

Photo-ID-based estimates of reproductive patterns in female harbor seals

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ABSTRACT

Variations in reproductive patterns offer important insights into the dynamics of pinniped populations, but collecting data on reproduction for species that spend much of the breeding season in the water is problematic. We used land-based photo-identification techniques to collect individual-based data on the timing of pupping, total pup production, and lactation duration in a population of harbor seals in NE Scotland. Capture–Mark–Recapture (CMR) techniques were used to overcome potential biases due to changes in probability of capture, and provide estimates of lactation duration based upon changes in the “survival” of mother–pup bonds. A mean birth date of 20 June is the first direct estimate of parturition date for UK harbor seals. Information on cumulative births indicated that the peak daily haul-out count accounted for 77% of total pup production. CMR-based estimates of lactation duration suggest that 50% of mothers had weaned their pups, when pups were 21-d old. These results highlight the potential for using photo-ID techniques to study harbor seal reproductive patterns at sites where intensive capture and marking is not possible for logistic, legislative, or ethical reasons.

Key words: phenology, *Phoca vitulina*, harbor seal, individual identification, reproduction, photo-ID.

In recent decades, harbor seal populations have exhibited marked variation in population trends; ranging from exponential increases to dramatic declines (*e.g.*, Pitcher 1990, Bowen *et al.* 2003, Härkönen *et al.* 2006, Lonergan *et al.* 2007). However, study of the factors driving these trends is constrained by the harbor seals' aquatic breeding habits, which often make it difficult to collect data on the most basic of population parameters.

In other species, variations in productivity and reproductive patterns have provided sensitive and informative indicators of population responses to environmental variability and climate change (Roy and Sparks 2000, Walther *et al.* 2002, Sims *et al.*

2004). Similarly, variability in pregnancy and lactation duration has been shown to reflect resource availability in some pinnipeds (Boyd 1996). However, collecting reliable data on the timing of pupping and duration of lactation in harbor seals is problematic at most sites throughout their range. Most detailed reproductive data for this species are therefore derived from Sable Island in Canada where, uniquely, mothers and pups remain ashore throughout lactation (*e.g.*, Bowen *et al.* 1994, 2001, 2003). Potentially, variations in reproductive patterns may help us understand harbor seal population dynamics. But to achieve this, we need to develop techniques to collect comparative reproductive data from other populations.

One promising area of research builds on the observation that the mean pupping date has shifted in relation to changes in abundance in several harbor seal populations (Jemison and Kelly 2001, Bowen *et al.* 2003). Not only does this provide interesting potential for understanding the factors driving population change, but an understanding of the mechanisms underlying these changes is also required because changes in the timing of pupping may affect the efficiency of standardized survey programs (Boveng *et al.* 2003, Jeffries *et al.* 2003, Härkönen *et al.* 2006). One possibility is that year-to-year changes in the timing of pupping reflect resource variability, potentially offering a useful indicator of population responses to environmental change (Bowen *et al.* 2003). Alternatively, given the recognized influence of age on the timing of reproduction, observed changes in mean pupping date could reflect longer-term changes in population age structure (Boyd 1996, Jemison and Kelly 2001). Further exploration of these alternative hypotheses therefore requires individual-based data from known females.

Recent studies in the NE Scotland have highlighted the potential for using photo-identification (photo-ID) to recognize individual harbor seals from their pelage patterns (Mackey *et al.*, in press). Only a few haul-out sites used by this population can be approached closely enough to obtain suitable high-resolution photographs, but 30–40 mothers use one such site regularly as a birthing site. This permits birth dates to be estimated from repeat sightings of each female, when they were last seen pregnant and when they were first seen with a newborn pup. However, telemetry studies at nearby sites indicate that females make offshore feeding trips around the time of weaning and may subsequently use alternative haul-out sites (Thompson *et al.* 1994). Thus, females are less easily observed later in the summer, meaning that weaning date cannot be reliably estimated in a similar way. To overcome this, we used our photographic resightings of identifiable mothers that were suckling pups in a capture–mark–recapture (CMR) framework (White and Burnham 1999), thereby allowing us to estimate the “survival” of the mother–pup bond while accounting for variations in recapture probability. In particular, we aimed to assess whether these methods could be used to provide a standardized approach to collecting comparative data on the timing of pupping, pup production, and lactation duration in harbor seals.

METHODS

Shore-based observations were made in 2006 at a haul-out site in Loch Fleet National Nature Reserve, in the Moray Firth, Scotland (see Thompson *et al.* 1997 for further details about the study area and local population structure). From mid-May, observations were made during the period ± 3 h of low tide every 2 d. Following the birth of the first pups (27 May), observations were then made daily until no mothers

and pups had been seen together for at least 2 d (20 July). The only exception to this was when the site could not be visited on 15 and 16 July.

Seals were counted with a 20–60 × 80-mm Swarovski HD-ATS 80 telescope (Swarovski UK Ltd., Surrey, UK) at a distance of approximately 130 m from a public road, and the maximum number of pups and seals of all other age classes were recorded for each day. Following counts, photographs were taken of both the left and right side of the head and neck region of all adult females that were present on the site. Photos were taken using a Nikon Coolpix 4500 camera (Nikon UK Ltd., Kingston, UK) attached to the telescope using commercially available digiscoping equipment (<http://digiscoping.swarovski-optik.info>).

Photographs were later matched to a catalog of previously identified individuals, resulting in identifications of both sides of 35 mothers. Capture histories of these individuals were constructed for the period that they were with pups. In addition, we used photographic captures to determine both the last day that a female was seen without a pup, and the first day that she was seen with a pup. Each individual female's date of parturition was assumed to be the midpoint between these two photographic captures. In five cases, more than 3 d elapsed between these two photographic captures. Estimates of mean date of pupping were produced both with and without these individuals, but they were excluded from analyses of lactation duration.

Lactation duration was estimated using two different methods. First a simple estimate of each female's minimum lactation duration was determined from her estimated date of pupping and the last day on which the mother and pup were photographed together. Second, we estimated time-dependant "survival" (Φ) of the mother–pup bond using a Cormack–Jolly–Seber model in the program MARK (White and Burnham 1999). A matrix of photographic captures of individually recognizable mothers was created using a 3-d sampling window, and by re-arranging the capture matrix so that the first 3-d sampling occasion related to the birth date. We compared the fit of four different models, using AIC values. These models were: (1) time-dependant survival ($\Phi [t]$) and constant capture probability ($P [·]$), (2) time-dependant survival and time-dependant capture probability ($P [t]$), (3) time-dependant survival with capture probability modeled as a linear trend ($P [\text{linear trend}]$), and (4) both survival and capture probability modeled as a linear trend. A logit link function was used, and goodness of fit was assessed from the model deviance. The proportion of females that had ended lactation at the end of each 3-d sampling period was then estimated as 1 minus the estimate of survival to that time point. Changes in this proportion were modeled using logistic regression to determine the point at which of 50% of females had weaned.

RESULTS

The maximum daily count recorded (not including pups) was of 65 harbor seals, and the mean count during the study period was 43 (SD = 13). Parturition dates ranged from 27 May to 6 July, with an overall mean for live births of 20 June \pm 7 d. Excluding data from the five females whose parturition date could only be assigned to a 3-d window had no effect on this estimate, and the mean remained at 20 June. Two stillborn pups were born early in the season on the 8 and 9 June, and are not included in daily totals or cumulative totals of pups.

The cumulative number of pups born is shown in Figure 1, together with daily maximum counts of pups. The peak daily count of 27 pups represented 77% of the cumulative total of 35.

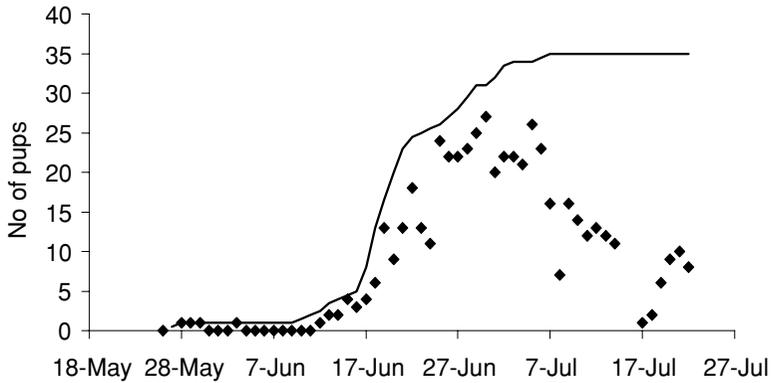


Figure 1. Daily maximum counts of harbor seal pups hauled out at the study site in Loch Fleet, together with the cumulative total of pups born (solid line), based upon observations of individually recognizable females.

The number of days that individually recognizable mothers were seen with a pup varied from 3 to 29 (Fig. 2), (mean = 17.00 ± 7.22 d; median = 17 d). As anticipated, the use of CMR models to account for variations in the probability of sighting individually recognizable females resulted in slightly longer estimates of lactation duration. Comparison of the results from the four different models used (Table 1) suggests that modeling both survival and capture probability with a linear (declining) trend provided the best-fitting model (Model 4). Using the parameter estimates from this model indicated that 50% of the females had weaned their pups after 21 d (Fig. 3). Using parameter estimates from the next best-fitting model had little effect on this result, with 50% of pups being weaned after 20 d.

DISCUSSION

Harbor seals can be observed from moderate distances in many parts of their range, but are easily disturbed by the close approaches that are required to identify

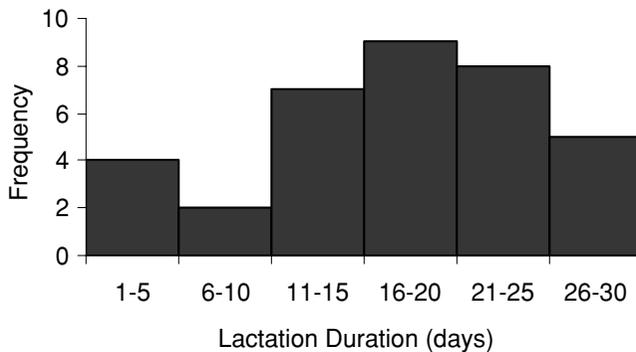


Figure 2. Frequency distribution of the length of time (days) during which individually recognizable females were recorded at the study site in the presence of their pup.

Table 1. Comparison of the performance of the four different models used to estimate survival and recapture probabilities.

Model description	AICc	No. of parameters	Deviance
(1) $\Phi(t), P(\cdot)$	286.04	12	115.20
(2) $\Phi(t), P(t)$	311.11	20	111.10
(3) $\Phi(t), P$ (linear trend)	296.71	13	114.31
(4) Φ (linear trend), P (linear trend)	280.64	4	118.50

individuals from conventional flipper tags. Opportunities to capture harbor seals and apply larger marks that would allow individual identification over several years are rare (Härkönen *et al.* 1999), thereby constraining the development of the individual-based studies that have underpinned demographic studies in many other species. As a result, much of our detailed understanding of reproductive patterns in this species is based either upon analyses of carcasses (*e.g.*, Harrison 1960, Bigg 1969), or of field studies on Sable Island, Canada. Our results build on an earlier study that used photo-identification to estimate harbor seal site fidelity and survival in Scottish waters (Mackey *et al.*, in press), and illustrate how the increasing availability of high-quality digital photographic equipment can be successfully exploited to develop studies of individual reproductive behavior. Here, we used a 4-megapixel camera with a 20–60 × 80-mm telescope, which provided suitable images at our working distance of around 130 m. Under the light and wind conditions experienced in our Scottish study area, this is probably close to the limit of the current generation of equipment. Nevertheless, higher quality images could be obtained at greater distances where light and wind conditions are more favorable.

Here, our main aim was to use repeat observations of individually observable females to estimate the total number of pups born at this site during the season, to

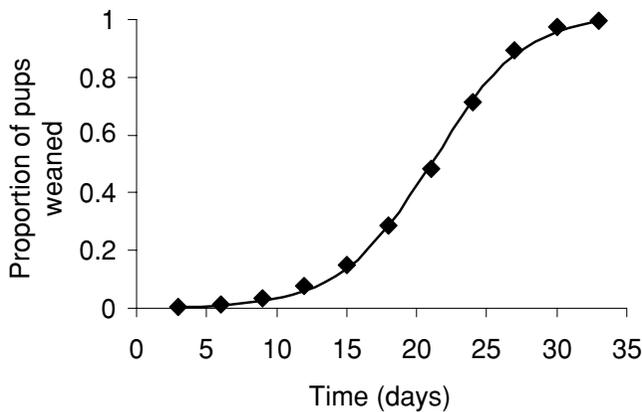


Figure 3. Estimated change in the proportion of individually recognizable females that had weaned their pups in relation to time in days from their birth date. Solid diamonds are estimates of mortality of the mother–pup bond from one 3-d sample to the next, estimated in program MARK using Model 4 (Table 1). The fitted line is a logistic regression through these data.

obtain data on the timing of parturition, and to estimate the duration of lactation. Overall, 35 identifiable mothers were recorded with pups during the study period. In contrast, the maximum number of pups hauled out at the study site on any one day was only 27, highlighting that counts alone can only provide an index of total pup production. This difference between the cumulative number of pups born and the peak count is likely to be due to a combination of early pup mortality, mother and pups spending low-tide haul-out periods at sea, and movements of mothers and pups to other haul-out sites. Some stillborn pups were observed, and additional early mortality seems likely where females were only seen with pups for <5 d. Currently, we have no additional data on likely rates of pup survival. However, if these were available, our modeling approach could be extended to include pup mortality as an additional parameter in the CMR model. Similarly, little information is available about the extent to which mother and pups may move between alternative haul-out sites. The nearest alternative haul-out site is >10 km away, but we cannot rule out the possibility that some females switched haul-out site early in lactation. Furthermore, we cannot be sure that we photographed and identified all mothers that gave birth at this site. Nevertheless, the proportion of our estimated total pup production that was present during the peak count (77%) is similar to that recorded on Sable Island (Godsell 1988).

Earlier radio-tracking studies of a small sample of females from this population indicate that mothers restrict their foraging range and haul out regularly for a few days prior to parturition (Thompson *et al.* 1994). In all but five cases, repeat sightings of mothers when pregnant and with their newborn pup meant that their birth date was known to occur within a 3-d window. Assuming that births occurred in the midpoint between these sightings, all births occurred within a 6-wk window, with a mean birth date of 20 June. To the best of our knowledge, this represents the first direct estimate of mean parturition date in any population of European harbor seals. This is 10 d earlier than the mean pupping date predicted for 58°N by the latitudinal gradient equation developed by Temte *et al.* (1991) and updated in Dube *et al.* (2003). Similarly, the mean pupping date for harbor seals in the St Lawrence River was 9 d earlier than the predicted date based on Temte's equation. The original relationship between latitude and timing of pupping was explored using a variety of data sets, many of which were based on indirect estimates of mean pupping date, or on captive studies. More direct field estimates of mean pupping date will help improve our understanding of the role of latitude and photoperiod on reproductive patterns in this species, and we hope these findings encourage others to develop comparative studies across a wider geographical range. More recent work has also shown that the timing of pupping within particular harbor seal populations may change by up to 14 d. These changes have coincided with marked population declines (*e.g.*, Jemison and Kelly 2001, Bowen *et al.* 2003), but the direction of change has varied. On Sable Island, for example, Bowen *et al.* (2003) suggested that a delay in pupping was related to nutritional stress due to competition with an expanding gray seal population. In contrast, in the Gulf of Alaska, harbor seal pups were born earlier following a decline in abundance (Jemison and Kelly 2001). This too could be a positive response to an increase in resource levels following a decrease in intraspecific competition. Alternatively, changes in age structure during these declines could affect mean pupping date (Jemison and Kelly 2001). Discrimination between these hypotheses requires a better understanding of how an individual female's date of parturition varies in relation to her age and resource availability. Similar uncertainty exists over the key factors driving recent declines of harbor seals in Scotland (Loneragan *et al.* 2007, Thompson *et al.* 2007). These

photo-ID techniques now provide a practical non-invasive method for studying temporal changes in the timing of parturition within an individual, and further work is now planned to explore this question.

Previous estimates of the duration of lactation in harbor seals vary between 23 and 42 d (Bowen 1991). Potentially, these spatial and temporal variations in lactation patterns could also provide an indication of the status of different populations and their responses to environmental variability. Currently, however, comparison among the few estimates available is constrained by the different methodologies used. For example, early estimates, including those available for UK waters, are typically in the range of 28–42 d (Bigg 1969, Bonner 1972). However, these are based on cross-sectional studies and are likely to be positively biased, reflecting the period when suckling females are seen in the population at large rather than an individual female's lactation period. More robust data on lactation duration come from longitudinal studies of tagged females on Sable Island (Bowen 1991, Muelbert and Bowen 1993). Here, the lactation duration of 52 mothers ranged from 15 to 30 d, with a mean of 24 d. The problem with collecting comparative data at other sites is twofold. First, females and pups are more easily disturbed and longitudinal studies require a method for identifying individual females at greater observation distances. Second, females and pups spend much of their time in the water (Bekkby and Bjorge 2003), such that the probability of sighting the pair together at the haul-out site on any particular day during the lactation period is <1 . In some areas, direct captures have allowed females or their pups to be marked and followed (Dube *et al.* 2003), but at many sites, including the one used in our study, this would cause unacceptable levels of disturbance. Even if this is not an issue, capture and tagging a representative sample of mothers and or pups requires considerable resources. In this study, photo-ID provided a low-cost, non-invasive technique that allowed us to follow individual mothers throughout a single breeding season. The application of CMR methodology to these resighting data also provided a more robust framework for accounting for the fact that the probability of sighting lactating females was <1 . As expected, our CMR estimate of mean lactation duration (21 d) was longer than the estimates based on resightings alone (Fig. 2). While within 3 d of Muelbert and Bowen's (1993) estimate of 24 d for Sable Island, this is the lowest recorded for this species. Whether this is due to genuine differences between these populations, or methodological differences, remains unclear. Estimates from both studies are considerably shorter than the 36 d recorded for captive harbor seals, and it seems likely that the need for many harbor seals to forage in late lactation could lead to variability in the pattern or duration of lactation in relation to spatiotemporal variations in local resources. However, it is likely that our CMR estimate of the time of weaning is less robust than our direct estimate of the date of parturition. Ideally, one would use a similar approach for estimating weaning to that used for estimating birth dates; using the last sighting of the females with her pup and the first sighting of the female once the pup had weaned. However, because females tend to go off on long foraging trips and may switch haul-out sites post weaning (Thompson *et al.* 1994), the probability of sighting females once they are without their pup drops even further. While this might be overcome by increasing sampling effort at this time, this is also the time that females start to molt (Thompson and Rothery 1987), further constraining opportunities for photo-ID (Mackey *et al.*, in press). To overcome this, we focused our photo-ID effort on pregnant females and females with pups, and used CMR to estimate the survival of the mother–pup bond. However, like most estimates of CMR survival, this relates only to local survival. While we cannot exclude the possibility that some females and pups move

to alternative sites during lactation, the continued presence of weaned pups at the study site suggests that this is not a major issue. In future, an alternative approach to address this question would be extending our surveys to all other haul-out sites in adjacent areas. The nature of these sites precludes wider scale photo-ID surveys, but regular counts of the proportion of pups that were still suckling could be used to produce an alternative estimate of the mean date of weaning. This approach was used in the St Lawrence River, where cross-sectional data on weaning were compared with an estimate of mean pupping date derived from captures and measurements of newborn pups (Dube *et al.* 2003).

In conclusion, this study has shown that photo-ID can provide a practical method for studying harbor seal reproduction. Using this technique, we have obtained direct estimates of total pup production, the timing of pupping, and lactation duration, that now provide baseline data on these parameters for Scottish harbor seals. Further photo-ID studies now provide the potential for a more detailed understanding of the factors that influence temporal and geographical variation in reproductive patterns in this species.

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LITERATURE CITED

- BEKKBY, T., AND A. BJORGE. 2003. Joint diving behaviour of harbour seal (*Phoca vitulina*) females and pups in the lactation period. *Sarsia* 88:369–372.
- BIGG, M. 1969. The harbour seal in British Columbia. Fisheries Research Board of Canada Bulletin 172. 33 pp.
- BONNER, W. 1972. The grey seal and common seal in European waters. *Oceanography and Marine Biology Annual Review* 10:461–507.
- BOVING, P. L., J. L. BENGTSON, D. E. WITHROW, J. C. CESARONE, M. A. SIMPKINS, K. J. FROST AND J. J. BURNS. 2003. The abundance of harbor seals in the Gulf of Alaska. *Marine Mammal Science* 19:111–127.
- BOWEN, W. D. 1991. Behavioural ecology of pinniped neonates. Pages 66–127 *in* D. Renouf, ed. *Behaviour of pinnipeds*. Chapman & Hall, London, UK.
- BOWEN, W. D., O. T. OFTEDAL, D. J. BONESS AND S. J. IVERSON. 1994. The effect of maternal age and other factors on birth mass in the harbor seal. *Canadian Journal of Zoology* 72:8–14.
- BOWEN, W. D., S. J. IVERSON, D. J. BONESS AND O. T. OFTEDAL. 2001. Foraging effort, food intake and lactation performance depend on maternal mass in a small phocid seal. *Functional Ecology* 15:325–334.
- BOWEN, W. D., S. L. ELLIS, S. J. IVERSON AND D. J. BONESS. 2003. Maternal and newborn life-history traits during periods of contrasting population trends: Implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. *Journal of Zoology* 261:155–163.
- BOYD, I. L. 1996. Individual variation in the duration of pregnancy and birth date in Antarctic fur seals: The role of environment, age, and sex of fetus. *Journal of Mammalogy* 77:124–133.
- DUBE, Y., M. O. HAMMILL AND C. BARRETTE. 2003. Pup development and timing of pupping in harbour seals (*Phoca vitulina*) in the St. Lawrence River estuary, Canada. *Canadian Journal of Zoology* 81:188–194.

- GODESELL, J. 1988. Herd formation and haul-out behavior in harbor seals (*Phoca vitulina*). *Journal of Zoology* 215:83–98.
- HÄRKÖNEN, T., K. C. HARDING AND S. G. LUNNERYD. 1999. Age- and sex-specific behaviour in harbour seals *Phoca vitulina* leads to biased estimates of vital population parameters. *Journal of Applied Ecology* 36:825–841.
- HÄRKÖNEN, L., R. DIETZ, P. REIJNDERS, J. TEILMANN, K. HARDING, A. HALL, S. BRASSEUR, U. SIEBERT, S., J. GOODMAN, P. D. JEPSON, T. D. RASMUSSEN AND P. THOMPSON. 2006. The 1988 and 2002 phocine distemper virus epidemics in European harbour seals. *Diseases of Aquatic Organisms* 68:115–130.
- HARRISON, R. 1960. Reproduction and reproductive organs in common seals (*Phoca vitulina*) in the Wash, East Anglia. *Mammalia* 24:372–385.
- JEFFRIES, S., H. HUBER, J. CALAMBOKIDIS AND J. LAAKE. 2003. Trends and status of harbor seals in Washington state: 1978–1999. *Journal of Wildlife Management* 67:207–218.
- JEMISON, L. A., AND B. P. KELLY. 2001. Pupping phenology and demography of harbor seals (*Phoca vitulina richardsi*) on Tugidak Island, Alaska. *Marine Mammal Science* 17:585–600.
- LONERGAN, M., C. D. DUCK, D. THOMPSON, B. L. MACKEY, L. CUNNINGHAM AND I. L. BOYD. 2007. Using sparse survey data to investigate the declining abundance of British harbour seals. *Journal of Zoology* 271:261–269.
- MACKEY, B. L., J. W. DURBAN, S. J. MIDDLEMAS AND P. M. THOMPSON. 2007. A Bayesian estimate of harbour seal survival using sparse photo-identification data. *Journal of Zoology*, July 28, 2007; doi: 10.1111/j.1469-7998.2007.00352.x
- MUELBERT, M. M. C., AND BOWEN, W. D. 1993. Duration of lactation and postweaning changes in mass and body-composition of harbor seal, *Phoca-Vitulina*, pups. *Canadian Journal of Zoology* 71:1405–1414.
- PITCHER, K. W. 1990. Major decline in number of harbor seals, *Phoca vitulina richardsi*, on Tugidak Island, Gulf of Alaska. *Marine Mammal Science* 6:121–134.
- ROY, D. B., AND T. H. SPARKS. 2000. Phenology of British butterflies and climate change. *Global Change Biology* 6:407–416.
- SIMS, D. W., V. J. WEARMOUTH, M. J. GENNER, A. J. SOUTHWARD AND S. J. HAWKINS. 2004. Low-temperature-driven early spawning migration of a temperate marine fish. *Journal of Animal Ecology* 73:333–341.
- TEMTE, J. L., M. A. BIGG AND O. WIIG. 1991. Clines revisited—the timing of pupping in the harbor seal (*Phoca vitulina*). *Journal of Zoology* 224:617–632.
- THOMPSON, P., AND P. ROTHERY. 1987. Age and sex-differences in the timing of moult in the Common Seal, *Phoca vitulina*. *Journal of Zoology* 212:597–603.
- THOMPSON, P. M., D. MILLER, R. COOPER AND P. S. HAMMOND. 1994. Changes in the distribution and activity of female harbour seals during the breeding season—implications for their lactation strategy and mating patterns. *Journal of Animal Ecology* 63:24–30.
- THOMPSON, P. M., D. J. TOLLIT, D. WOOD, H. M. CORPE, P. S. HAMMOND AND A. MACKAY. 1997. Estimating harbour seal abundance and status in an estuarine habitat in north-east Scotland. *Journal of Applied Ecology* 34:43–52.
- THOMPSON, P. M., B. L. MACKEY, T. R. BARTON, C. DUCK AND J. R. A. BUTLER. 2007. Assessing the potential impact of salmon fisheries management on the conservation status of harbour seals in NE Scotland. *Animal Conservation* 10:48–56.
- WALTHER, G. R., E. POST, P. CONVEY, A. MENZEL, C. PARMESAN, T. J. BEEBEE, J. M. FROMENTIN, O. HOEGH-GULDBERG AND F. BAIRLEIN. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:120–139.

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