in Britain attempted to combine estimates of pup production and population size and took place during June or July (Summers 1979; NERC 1985). During this study, however, regular counts in a sample area showed that the number of pups ashore decreased steadily after a peak in mid-June (Fig. 5). Previous boat surveys, over areas such as Orkney or Shetland, took 2–3 weeks to complete. Consequently, within-year variation in the number of pups ashore is likely to have been too great to allow useful comparison either between years, or between areas, and probably explains the wide variation in pup numbers noted in different surveys (e.g. Anderson 1981; Warner 1983). Reijnders (1978) also noted decreases in the number of pups ashore throughout the lactation period, which he attributed to pup mortality. In contrast, pup numbers on Sable Island, Nova Scotia, remained high until well after pups were weaned (Boulva & McLaren 1979). Although mortality will have contributed to the observed decline in this study, changes in haul-out behaviour are also likely to have had an important effect. Very few marked pups were seen in late July and August, but numbers increased slightly in September (P. M. Thompson, unpubl. data). How much time pups spend ashore during the post-weaning period may therefore vary between populations, in relation to factors such as local changes in food availability or the relative abundance of aquatic and terrestrial predators.

If estimates of pup production are needed, separate surveys must therefore be made during June, specifically to count pups. Ideally, these surveys should involve a series of counts, within a single year, so that the peak in pup numbers can be identified using methods similar to those used for grey seal population surveys (Ward, Thompson & Hiby 1988). Peak annual pup counts obtained in this way would provide a more useful index of pup production than previous estimates from boat surveys, but further research would be needed before they could be related to annual pup production. In particular, changes in the behaviour of adult females and their pups would need to be monitored throughout the lactation period, and attempts made to estimate pup mortality. Telemetric techniques would allow data to be collected on haul-out behaviour, but estimating common seal pup mortality presents enormous problems. Instead, effort should perhaps be concentrated on identifying the time of peak pup numbers in order to produce a more reliable index of pup production.

Survey methodology

Common seal surveys during the moult period involve counting groups of several hundred individuals, while pup surveys would need to cover large areas during the relatively short peak in numbers. Consequently, the only practical way to make such surveys is from the air.

Comparison of photographic counts and visual estimates, made from the air, suggests that the precision of counts can be improved greatly by photographing groups of seals, and that the use of high speed colour film allows common seals to be distinguished from a rocky shore background. Although made on different days, aerial and ground counts of the number of seals present on Eynhallow were of a similar size (Fig. 4). Ground counts of common seals cannot be considered 'truth' counts as, for example, when grey seal pups can be marked, counted, and compared with aerial counts (Wyile & Thompson (1985), but the similarity between these figures is nonetheless reassuring.

Although photography may improve the precision of counts, there remains the problem of assessing the accuracy with which groups of seals are detected. Groups of common seals are probably easier to find than some terrestrial mammals (e.g. Caughley 1974; Caughley, Sinclair & Scott Kemmis 1976) or ice-breeding seals (e.g. Eberhardt *et al.* 1979; Helle 1980) because of the lack of cover and the limited inter-tidal area which is available for hauling-out. However, a substantial bias could be generated if even a few large aggregations were missed. The risk of this was minimized by using a helicopter which was manoevrable enough to follow the coastline closely and slowly. As a result, we suggest that only solitary individuals and small groups were missed, but further work is required to assess the extent of this problem. Common seals appear to use the same haul-out site consistently from year to year (Anderson 1981; Thompson 1989) so that, once the major sites in an area have been identified, future surveys will be less likely to miss large aggregations. However, it would be unwise to design surveys on the assumption that seals will only be found at traditional sites. The absence of seals from such sites may, however, be a useful indicator of recent disturbance, which can have a dramatic effect on the number of seals ashore (Allen *et al.* 1984). The presence of fishing boats or large groups of seals in the water may also allow some assessment of the degree of disturbance. Ideally, however, repeat counts should be made over each area, on different days, so that these effects can be minimized.

Population estimates

In order to produce a total population estimate from the corrected survey results, a number of basic assumptions had to be made. This first estimate is crude, and the methods used in its production should be modified with further research. However, as long as survey techniques are standardized, the improved methods can then be used to re-evaluate old survey data.

In particular, data are needed on the behaviour of females and sub-adult common seals during August. However, obtaining such data would require a different method for attaching radio-tags because they have previously been glued to the hair of seals (Thompson *et al.* 1989) and females and juveniles moult before adult males (Thompson & Rothery 1987). The diurnal haul-out behaviour of four radio-tagged males followed during August appeared highly predictable (Thompson *et al.* 1989), but a larger sample of animals is needed to confirm whether or not all males do come ashore each day.

Casual observations supported the assumption that a negligible number of pups hauled-out during August, but this could be tested in the future by carrying out a large-scale pup-marking or radio-tracking programme.

It was assumed that the sex ratio of this population was 1 : 1. Varying the sex ratio over the range of values found in the literature (Bishop 1968; Bigg 1969; Pitcher 1977; Boulva & McLaren 1979) had little effect on the total population estimate. Therefore, other sources of error would need to be reduced considerably before it became important to collect data on the sex ratio of this population.

The variance in the estimate of population size has two components (see Appendix): one due to variability in $\hat{c}_i$ and the other due to variability in $\hat{h}$. The variance could therefore be reduced by improving the estimates of these parameters. However, there appears to be no particular advantage in concentrating effort on particular c_i or h values.

Two-thirds of the seals were counted between 14.00 and 17.59 h and for this period the estimates of c_t and their variances are broadly similar to those for h. Thus, a 10% reduction in the variance of $\hat{c}_t$ would have a similar effect on the variance of N as a 10% reduction in the variance of $\hat{h}$.

Implications for the size of the British population

The mean total population estimate of 9331 was approximately three times the size of previous estimates for the Orkney common seal population (Vaughan 1975; McConnell 1985), showing that the number of common seals seen ashore at any one time represents a small proportion of the total population.

Current estimates of the British common seal population are based almost entirely on estimates from maximum haul-out counts (NERC 1985), the only area with a reliable total population estimate being the Wash (Summers & Mountford 1975). Consequently, the British population estimate of 21 600 (NERC 1985) is likely to be a gross underestimate. Haul-out behaviour during the pupping period is very variable (Thompson *et al.* 1989). Furthermore, several areas of Britain have not been surveyed for over 10 years (NERC 1985). Although the results of earlier surveys made during the pupping season must therefore be treated with caution, they can give some indication of the degree of underestimation involved. If we assume that the size of the population in other rocky shore habitats was underestimated to a similar extent to that in Orkney, the total population in Orkney, Shetland, the Western Isles and the west coast of Scotland is more likely to be in the region of 38–39 000 than the current estimate of 14 000. If this is so, the total British population, prior to the 1988 morbilli virus epizootic, may have been around 46–47 000. Clearly, surveys of these other areas, using methods comparable with those used in Orkney in 1985, are required. Once such a baseline has been established for the British population, it will then be possible to monitor population trends over future years.

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APPENDIX

Estimating the variance of N

Equation (1) can be rewritten as:

$$N = \sum_{i=1}^{L} \sum_{t=1}^{K} n_{it}/C_t$$

where $C_t = c_t h$, L = number of sites surveyed, K = number of time intervals.

Then $$\mathrm{var}(C_t) = h^2\mathrm{var}(c_t) + c_t^2\mathrm{var}(h) + \mathrm{var}(c_t),\mathrm{var}(h)$$

and $$\mathrm{var}(N) = \sum_{i=1}^{L} \sum_{t=1}^{K} n_{it}^2 C_t^{-4}\mathrm{var}(C_t)$$