# A modelling framework to optimize timing of haulout counts for estimating harbour seal (*Phoca vitulina*) abundance

Michelle. A. Cronin<sup>1</sup>, Alain. F. Zuur<sup>2</sup>, Simon. N. Ingram<sup>3</sup> and Emer Rogan<sup>3</sup>.

- <sup>1</sup> Coastal & Marine Resources Centre, ERI, University College Cork, Naval Base, Haulbowline, Cobh, Co. Cork, Ireland
- <sup>2</sup> Highland Statistics Ltd., 6 Laverock Road, AB41 6FN Newburgh, Scotland, United Kingdom
- <sup>3</sup> Department of Zoology, Ecology & Plant Science, University College Cork, North Mall, Cork, Ireland

#### **ABSTRACT**

The time of year and day, the state of the tide and prevailing environmental conditions significantly influence seal haulout behaviour. Understanding these effects is fundamentally important in deriving accurate estimates of harbour seal abundance from haulout data. We present a modelling approach to assess the influence of these variables on seals' haulout behaviour and, by identifying the combination of covariates during which seal abundance is highest, predict the optimal time and conditions for future surveys. Count data of harbour seals at haulouts in southwest Ireland collected during 2003-2005 were included in mixed additive models together with environmental covariates, including season, time of day and weather conditions. The models show maximum abundance at haulout sites occurred during midday periods during August and in late afternoon/early evening during September. Accurate national and local population estimates are essential for the effective monitoring of the conservation status of the species and for the identification, management and monitoring of Special Areas of Conservation (SAC) in accordance with the EU Habitats Directive. Our model based approach provides a useful tool for optimising the timing of harbour seal surveys in Ireland and the modelling framework is useful for predicting optimal survey periods for other protected, endangered or significant species worldwide.

Cronin, M.A., Ingram, S.N., Zuur, A.F. and Rogan, E. 2010. A modelling framework to optimize timing of haulout counts for estimating harbour seal (*Phoca vitulina*) abundance. *NAMMCO Sci. Publ.* 8:213-226.

## INTRODUCTION

Deciding on the optimal time to conduct a survey of an animal population to determine the size of the population is a challenging task. Such surveys are necessary for reasons such as basic ecological audits for conservation management and planning decisions or population estimate and trend analyses for assessing the conservation status of endangered or protected species. They are also essential in policy making for the protection of the environment. It is rare that all individuals in a population can be counted during an assessment of population size, making accurate estimates of population size difficult to obtain. Various approaches have been used to overcome this problem including mark-recapture models, distance sampling techniques and

derived population estimates based on known births and deaths. It is especially difficult with semi-aquatic or aquatic and/or migratory species that are inaccessible or unavailable for counting during a significant part of their life histories. With such species there is often a window in time where a consistent fraction of the population is available for counting and that provides an opportunity to obtain reliable estimates of abundance. Identifying such periods is a challenge and requires survey effort and statistical manipulation of the resulting data.

Here we provide an example of a modelling technique that can be used to identify annual peaks in abundance of a population of seals, and to examine the relationship between seal numbers and environmental variables that affect the numbers that come ashore. This allows us to predict optimal survey periods to estimate abundance and trends and to account for the influence of environmental variables on the numbers ashore.

The harbour seal (*Phoca vitulina* L.) is a widelydistributed pinniped, inhabiting cold-temperate and temperate waters in the North Atlantic and North Pacific (Bigg 1981). In Europe the harbour seal is listed as an Annex II species under the EU Habitats Directive (92/43/EEC) *i.e.* a protected species whose conservation requires the designation of special areas of conservation. Accurate assessment of population size, terrestrial and aquatic distribution and range are essential for the effective monitoring of the conservation status of the species. In some parts of the harbour seals range, such information is lacking or incomplete. Recent efforts have addressed the shortfall in fundamental population data on the harbour seal in Ireland, including a national census to establish a minimum population estimate (Cronin et al. 2007). Such efforts, whilst providing fundamental baseline information on population size and distribution, fall short at enabling us to understand year-round changes in population parameters and the environmental forcing on haulout behaviour.

Seasonal changes in the numbers of harbour seals at haulout sites, resulting from changes in the haulout behaviour of various age-sex classes have been described from previous studies (Thompson and Rothery 1987, Thompson 1989, Thompson et al. 1989, Thompson and Miller 1990, Härkönen et al. 1999). Generally, two seasonal peaks in abundance at haulout sites have been identified across the harbour seals' geographical range, a peak during May/June associated with pupping and during August/September associated with moulting (Thompson and Harwood 1990, Thompson et al. 1997, Jemison and Kelly 2001, Huber et al. 2001, Reijnders et al. 2003). Largescale surveys to obtain population estimates at regional and national scales are generally conducted during one of these peaks in abundance (Thompson and Harwood 1990, Huber et al. 2001, Boveng et al. 2003, Reijnders et al. 2003, Duck et al. 2005) when the most consistent fraction of the population is understood to be ashore.

As the actual timing of such peaks has been shown to vary geographically and temporally (Matthews and Kelly 1996, Huber et al. 2001, Jemison and Kelly 2001), understanding seasonal patterns on haulout behaviour is essential for identifying the optimal time for carrying out large-scale surveys. A national harbour seal survey conducted during the 2003 moult in the Republic of Ireland, provided a minimum population estimate of 2,905 harbour seals (Cronin et al. 2007), but was essentially a 'snap-shot' of harbour seal distribution and abundance at haulout sites on the Irish coast during that survey period. Moreover the timing of the survey was based on information on peak haulout counts of harbour seals in other parts of their geographical range as such information did not exist for the Irish population. More detailed information on the year-round abundance of harbour seals at haulout sites in Ireland, hitherto unavailable, provides a means of identifying seasonal peaks and optimal periods for future large-scale surveys. Such information also helps explain temporal trends at the population level, provides a means to examine the variables that effect haulout behaviour and helps explain between year variability in abundance resulting from for example redistribution, changes in habitat use and fluctuations in demographic parameters such as pup production or survival.

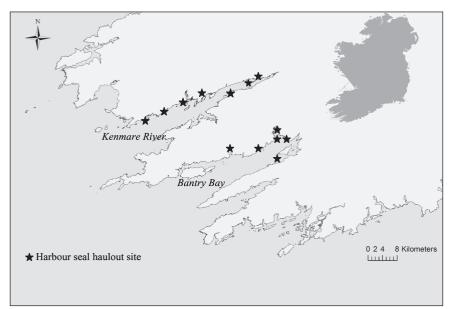


Fig. 1.
Haulout locations within the 2 study sites,
Bantry Bay
and Kenmare
River.

Other influences on seal haulout behaviour. apart from the time of year, include the time of day, tidal effects, disturbance and local weather (Stewart 1984, Yochem et al. 1987, Thompson et al. 1989, 1994, 1997, Thompson and Harwood 1990, Thompson and Miller 1990, Grellier et al. 1996, Reder et al. 2003). The influence of covariates on estimates of harbour seal population trend has been found to be substantial (Frost et al. 1999, Olesiuk 1999, Simpkins et al. 2003). Statistical models of the relationship between survey counts and environmental conditions at haulout sites have proven useful in enhancing survey design and improving the accuracy of population abundance estimates and trend analyses by adjusting counts to a standard set of environmental conditions (Watts 1996, Frost et al. 1999, Adkinson et al. 2003, Boveng et al. 2003, Small et al. 2003). The data that these previous models were based on were collected over a relatively short part of the annual cycle, during the breeding or moult periods namely, none of the studies to date looked at the full annual cycle.

Understanding year-round changes in seal haulout behaviour is essential for identifying peaks in haulout abundance. Moreover it contributes to the monitoring obligations under the Habitats Directive for Annex II species and to the understanding of national population

trends. Over one third of harbour seals in Ireland use haulout sites in the southwest region (Cronin *et al.* 2007). Most of the haulout sites in this region are located within Bantry Bay and the Kenmare River and Special Areas of Conservation (SACs) have been designated for the harbour seal at each of these sites in accordance with the Habitats Directive.

The objectives of this study were to investigate the effects of covariates such as month, time of day and weather on harbour seal abundance at haulout sites in SACs in southwest Ireland, to identify the peak in haulout counts and to determine the optimal timing and environmental conditions under which to conduct haulout counts in order to increase the accuracy of population estimates for the species in Ireland.

#### **METHODS**

#### Study area

Bantry Bay, County Cork (51°36'N, 9°50'W), a flooded river valley, is the longest marine inlet in southwest Ireland with a coastline ranging from exposed rocky shores to sheltered sediment shores. Haulout sites used by harbour seals within Bantry Bay are principally located on rocky inter-tidal skerries and islands in the northeastern region of the bay. The Kenmare River, County Kerry (51°43'N, 10°05'W), is a shallow,

partially mixed estuary where inter-tidal areas are dominated by rocky shores. Haulout sites used by harbour seals within the Kenmare River are predominantly located on rocky inter-tidal skerries within sheltered bays on the northern shore (Fig. 1).

#### **Survey methods**

Comprehensive scoping surveys of Bantry Bay and the Kenmare River were carried out in April 2003 in a Rigid Inflatable Boat (RIB) to locate harbour seal haulout sites. Subsequently, between April 2003 and November 2005 regular standardised haulout count surveys of both bays were carried out by boat at all key sites. Counts of seals at each haulout site were carried out independently and simultaneously by two observers, initially from a distance of approximately 200m from the haulout site and at progressively closer ranges whilst minimising disturbance to the seals.

Surveys were carried out at least monthly year-round and weekly during the summer and autumn, weather permitting. Surveys were scheduled to occur within two hours either side of low tide (as most haulout sites in the area are inter-tidal) and during daylight hours. Surveys began at the head or mouth of the bay on alternate survey dates so that haulout sites would not always be surveyed in the same order within the 4-hour tidal period. On each survey the coastline between

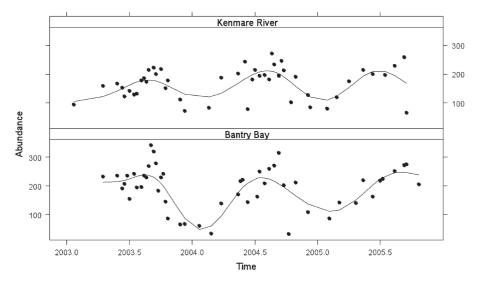
haulout sites was also checked for the presence of seals to ensure that all possible haulout sites used over the study period were identified.

## Statistical modelling

Models were designed to examine the effects of environmental variables on the numbers of seals hauled out during surveys of both bays. The environmental variables investigated included month, time of day, wind speed, wind direction and weather. The effect of tide was not examined as this effect was 'controlled' for by surveying in a 4-hour period around low tide. Abundance data from haulouts within each bay were combined to give a total count for each bay. Following Wood (2006) and Zuur et al. (2009) all variables were treated as categorical variables except for time of the day and month. The bays were surveyed independently and a categorical variable 'site' was included in the models to represent each bay.

Time of the day was included as a variable in our models as this variable has been shown to significantly affect harbour seal haulout behaviour throughout its geographical range (Stewart 1984, Yochem *et al.* 1987, Thompson *et al.* 1989, Thompson and Miller 1990, Thompson *et al.* 1997, Rehberg and Small 2001, Reder *et al.* 2003, Small *et al.* 2003) and is a relatively simple variable to control for in the determination of optimal survey conditions. Seasonal and temporal patterns in haulout count data





(Figs 2 and 3) indicate that we need a statistical methodology that can cope with non-linear patterns, seasonal effects, and potential autocorrelation of count data. We used an Additive mixed modelling framework, a combination of a Generalised Additive Modelling (GAMs) and mixed models (Wood 2006, Zuur et al. 2007, 2009). GAMs use smoothing curves to model non-linear relationships between variables (Hastie and Tibshirani 1990). Mixed effects models can have both fixed and random components together and are used when the data have a hierarchical or nested structure or include longitudinal or spatial elements (Zuur et al. 2007, 2009). All statistical analyses were carried out in R (R Development Core Team, 2007) using the mgcv package (Wood 2003, 2006).

To derive the optimal model in our additive mixed framework we selected the most optimal random components from within a "just beyond optimal model" comprised of fixed components. Once the random components were selected, the most optimal model in terms of fixed components was explored (Fitzmaurice et al. 2004). The optimal model in terms of random components allowed for heterogeneity of variances at least by season. Auto-correlation was added in the form of an auto-regressive model of order 1, allowing for correlation between residuals of sequential weeks of each site. To determine the most optimal model in terms of fixed terms, a backward selection was

carried out and those explanatory variables that were found not to be significant in explaining seal abundance (*p* values >0.05) were dropped sequentially. From our haulout count data (Fig. 3) we expect that, the effect of time of day on seal abundance at haulout sites may change over the year and to accommodate this effect we incorporated a 2-dimensional smoother for the variables 'month' and 'time of day' in the additive mixed model (it allows for an interaction between these two terms).

The variable 'week' was included to explore potential significant variation in the patterns in seal abundance over the entire study period (see also Fig. 2). It was calculated as {year + (week number-1)/52}. It represents the long-term trend. Other terms included were wind direction (1=north/northeast, 2=east/southeast, 3=south/southwest, 4= west/northwest), wind speed (Beaufort 0-5) and weather (1=rain, 2= overcast >50% cloud cover, 3 =sunny). Hence, the starting point of the analysis is the following model:

$$A_j = \text{Site }_j + f_1(\text{Month }_j, \text{TimeofDay }_j) + f_2(\text{WeekTime }_j) + \text{WindDir}_j + \text{WindSpeed}_j + \text{Weather }_j + \text{Year }_j + \text{Year }_j + \epsilon_j$$
where:

 $A_j$  = the seal abundance for observation j, (j=1...97)

 $f_1$  and  $f_2$  stands for smoothing function.  $\epsilon_j$  = residuals (are normally distributed with mean 0)

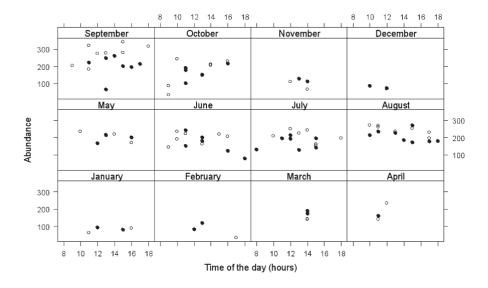
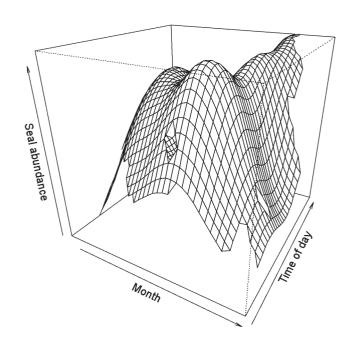


Fig. 3.
Abundances
versus time of
the day for each
month. Open
circles are for
site 1 (Bantry
Bay) and filled
circles for site 2
(Kenmare
River).

Fig. 4. GAMM 2D smoothing curves fitted to partial effects of explanatory variables on abundance of harbour seals in Bantry Bay and Kenmare River in 2003-2005. Abundance is represented as a function of month (1 to 12) and time of day (08.00 to 18.00).



The variance depends on the season. The observations from months 12, 1 and 2 have a variance  $\sigma_1^2$ , the observations from months 3, 4 and 5 have variance  $\sigma_2^2$  months 6, 7 and 8  $\sigma_3^2$  and the remaining months have variance  $\sigma_4^2$ . Within linear regression, a model with multiple variances is estimated with generalized least squares (Pinheiro and Bates 2000, Zuur et al. 2007). Besides different variances, we also allowed for an auto-correlation structure between residuals at the same site. For those covariates that were significant, predictive plots of seal abundance were created for the full range of these covariates. A full model validation was carried out in which we investigated the residuals for violation of homogeneity, independence, lack of fit, and normality. All assumptions were met.

### **RESULTS**

A strong seasonal pattern in harbour seal abundance at haulout sites was evident during the study period in both bays (Fig. 2). Highest numbers were observed during August/September, with numbers declining rapidly during October and November to a minimum over the months December to February. This pattern in abundance was evident throughout the study period in both bays.

Modelling count data as a function of the covariates enabled the determination of the extent of the covariate effects. The optimal model contained a random structure allowing for a different residual spread per month (Likelihood ratio = 15.43, df= 3, p <0.01) and

**Table 1.** Output from ANOVA showing individual probability (*p*) values for explanatory variables fitted as parametric terms, significant in explaining patterns of abundance in harbour seals in Bantry Bay and Kenmare River during 2003-2005.

	Estimate	p value
Intercept (Wind direction 1)	185.17	<0.001
Wind direction 2	- 22.16	0.0808
Wind direction 3	15.13	0.1791
Wind direction 4	20.143	<0.05
Site 2	-22.97	<0.01

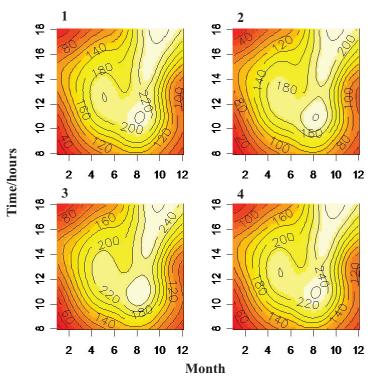


Fig. 5.
Contour plots of harbour seal abundance in Bantry Bay for specified wind direction 1:north/northeast, 2:east/southeast, 3:south/southwest 4: west/northwest).

an auto-correlation structure. Although the auto-correlation term is not significant, it was retained in the models due to the nature of the data. The optimal fixed structure contained terms for month, time of day, wind direction and site.

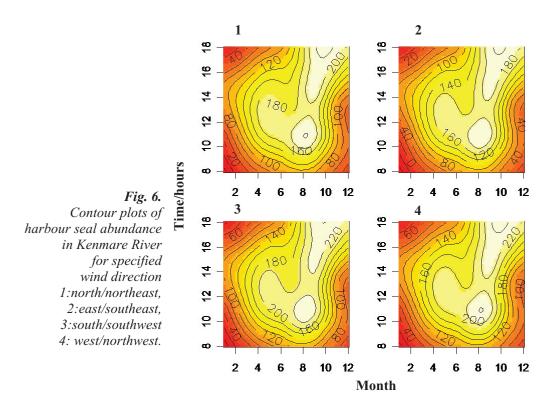
There was a significant effect of month and time of day (estimated degrees of freedom = 19.07, F = 15.15, p < 0.001), wind direction (F = 4.33, df = 3, p < 0.01), and site (F = 11.08, df = 1, p < 0.001) on the abundance of seals at haulout sites in both bays. Table 1 shows estimated values and significance levels per individual level of the categorical variables. Lowest numbers of seals were present in east-southeasterly winds and significantly higher numbers in west-northwesterly winds. There was a 'site' effect with a significantly lower abundance of seals at sites in the Kenmare River (site 2).

The residual variation in months 12, 1 and 2 is considerably smaller than in months 3-8. The largest residual variation is obtained in months 9-11. We also checked whether the model with no interaction between time of day and month (two 1-dimensional smoothers) was any better than the model with the interaction term (one 2-dimensional smoother). The AIC and the like-

lihood ratio test slightly favoured the model with the interaction. The model with the 2-d smoother was less complex in terms of degrees of freedom. The likelihood ratio test was L=0.5812034, df=1, p=0.4458, indicating that the more simple model, with the 2-d smoother is more optimal.

A 2-D smoother of month and time of day shows how the time of day effect changes with month (Fig. 4). The shape of this smoother suggests that the maximum numbers of seals are hauled out close to midday in August. Additionally, time of day appears to have less of an effect on abundance at this time of year as the 'spine' of the smoother suggests, with seal abundance remaining high at haulout sites later in the day. The time of day appears to have much less of an influence on the abundance of seals at haulout sites later in the year, while the reverse is true early in the year with abundance increasing in the afternoon.

Fitted values for seal abundance at haulout sites in Bantry Bay and the Kenmare River were obtained from the optimal model for different wind direction (Figs 5 and 6). These contour plots predict seal numbers at different times of



the day and year based on the data in the model from the period 2003 to 2005. Highest seal numbers of 260 in Bantry Bay (site 1) and 240 in the Kenmare River (site 2) are predicted between 10 AM and midday in August and between 4 PM and 6 PM in September with west/northwesterly winds (wind direction 4).

# DISCUSSION

An obvious seasonal pattern in harbour seal abundance at haulout sites in both Bantry Bay and the Kenmare River was apparent during the course of this study, with the lowest numbers of seals observed in December and January. Numbers at haulout sites increased gradually between January and July followed by a steep increase until August/September, when the peak in abundance was evident. The number of seals declined steadily thereafter throughout the remainder of the year. Generally, two seasonal peaks in abundance at haulout sites have been identified across the harbour seals' geographical range, a peak during May/-June associated with pupping and during August/September associated with moulting

(Thompson and Harwood 1990, Thompson *et al.* 1997, Jemison and Kelly 2001, Huber *et al.* 2001, Harris *et al.* 2003, Reijnders, *et al.* 2003). The timing of the moult of harbour seals in Ireland has not been established. Moulting of harbour seals in nearby Britain occurs from late July through August (Bonner 1972). It is likely that the prominent peak in counts in August/September in southwest Ireland was associated with the annual moult. The peak is typical of that described in other studies of harbour seal haulout behaviour in a rocky shore environment (Thompson *et al.* 1989, Heide-Jørgensen and Härkönen 1988, Thompson and Harwood 1990).

Understanding the seasonal patterns in haulout behaviour is important for identifying the optimal time for carrying out large-scale surveys. Predictive plots indicate that haulout abundance is highest at both Bantry Bay and Kenmare River around midday in August and in the late afternoon/early evening during September. Two peaks in abundance have been explained in other studies as differences in peaks between demographic classes (Thompson and Rothery 1987, Thompson *et al.* 1989,

Härkönen et al. 1999). As it was unfeasible to identify age and sex ratios of haulout groups from the boat during counts, it is impossible to ascertain this in this study. Seal abundance at haulout sites is predicted to be highest during west/north-westerly winds. Such information is useful for determining the timing of future surveys in the area to coincide with peak counts to examine local population trends. These surveys, repeated at annual intervals would provide information on the status of harbour seals within the SACs in Bantry Bay and the Kenmare River. Efforts should also be made to regularly monitor the status of harbour seals outside of protected areas to assess the success of SAC management plans, to identify any potential changes in harbour seal abundance and/or distribution and to better understand national population trends.

The optimal timing and conditions for annual surveys of harbour seals during peak abundance at the rocky haulout sites in the study area identified by the described approach will not necessarily apply to haulout sites outside of the study area, as the influence of covariates has been shown to be associated with haulout substrate type (Thompson et al. 1997). Local data and habitat specific data are needed to produce accurate predictive models. As the timing of peaks in abundance has been shown to vary geographically and temporally (Matthews and Kelly 1996, Jemison and Kelly 2001, Huber et al. 2001) it is recommended that effort be directed at identifying optimal survey times and conditions across the full range of haulout habitat in Ireland rather than using information from other studies on harbour seal haulout behaviour in other parts of their geographical range. However, it is also acknowledged that site specific studies of such detail would be logistically and financially demanding. As the majority of haulout sites used by harbour seals on the Irish coast is on rocky substrate (Cronin, unpublished data) similar to that in the study area and approximately one third of the national population of harbour seals use sites in the study area, we suggest that the results presented here on the optimal period for surveying seals be applied with caution on a national scale, until further data become available. This will have applied implications for the planning of a future census of this Annex II species whose conservation and protection requires frequent assessment of population size and distribution on a national scale.

The effect of the time of day on the seal counts in both bays was observed to change across the year and to be most influential during the summer and autumn months with a peak in abundance evident around midday in August/September. Abundance at haulout sites remained high later in the day at this time of year in contrast to other times of the year when lower numbers were recorded in the evening. A decrease in numbers of seals at haulout sites in the evening may be related to foraging behaviour. It has been suggested that seals feed nocturnally in response to changes in the vertical distribution or schooling behaviour of their prey (Croxall et al. 1985, Thompson et al. 1989). Harbour seals spend a higher proportion of their time ashore during the annual moult (Stevik et al. 2002) and this may explain the temporal change in diurnal haulout patterns observed during the moulting period. The time of day appears to have less of an influence on the abundance of seals at haulout sites in winter, however there is a potential sampling effect as survey effort was much lower in winter. The seasonal change in the patterns in haulout behaviour was also evident from telemetry data from tagged seals in the study area and in spring and summer a distinct diurnal pattern was evident with peak haulout activity during early to mid-afternoon (Cronin et al. 2009). Seasonal changes in the effects of photoperiod influences on haulout behaviour of harbour seals have been observed in Norway, Scotland and Alaska, where strong circadian rhythms were apparent during summer months (Reder et al. 2003, Thompson et al. 1989, Rehberg and Small 2001).

The strength of the wind did not significantly affect haulout behaviour as has been described in other studies (Venables and Venables 1955, Bishop 1968, Boveng *et al.* 2003). Wind direction, however, was observed to have an effect on haulout behaviour with less seals hauled-out during east/south-easterly winds. The prevailing winds in the region are west, south-westerly and its possible that haulout sites are selected that

afford shelter from these winds. As harbour seals show a high degree of site fidelity (Härkönen and Harding 2001) it is possible that they choose not to haulout in onshore east/south-easterly winds at these sites. The variable 'weather', which takes into account the potential affect of rain, cloud and sun on numbers of seals hauled out, was not included in the final model. Studies have shown that less seals are ashore during heavy rain (Pauli and Terhune 1987, Olesiuk et al. 1990, Grellier et al. 1996, Boveng et al. 2003). It is probable that the reason 'weather' was found to be insignificant in the final model is because surveys were not conducted during heavy rain due to limited visibility for the observers, and the category rain included light drizzle/showers only.

The modelling based approach we have developed here is applicable to other sites and habitats. By extending its application to other coastal areas including different haulout substrates, the accuracy of larger scale censuses will be greatly improved. Specifically, the application of covariate models will help improve the accuracy of population estimates over a wide geographical area by 'controlling' for or

standardising environmental conditions and accounting for covariate associated variation in counts. As the influence of covariates can vary spatially at the site and regional scale and temporally across years (Simpkins *et al.* 2003), it would be pragmatic to continue to collect as much information on potential covariates as possible during future seal surveys. We suggest that the modelling approach could also be applied to population survey data of other species in a range of habitat types to identify environmental or other influences on population size and to potentially identify optimal periods for surveying.

#### **ACKNOWLEDGEMENTS**

Many thanks to Mick Mackey, Daphne Roycroft and Tom Hubbard for providing assistance in the field during seal surveys. Thanks also to the anonymous reviewers of the manuscript for their useful comments. The study was funded by the Higher Education Authority (HEA) of Ireland under the PRTLI3 funding mechanism.

# **REFERENCES**

- Adkinson, M.D., Quinn, T.J. and Small, R.J. 2003. Evaluation of the Alaska harbour seal (*Phoca vitulina*) population survey: A simulation study. *Mar. Mamm. Sci.* 19:764-790.
- Bigg, M.A. 1981. Harbour seal *Phoca vitulina* Linnaeus, 1758, and *Phoca largha*, Pallas, 1811. In: Ridgeway, S.H. and Harrison, R.J. (eds.); *Handbook of Marine Mammals*. Academic Press Inc. Ltd, London, 1-77.
- Bishop, R H. 1968. (MS). Reproduction, age determination and behaviour of the harbour seal (*Phoca vitulina* L.) in the Gulf of Alaska. [MSc thesis]. University of Alaska, Fairbanks, AK, USA. 113pp.
- Bonner, W.N. 1972. The grey seal and common seal in European waters. Oceanogr. *Mar. Biol. Ann. Rev.* 10:461-507.
- Boveng, P.L., Bengston, J.L., Withrow, D.E., Cesarone, J.C., Simpkins, M.A., Frost K. J. and Burns, J.J. 2003. The abundance of harbour seals in the Gulf of Alaska. *Mar. Mamm. Sci.* 19:111-127.
- Cronin, M., Duck, C., O'Cadhla, O., Nairn, R., Strong, D. and O'Keefe, C. 2007. An assessment of population size and distribution of harbour seals *(Phoca vitulina vitulina)* in the Republic of Ireland during the moult season in August 2003. *J. Zool.* 273:131-139.
- Cronin, M., Zuur, A., Rogan, E. and McConnell, B. 2009. Using mobile phone technology to investigate the haulout behaviour of harbour seals. *Endang. Spec. Res. Forthcoming*
- Croxall, J.P., Everson, I., Kooyman, G.L., Ricketts, C. and Davis, R.W. 1985. Fur seal diving behaviour in relation to vertical distribution of krill. *J. Anim. Ecol.* 54:1-8.
- Duck, C.D., Thompson, D. and Cunningham, L. 2005. The status of British common seal populations. In: *Scientific Advice on Matters Related to the Management of Seal Populations*. Briefing Paper, 05/4, 54-65.
- Fitzmaurice, G.M., Laird, N.M. and Ware, J.H. 2004. *Applied Longitudinal Analysis*. Wiley. 536pp.
- Frost, K.J., Lowry, L.F. and Ver Hoef, V.M. 1999. Monitoring the trend of harbour seals in Prince William Sound, Alaska after the Exxon Valdez oil spill. *Mar. Mamm. Sci.* 15:494-506.
- Grellier, K., Thompson, P.M. and Corpe, H.M. 1996. The effect of weather conditions on harbour seal (*Phoca vitulina*) haulout behaviour in the Moray Firth, northeast Scotland. *Can. J. Zool.* 74:1806-1811.
- Härkönen, T., Harding, K.C. and Lunneryd, S.G. 1999. Age and sex specific behaviour in harbour seals *Phoca vitulina* leads to biased estimates of vital population parameters. *J. Appl. Ecol.* 36:825-841.
- Härkönen T. and Harding K.C. 2001. Spatial structure of harbour seal populations and the implications thereof. *Can. J. Zool.* 79:2115-2127.

- Harris, D.E., Lelli, B. and Gupta, S. 2003. Long-term observations of a harbour seal haulout site in a protected cove in Casco Bay, Gulf of Maine. *Nor. Natur.* 10:141-148.
- Hastie, T.J. and Tibshirani, R. J. 1990. *Generalised Additive Models*. Chapman & Hall, London. 356pp.
- Heide-Jorgensen, M.P. and Härkönen, T. 1988. Rebuilding seal stocks in the Kattegat-Skagerrak. *Mar. Mamm. Sci.* 4:231-246.
- Huber, H.R., Jeffries, S.J., Brown, R.F., Delong, R.L. and Vanblaricom, G. 2001. Correcting aerial survey counts of harbour seals (*Phoca vitulina richardsi*) in Washington and Oregon. *Mar. Mamm. Sci.* 17:276-293.
- Jemison, L.A. and Kelly, B.P. 2001. Pupping phenology and demography of harbour seals (*Phoca vitulina richardsi*) on Tugidak Island, Alaska. *Mar. Mamm. Sci.* 17:585-600.
- Matthews, E.A. and Kelly, B.P. 1996. Extreme temporal variation in harbour seal *(Phoca vitulina richardsi)* numbers in Glacier Bay, a glacial fjord in S.E. Alaska. *Mar. Mamm. Sci.* 12:483-489.
- Olesiuk, P.F. 1999. *An assessment of the status of harbour seals* (Phoca vitulina) *in British Columbia*. Canadian Stock Assessment Secretariat Research Document 99/33. Fisheries and Oceans Canada, Ottawa, Ontario, Canada. 130 pp.
- Pauli, B.D. and Terhune, J.M. 1987. Tidal and temporal interaction on harbour seal haul-out patterns. *Aquat. Mamm.* 13:93-95.
- Pinheiro, J.C. and Bates, D.M. 2000. *Mixed-effects models in S and S-Plus*. New York, Springer. 528 pp.
- R Development Core Team 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.
- Reder, S., Lydersen, C., Arnold, W. and Kovacs, K. 2003. Haulout behaviour of high Arctic harbour seals *(Phoca vitulina vitulina)* in Svalbard, Norway. *Polar Biol.* 27:6-16.
- Rehberg, M. J. and Small, R. J. 2001. Dive behaviour, haulout patterns and movements of harbour seal pups in the Kodiak archipelago, 1997-2000. In: *Harbour seal investigations in Alaska*. Annual report for NOAA, award NA87FX0300. Alaska Department of Fish & Game, Division of Wildlife Conservation, Anchorage, AK, p 209-238.
- Reijnders, P., Abt, K., Brasseur, S., Tougaard, S., Siebert, U. and Vareschi, E. 2003. Sense and sensibility in evaluating aerial counts of harbour seals in the Wadden Sea. *Wadden Sea Newsletter* 1:9-12.
- Simpkins, M.A., Withrow, D.E., Cesarone, D.E. and Boveng, P.L. 2003. Stability in the proportion of harbour seals hauled out under locally ideal conditions. *Mar. Mamm. Sci.* 19:791-805.
- Small, R.J.G., Pendleton, W. and Pitcher, K.W. 2003. Trends in abundance of Alaska harbour seals, 1983-2001. *Mar. Mamm. Sci.* 19:344-362.

- Stevik, P.T., McConnell, B.J. and Hammond, P.S. 2002. Patterns of movement. In: Hoelzel A.R. (ed.); *Marine Mammal Biology, An Evolutionary Approach*. Blackwell Science Ltd., 185-216.
- Stewart, B.S. 1984. Diurnal patterns of harbour seals at San Miguel Island, California. *J. Wildl. Manage.* 48:1459-1461.
- Thompson, P.M. and Rothery, P. 1987. Age and sex differences in the timing of moult in the common seal, *Phoca vitulina*. *J. Zool.* 212:597-603.
- Thompson, P.M. 1989. Seasonal changes in the distribution and composition of common seal (*Phoca vitulina*) haulout groups. *J. Zool.* 217:281-294.
- Thompson, P.M., Fedak, M., McConnell, B. and Nicholas, K.S. 1989. Seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*). *J. Appl. Ecol.* 26:521-535.
- Thompson, P.M. and Harwood, J. 1990. Methods for estimating the population size of common seals *Phoca vitulina*. *J. Appl. Ecol.* 27:924-938.
- Thompson, P.M. and Miller, D. 1990. Summer foraging activity and movements of radio-tagged common seals (*Phoca vitulina*) in the Moray Firth, Scotland. *J. Appl. Ecol.* 27:492-501.
- Thompson, P.M., Miller, D., Cooper, R. and Hammond, P.S. 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, P.M., Tollit, D.J., Wood, D., Corpe, H.M., Hammond, P.S. and Mackay, A. 1997. Estimating harbour seal abundance and status in an estuarine habitat in north-east Scotland. *J. Appl. Ecol.* 34:43-52.
- Venables, U.M. and Venables, L.S.V. 1955. Observations on a breeding colony of the seal *Phoca vitulina* in Shetland. *Proc. Royal Zool. Soc. Lond.* 125:521-532.
- Watts, P. 1996. The diel hauling out cycle of harbour seals in an open marine environment: Correlates and constraints. *J. Zool.* 240:175-200.
- Wood, S.N. 2003. Thin-plate regression splines. Jour. Royal Stat. Soc. B 65: 1, 95-114.
- Wood, S.N. 2006. *Generalized Additive Models: An Introduction with R*. Chapman and Hall/CRC., 410 pp.
- Yochem, P.K., Stewart, B.S., Delong, R.L., and DeMaster, D.P. 1987. Diel haulout patterns and site fidelity of harbour seals (*Phoca vitulina richardsi*) on San Miguel Island, California in Autumn. *Mar. Mamm. Sci.* 3:323-332.
- Zuur, A.F., Ieno, E.N. and Smith, G.M. 2007. Analysing Ecological Data. Springer Verlag.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. and Smith, G.M. 2009. *Mixed effects models and extensions in ecology with R.* Springer Verlag, 562 pp.