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Mark-resight estimates of seasonal variation in harbor seal abundance and site fidelity

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Abstract Monitoring trends in abundance of pinnipeds typically involves counting seals at terrestrial haul-out sites during the breeding season. Counts of seals made at other times of the year are typically lower; however, it is often unknown whether this is because fewer animals are present or whether lower counts simply reflect a reduction in haul-out probability. Here we illustrate how photo-identification data from an individual-based study of harbor seals (*Phoca vitulina*) can be used to estimate seasonal variation in abundance and site fidelity. Monthly data collected over a two-year period were analyzed using a mark-recapture mark-resight model accounting for individuals transitioning between observable and unobservable states. Levels of site fidelity were high throughout the year and abundance estimates showed no seasonal pattern. This suggests that individual seals used haul-out sites to the same extent throughout the year, and that peaks in counts during the breeding season are a result of seasonal changes in haul-out probability. The results of this study have implications for understanding population sub-structuring, gene flow and disease spread.

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Introduction

Monitoring trends in population abundance plays an important role in conservation efforts (Yoccoz et al. 2001; Taylor et al. 2007). For pinniped species, this typically involves counting seals at their terrestrial haul-out sites during the breeding season or molt when seals are most likely to be observed out of the water (Braham et al. 1980; Bowen et al. 2003; Jeffries et al. 2003; Baker and Johanos 2004). Less effort is usually applied at other times of the year but, where information exists, counts are generally lower (Sullivan 1980; Hindell and Burton 1988; Thompson et al. 1996, 1997; Salwicka and Sierakowski 1998). However, it is often unknown whether fewer individuals are present at these other times of year, or whether temporal variation in counts reflects a change in haul-out probability. This can make it difficult for conservation managers to assess the importance of different haul-out sites outside the breeding season; constraining management decisions where these are based on count data alone.

Understanding levels of site fidelity can provide crucial information on population sub-structuring and connectivity, which are important metrics for effective conservation management and understanding disease spread. Many colonial species, both sedentary and migratory (Blancher and Robertson 1985; Cooch et al. 1993; Ganter and Cooke 1998; Pomeroy et al. 2000; Matthiopoulos et al. 2005; Gamble et al. 2007), exhibit site fidelity. However, in the literature this concept is generally described in relation to between or within-year breeding season site fidelity, whereas less is known about the function and use of these sites at other times of the year. While less relevant for migratory species that move to wintering grounds, many pinnipeds rely on terrestrial sites for resting throughout the year. Both genetic and re-sighting studies of pinnipeds

have shown evidence of site fidelity or philopatry to certain sites or areas (Kretzmann et al. 1997; Pomeroy et al. 2000; Fabiani et al. 2006; Hoffman et al. 2006; Campbell et al. 2008). These studies also indicate that, although a population may appear continuous, sub-structuring and genetic differentiation may still occur, which may have implications for the efficacy of management if this has not been identified (Hoffman et al. 2006).

In Europe, conservation measures to protect European harbor seal (*Phoca vitulina*) populations have been developed in response to the EU Habitats and Species Directive (Council Directive 92/43/EEC). These include the designation of protected areas (e.g., Special Areas of Conservation), primarily haul-out sites and surrounding waters, to conserve their vital habitat (Baxter 2001). Information from the monitoring programs associated with these designations can inform understanding of various aspects of their population dynamics, including levels of population sub-structuring and connectivity (e.g., Goodman 1998), disease spread (e.g., Härkönen et al. 2006), and the impacts of anthropogenic stressors (e.g., Inger et al. 2009). As in many other groups of animals (e.g., Hestbeck et al. 1991), a major constraint of such data is the lack of the ability to follow individuals over time, limiting inferences about the extent to which changes in abundance at different sites are driven by either movement or distinct local dynamics. Marking and telemetry studies can be used to explore this issue (Härkönen and Harding 2001; Sharples et al. 2009; Hamilton et al. 2014). However, these are typically constrained by a small sample of individuals, low re-sighting rates of visual tags, and the relatively short time period over which telemetry devices can be attached to seals. Critically, most telemetry devices are glued on to the seals' fur and are therefore lost during the molt if not sooner, preventing year-round data collection. Furthermore, repeat captures of individual harbor seals to attach telemetry devices or read tags cannot be achieved with any certainty because of their more aquatic breeding habits. Alternatively, harbor seals have natural and distinctive individual markings, which offer a unique and low cost opportunity to follow individuals over time using photo-identification techniques (Thompson and Wheeler 2008; Hastings et al. 2012; Cordes and Thompson 2013, 2014). Due to the inaccessibility of most haul-out sites, only a few areas in the world have proved suitable for this type of data collection (Hastings et al. 2008, 2012; Mackey et al. 2008; Cunningham 2009; Cordes and Thompson 2013, 2014). Nevertheless, new monitoring techniques may make photo-identification studies of harbor seals and other pinnipeds more manageable. Here, we aim to estimate seasonal variation in mean re-sighting rate, site fidelity, and abundance of harbor seals using photo-identification and mark-recapture modeling techniques.

Methods

Photo-identification surveys

The study was carried out in NE Scotland, within the Loch Fleet National Nature Reserve (Thompson and Wheeler 2008; Cordes et al. 2011; Cordes and Thompson 2013, 2014). At low tide, harbor seals haul-out on inter-tidal sandbanks approximately 130 m from the shore, allowing individual seals to be recognized by photographic identification (see Cordes and Thompson 2013, 2014). In 2008 and 2009, daily photo-identification surveys were carried out during the breeding seasons (June–July), while two to six (mean = 3.2 ± 0.3 SE) surveys were conducted each month outside the breeding season (August–May). In order to balance the number of surveys per month two surveys closest in time were chosen for this analysis. Individual seals were recognized from photographs of the head and neck region using a digital camera (Nikon Coolpix 5100) and a telescope ($20 - 60 \times 80$ mm Swarowski HD-ATS 80) (as described in Cordes and Thompson 2013, 2014). Photographs of individual seals were matched by eye to a catalogue containing left and right headshots of all seals that had been photographed since the beginning of the study in 2006 by the same experienced observer (LSC). Counts of seals on the sandbanks were carried out on the same days as photo-identification surveys.

Statistical analysis

Estimating seasonal variation in site fidelity, mean re-sighting rate and abundance

The mark-resight model developed by McClintock and White (2009) integrates sightings of known marked individuals that transition between observable (individuals present in the study area) and unobservable (individuals outside the study area or in the water) states, as well as the number of "unmarked" and "marked but unidentified" individuals. In this study, a large proportion of the unmarked individuals were juveniles, which were difficult to identify consistently due to their coat characteristics, but also included light pelage adults. "Marked but unidentified" individuals included animals that occasionally could not be identified because of their position on the sandbank and those that were molting between late summer and early autumn. Since the number of marked individuals in the population at any one time was not known, the poisson-log normal mark-resight model developed by McClintock et al. (2009) was used to estimate the monthly abundance at our study site. This situation is common when individuals are recognized by natural markings rather than caught for tagging prior to sampling. Seals could also be

photographed more than once within secondary occasions (i.e., sampling with replacement). This model assumed closure within primary occasions (month), whereas periods between primary occasions were open to births, deaths, and movement. For this reason we chose secondary occasions within months that were closest in time [mean number of days between secondary occasions was 2.96 ($\pm$ 0.64 SE)]. Furthermore, as seals were identified by markings in their pelage, it was assumed that no marks were lost over time. The number of "marked and identified", "unmarked", and "marked but unidentified" individuals per month ranged from 19 to 63, 0 to 17 and 0 to 6, respectively. A total of 129 individuals were included in the analysis. Sex was not included as a covariate as it was not possible to consistently determine the sex of the "marked but unidentified" and "unmarked" individuals.

Models were built with constant and time variation on mean re-sighting rate (α), individual heterogeneity (σ), and transition probabilities (γ' and γ''). We allowed for time variation on the number of unmarked individuals in the population during primary periods (U), while apparent survival (ϕ) was held constant, as this was not part of the objectives of the study (see Table 1). In addition we tested for a seasonal pattern in α by grouping months into periods whereby October–February contained the winter period, March–April and August–September incorporated the periods pre and post breeding season, while May–July encompassed the breeding season. We ran two models which included this seasonal pattern in mean re-sighting rate: one where the seasonal pattern was the same between years, α(season), and another that allow seasonal patterns to be different between the 2 years, α(season + year). We use the transition probability from observable to observable as a proxy for site fidelity. This probability was obtained by subtraction ($1 - \gamma_j''$). For each primary occasion (month) the derived parameters population size (N) and the overall

mean re-sighting rate (λ) were estimated. We assume that the sighting probabilities of the sample of marked individuals are representative of the entire population. Furthermore, we assume that the time interval between secondary occasions is short enough to satisfy the assumption of closure (see Neal et al. 1993). The statistical analysis was carried out in MARK (White and Burnham 1999), and models were assessed based on AIC$_c$ scores and AIC$_c$ weight (Burnham and Anderson 1998).

Results

The mark-resight analysis revealed one top model $\{\alpha(t)\ \sigma(.)\ U(t)\ \phi(.)\ \gamma''(.)\ \gamma'(.)\}$, which accounted for 0.999 of the AIC$_c$ weight, and was 14 AIC$_c$ scores better than the second top model (Table 2). Overall mean re-sighting rates (λ) showed a distinct seasonal pattern peaking around June–July in both years (Fig. 1). The model showed no support for temporal variation in transition probabilities (γ'' and γ'), and site fidelity ($1 - \gamma''$) was estimated at 0.89 [95 % CI (0.85, 0.93)]. The constant individual heterogeneity level (σ_j^2; log scale) was estimated at 0.15 [95 % CI (0.01, 1.66)]. Abundance showed no seasonal variation and averaged around 90 seals per month (Fig. 2). Monthly mean counts of seals during 2008 and 2009 were variable, but generally higher during the summer months (Fig. 3).

Discussion

Here we have shown that although monthly counts of seals exhibit a seasonal peak during the breeding season, this did not equate to more individuals being present during this period, as the estimated abundance of seals remained fairly constant across months in both years. Rather this seasonal

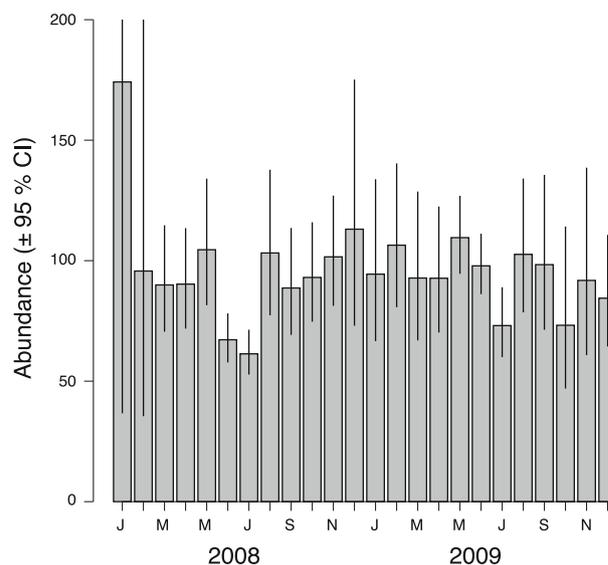**Table 1** Mark-resight model parameters, derived parameters, and descriptions

	Description
Parameters	
U_j	Number of unmarked individuals in the population during primary interval j
α_j	Intercept for mean re-sighting rate (log scale) during primary interval j. When there is no individual heterogeneity ($\sigma_j^2 = 0$) α_j can be interpreted as the overall mean resighting rate for the entire population (once back-transformed from the log scale)
σ_j^2	Individual heterogeneity level (log) during primary interval j
ϕ_j	Apparent survival between primary intervals j and $j + 1$
γ_j''	Probability of transitioning from an observable state at time j to an unobservable state at time $j + 1$. Equivalent to transition probability Ψ^{OU} of Kendall and Nichols (2002)
γ_j'	Probability of remaining at an unobservable state at time $j + 1$ when at an unobservable state at time j. Equivalent to $1 - \Psi^{UO}$ of Kendall and Nichols (2002)
Derived parameters	
λ_j	Overall mean re-sighting rate for primary occasion j
N_j	Total population size during primary occasion j ($U_j + n_j$), where n_j is the number of marked individuals in the population

Table 2 Mark-resight models with associated ΔAIC_c scores, weights, number of parameters, and deviance

	ΔAIC_c	AIC_c weight	Number of parameters	Deviance
$\alpha(t)\ \sigma(.)\ U(t)\ \phi(.)\ \gamma''(.)\ \gamma'(.)$	0.00	0.999	52	3980.7
$\alpha(t)\ \sigma(.)\ U(t)\ \phi(.)\ \gamma''(t)\ \gamma'(.)$	14.11	0.001	74	3943.6
$\alpha(t)\ \sigma(.)\ U(t)\ \phi(.)\ \gamma''(.)\ \gamma'(t)$	16.24	0.000	73	3948.1
$\alpha(\text{season})\ \sigma(.)\ U(t)\ \phi(.)\ \gamma''(.)\ \gamma'(.)$	22.82	0.000	30	4052.1
$\alpha(\text{season} + \text{year})\ \sigma(.)\ U(t)\ \phi(.)\ \gamma''(.)\ \gamma'(.)$	23.69	0.000	33	4046.5
$\alpha(t)\ \sigma(.)\ U(t)\ \phi(.)\ \gamma''(t)\ \gamma'(t)$	34.86	0.000	95	3912.6
$\alpha(t)\ \sigma(t)\ U(t)\ \phi(.)\ \gamma''(.)\ \gamma'(.)$	37.71	0.000	75	3964.8
$\alpha(.)\ \sigma(.)\ U(t)\ \phi(.)\ \gamma''(.)\ \gamma'(.)$	151.53	0.000	29	4182.9
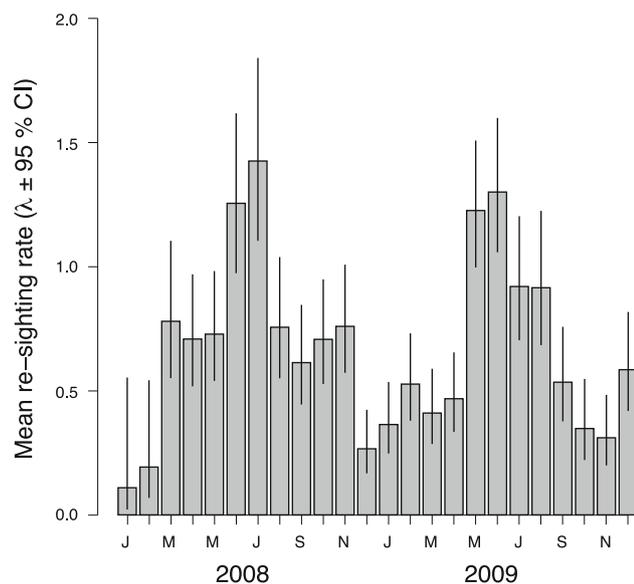
Fig. 1 Monthly variation in derived estimates of overall mean re-sighting rate (λ) with 95 % confidence limits throughout 2008 and 2009

Fig. 2 Monthly variation in derived estimates of abundance (N) with 95 % confidence limits throughout 2008 and 2009 (for clarity the y-axis was restricted to 200, however, the variability around the estimates for the first two months in 2008 was much greater with upper confidence limits reaching 827 and 258, respectively)

peak in counts likely reflects a temporal change in overall mean re-sighting rate, which also peaked during the breeding seasons. Female harbor seals spend more time hauled out during the breeding season nursing their pup before commencing foraging trips in July as pups are being weaned (Thompson et al. 1989, 1994), and males may be more likely to rest on sandbanks prior to the mating season in July–August during which they will spend more time in the water seeking mating opportunities (Van Parijs et al. 1997). Furthermore, the analysis did not support temporal variation in transition probabilities (γ'' and γ'), which we used as a proxy for site fidelity, suggesting that site fidelity ($1 - \gamma''$) remained at a constant and high level throughout the year. At our study site individual seals have also shown high levels of between-year site fidelity (between-year recapture probability = 0.97 [95 % CI (0.92, 0.99)]; Cordes and Thompson 2014) indicating that breeding groups may be relatively discrete, and highlighting the need for site-specific management.

Other photo-identification work found more monthly variation in abundance, however sample size was relatively small, recapture rates low and the study did not account for unmarked and marked but unidentified individuals (Cunningham 2009). Most telemetry studies involve gluing tags to the fur, meaning that data are unavailable around the molt. Consequently, these studies generally do not represent the same individuals throughout the year, and sample size is also limited by the number of individuals caught and the costs of tags (Thompson et al. 1989; Cunningham et al. 2009; Sharples et al. 2009). Nevertheless, similar to our study Sharples et al. (2009) found abundance estimates to be consistent across nearly 2 years for months outside the molting period, while count data varied substantially. There was some evidence of temporal variation in the proportion of time spent hauled out but again the summer breeding season and molt had very little if any coverage (Cunningham et al. 2009; Sharples et al. 2009). Thompson
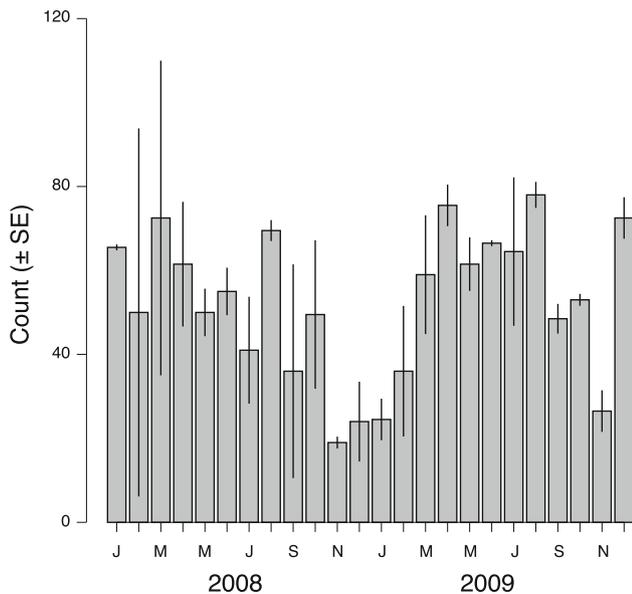
Fig. 3 Monthly mean haul-out counts with standard errors throughout 2008 and 2009

et al. (1989) found higher haul-out probabilities during the breeding season and early molt whereas individuals appeared to spend more time offshore during the winter, even though individuals continued to utilize local haul-out sites within the study area.

Previous understanding of long-term patterns of site fidelity in harbor seals has largely been dependent upon the results of a single intensive branding study in Swedish waters. There, intensive long-term and large-scale re-sighting effort revealed marked spatial segregation of harbor seals by sex and age (Härkönen and Harding 2001). Furthermore, that study suggested that, depending on context, single colonies could act as either isolated sub-populations or as part of a network of colonies. For example, low levels of dispersal could be enough to rapidly spread disease among colonies, but may be insufficient to prevent sub-structuring if females show natal site fidelity and dispersal primarily results from male movements. Our study highlights the value of photo-identification studies for identifying levels of site fidelity, opening up new opportunities for understanding population dynamics and applying appropriate conservation measures. Furthermore, our study highlights how this modelling framework can be applied to a wide range of species, which show seasonal changes in site use and where individuals cannot always be accurately identified (fur dye, ringing, tagging, or other natural markings). With recent advances in remote monitoring techniques (e.g., high definition surveys, drones; Anderson and Gaston 2013) multi-site photo-identification studies of harbor seals and other pinnipeds may now be more practicable (including ice-dependent species in remote locations), permitting the investigation of between

site movements and population sub-structuring that could provide new insights into their demography as well as potential gene flow and disease transmission.

References

Anderson K, Gaston KJ (2013) Lightweight unmanned aerial vehicles will revolutionize spatial ecology. Front Ecol Environ 11:138–146

Baker JD, Johanos TC (2004) Abundance of the Hawaiian monk seal in the main Hawaiian island. Biol Conserv 116:103–110

Baxter JM (2001) Establishing management schemes on marine special areas of conservation in Scotland. Aquat Conserv 11:261–265

Blancher PJ, Robertson RJ (1985) Site consistency in kingbird breeding performance: implications for site fidelity. J Anim Ecol 54:1017–1027

Bowen WD, McMillan J, Mohn R (2003) Sustained exponential population growth of grey seals at Sable Island, Nova Scotia. ICES J Mar Sci 60:1265–1274

Braham HW, Everitt RD, Rugh DJ (1980) Northern sea lion population decline in the Eastern Aleutian Islands. J Wildl Manag 44:25–33

Burnham KP, Anderson DR (1998) Model selection and inference. Springer, New York

Campbell RA, Gales NJ, Lento GM, Baker CS (2008) Islands in the sea: extreme female natal site fidelity in the Australian sea lion, *Neophoca cinerea*. Biol Lett 4:139–142

Cooch EG, Jeffries RL, Rockwell RF, Cooke F (1993) Environmental change and the cost of philopatry: an example in the lesser snow goose. Oecologia 93:128–138

Cordes LS, Thompson PM (2013) Variation in breeding phenology provides insights into drivers of long-term population change in harbour seals. Proc R Soc B Biol Sci 280:20130847

Cordes LS, Thompson PM (2014) Mark-recapture modeling accounting for state uncertainty provides concurrent estimates of survival and fecundity in a protected harbour seal population. Mar Mammal Sci 30:691–705

Cordes LS, Duck CD, Mackey BL, Hall AJ, Thompson PM (2011) Long-term patterns in harbour seal site-use and the consequences for managing protected areas. Anim Conserv 14:430–438

Cunningham L (2009) Using computer-assisted photo-identification and capture-recapture techniques to monitor the conservation status of harbour seals (*Phoca vitulina*). Aquat Mammals 35:319–329

Cunningham L, Baxter JM, Boyd IL, Duck CD, Lonergan M, Moss SE, McConnell B (2009) Harbour seal movements and haul-out patterns: implications for monitoring and management. Aquat Conserv Mar Freshw Ecosyst 19:398–407

Fabiani A, Galimberti F, Sanvito S, Hoelzel AS (2006) Relatedness and site fidelity at the southern elephant seal, *Mirounga leonina*, breeding colony in the Falkland Islands. Anim Behav 72:617–626

Gamble LR, McGarigal K, Compton BW (2007) Fidelity and dispersal in the pond breeding amphibian, *Ambystoma opacum*: implications for spatio-temporal population dynamics and conservation. Biol Conserv 139:247–257

Ganter B, Cooke F (1998) Colonial nesters in a deteriorating habitat: site fidelity and colony dynamics of lesser snow geese. Auk 115:642–652

Goodman SJ (1998) Patterns of extensive genetic differentiation and variation among European harbor seals (Phoca vitulina vitulina) revealed using microsatellite DNA polymorphism. Mol Biol Evol 15:104–118

Hamilton CD, Lydersen C, Ims RA, Kovacs KM (2014) Haul-out behaviour of the world's northernmost population of harbour seals (Phoca vitulina) throughout the year. PLoS One 9(1):e86055

Härkönen T, Harding KC (2001) Spatial structure of harbour seal populations and the implications thereof. Can J Zool 79:2115–2127

Härkönen T, Dietz R, Reijnders P, Teilmann J, Harding K, Hall A, Brasseur S, Siebert U, Goodman SJ, Jepson PD, Dau Rasmussen T, Thompson P (2006) A review of the 1988 and 2002 phocine distemper virus epidemics in European harbour seals. Dis Aquat Organ 68:115–130

Hastings KK, Hiby LA, Small RJ (2008) Evaluation of a computer-assisted photograph-matching system to monitor naturally marked harbour seals at Tugidak Island, Alaska. J Mammal 89:1201–1211

Hastings KK, Small RJ, Pendleton GW (2012) Sex- and age-specific survival of harbour seals (Phoca vitulina) from Tugidak Island, Alaska. J Mammal 93:1368–1379

Hestbeck JB, Nichols JD, Malecki RA (1991) Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. Ecology 72:523–533

Hindell MA, Burton HR (1988) Seasonal haul-out patterns of the southern elephant seal (Mirounga leonine L.) at Macquarie Island. J Mammal 69:81–88

Hoffman JI, Trathan PN, Amos W (2006) Genetic tagging reveals extreme site fidelity in territorial male Antarctic fur seals Arctocephalus gazelle. Mol Ecol 15:3841–3847

Inger R, Attrill MJ, Bearhop S, Broderick AC, Grecian WJ, Hodgson DJ, Mills C, Sheehan E, Votier SC, Witt MJ, Godley BJ (2009) Marine renewable energy: potential benefits to biodiversity? An urgent call for research. J Appl Ecol 46:1145–1153

Jeffries S, Huber H, Calambokidis J (2003) Trends and status of harbour seals in Washington State: 1978–1999. J Wildl Manag 67:207–218

Kendall WL, Nichols JD (2002) Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. Ecology 83:3276–3284

Kretzmann MB, Gilmartin WG, Meyer A, Zegers GP, Fain SR, Taylor BF, Costa DP (1997) Low genetic variability in the Hawaiian monk seal. Conserv Biol 11:482–490

Mackey BL, Durban JW, Middlemas SJ, Thompson PM (2008) A Bayesian estimate of harbour seal survival using sparse photo-identification data. J Zool 274:18–27

Matthiopoulos J, Harwood J, Thomas L (2005) Metapopulation consequences of site fidelity for colonially breeding mammals and birds. J Anim Ecol 74:716–727

McClintock BT, White GC (2009) A less field intensive robust design for estimating demographic parameters with mark-resight data. Ecology 90:313–320

McClintock BT, White GC, Antolin MF, Tripp DW (2009) Estimating abundance using mark-resight when sampling is with replacement or the number of marked individuals is unknown. Biometric 65:237–246

Neal AK, White GC, Gill RB, Reed DF, Olterman JH (1993) Evaluation of mark-resight model assumptions for estimating mountain sheep numbers. J Wildl Manag 57:436–450

Pomeroy PP, Twiss SD, Redman P (2000) Philopatry, site fidelity and local kin associations within grey seal breeding colonies. Ethology 106:899–919

Salwicka K, Sierakowski K (1998) Seasonal numbers of five species of seals in Admiralty Bay (South Shetland Island, Antarctica). Polish Polar Res 19:235–247

Sharples RJ, Mackenzie ML, Hammond PS (2009) Estimating seasonal abundance of a central place forager using counts and telemetry data. Mar Ecol Prog Ser 378:289–298

Sullivan RM (1980) Seasonal occurrence and haul-out use in pinnipeds along Humboldt County, California. J Mammal 61:754–760

Taylor BL, Martinez M, Gerrodette T, Barlow J, Hrovat YN (2007) Lessons from monitoring trends in abundance of marine mammals. Mar Mammal Sci 23:157–175

Thompson PM, Wheeler H (2008) Photo-ID-based estimates of reproductive patterns in female harbour seals. Mar Mammal Sci 24:138–146

Thompson PM, Fedak MA, McConnell BJ, Nicholas KS (1989) Seasonal and sex-related variation in the activity patterns of common seals (Phoca vitulina). J Appl Ecol 26:521–535

Thompson PM, Miller D, Cooper R, Hammond PS (1994) Changes in the distribution and activity of female harbour seals during the breeding season: implications for their lactation strategy and mating patterns. J Anim Ecol 63:24–30

Thompson PM, McConnell BJ, Tollit DJ, Mackey A, Hunter C, Racey PA (1996) Comparative distribution, movements and diet of harbour and grey seals from Moray Firth, N.E. Scotland. J Appl Ecol 33:1572–1584

Thompson PM, Tollit DJ, Wood D, Corpe HM, Hammond PS, Mackey A (1997) Estimating harbour seal abundance and status in an estuarine habitat in north-east Scotland. J Appl Ecol 34:43–52

Van Parijs SM, Thompson PM, Tollit DJ, Mackey A (1997) Distribution and activity of male harbour seals during the mating season. Anim Behav 54:35–43

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139

Yoccoz NG, Nichols JD, Boulinier T (2001) Monitoring of biological diversity in space and time. Trends Ecol Evol 16:446–453