UNIVERSITY OF TROMSØ UiT
FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS
DEPARTMENT OF ARCTIC AND MARINE BIOLOGY

Fine scale haul-out behaviour of harbour seals (*Phoca vitulina*) at different localities in northern Norway

Kristin Herstrøm

BIO-3950 Master's thesis in Biology

May 2013

INSTITUTE OF MARINE RESEARCH
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Front page photo: Harbour seals (*Phoca vitulina vitulina*) hauled out in Kongsfjord.
Photo: Kristin Herstrøm.

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Acknowledgements

I would like to thank all the people at the Institute of Marine Research in Tromsø, for creating such a friendly and inspiring atmosphere and an ideal place for writing a master thesis. In particular I am grateful to my supervisors, Kjell T. Nilssen and Virginie Ramasco, for giving me the opportunity to work on this topic, and for countless hours of supervision, corrections, suggestions and editing advice. A special thank you to Virginie Ramasco for being a fun and helpful fieldwork assistant and for patiently teaching me all the wonderful sides of R, and to Kjell T. Nilssen for achieving aerial survey photographs from the study areas and for allowing me to use the data obtained for my thesis. Thanks to: Michael Poltermann, for support in fieldwork, advice and help in reading aerial photographs, Tor Arne Øigård for help with statistics, calculations and general recommendations, and to Ulf Lindstrøm and Grégoire Certain for useful suggestions and comments. I would also like to thank my supervisor at the University of Tromsø, Nigel Yoccoz, for most helpful advice and suggestions, especially on the statistical analyses. An immense thank you also goes to my dad, not only for taking interest and participating in the fieldwork, but also for supplying crucial survival gear for cold summer days. (The Fjellduk made the countless hours of observation quite comfortable.) The rest of my family and friends also disserves a big thank you, for constantly supporting and encouraging me. A special thank you to Espen, for feedback on various drafts of the thesis, and for always motivating me and making me smile when the light at the end of the tunnel seems so far away.

Abstract

The haul-out behaviour of harbour seal (*Phoca vitulina vitulina*) is influenced by several factors such as the tidal state and environmental variables. Understanding these effects is important for designing counting-surveys providing data necessary to be able to estimate population size. The haul-out behaviour of harbour seals was investigated during the moulting period in three different localities by performing repeated land based visual counts at haul-out sites. The results from the counts were modelled using generalized additive mixed modelling to gain a better understanding of the relationship between the fine scale haul-out behaviour of harbour seals and the tidal cycle, as well as other sources of variability affecting the number of seals hauled out. In addition, results from aerial survey photographs of harbour seals from the same areas were compared to the results from the land based counts. The development of hauled out seals in time at haul-out sites was explained by the tidal cycle and other sources of variation on haul-out behaviour such as disturbance, time of day and movement of seals between haul-out sites were factors influencing seal numbers. The within-day variation in seal numbers along the tidal cycle was also investigated through the use of correction factors which revealed that counting-surveys should be performed around low tide when corrected estimates have a small uncertainty. The unexpected between-days variation in seal numbers, together with the investigated quality of aerial surveys, revealed the need for replicate counts at haul-out sites to provide a measure of uncertainty in the population estimates of Norwegian harbour seals.

Key words: harbour seal, *Phoca vitulina*, haul-out behaviour, within-day variation, between-days variation, correction factor, aerial survey.

Introduction

The harbour seal *Phoca vitulina* is the most widespread of all pinnipeds, with a distribution in temperate and subarctic areas along the eastern and western coast of the North Atlantic and the North Pacific Ocean. There are four recognised marine subspecies of the harbour seal: the eastern North Atlantic harbour seal *Phoca vitulina vitulina* (Linnaeus 1758), the western North Atlantic harbour seal *Phoca vitulina concolor* (DeKay 1842), the eastern North Pacific harbour seal *Phoca vitulina richardii* (Gray 1864), and the western North Pacific harbour seal *Phoca vitulina stejnegeri* (Allen 1902). In addition, there is a fifth subspecies, *Phoca vitulina mellonge* (Doutt 1942) of landlocked harbour seals in lakes and rivers connected with south eastern Hudson Bay. *Phoca vitulina* is a coastal, non-migratory seal and utilizes three distinct types of habitats: open rocky coast, deep fjords and estuarine sandbanks (Bjørge 1991). In Norway the distribution of *Phoca vitulina vitulina* extends along the entire coast, and continues along the Murman coast of Russia, making it the easternmost known habitat for this subspecies (Zyryanov and Egorov 2010). In addition, the world northernmost harbour seal population occurs in Svalbard waters (Prestrud and Gjertz 1990).

The harbour seal is a rather small species with sexual mature males and females weighing between 55 to 130 and 45 to 106 kg, respectively (Bonner 1999). It is an aquatic breeder, but pupping takes place on land. The pups shed the white coat (*lanugo*) *in utero* and the juvenile pelage allow them to enter the water within a few hours from birth (King 1964, Henriksen and Røv 2004). Sexual maturation occurs at around four years of age for females, and five to seven years of age for males (Bjørge 1992). Harbour seals are opportunistic feeders, foraging in shallow waters close to land (Lowry *et al*. 2001). In Norwegian waters they feed mainly on small specimens and small species of codfishes such as saithe (*Pollachius virens*), cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), blue whiting (*Micromesistius poutassou*), Norway pout (*Trisopterus esmarkii*) and pour cod (*Trisopterus minutus*), and other smaller fish species such as sand eel (*Ammodytes* sp.), herring (*Clupea harengus*), and sprat (*Sprattus sprattus*) (Berg *et al*. 2002, Olsen and Bjørge 1995). Harbour seals have also been observed preying on salmon near river mouths (Brown and Mate 1983). Regional and seasonal pattern in the diet of harbour seals appear to coincide with changes in prey availability (Olsen and Bjørge 1995, Brown and Pierce 1998).

In 1997, a new management policy was executed for harbour seals in Norway to ensure viable stocks within their natural distribution areas, also considering the conflict between seals and fisheries. Hunting could be used to control population size, although the population structure along the Norwegian coast was unresolved. Due to a decline in the population during the last two decades (Bjørge *et al*. 2007), the harbour seal was listed as a vulnerable species on the Norwegian Red List in 2006 (Kålås *et al*. 2006). The minimum population of harbour seal in Norway was estimated to be 6,705 in 2004-2006 (Nilssen *et al*. 2010).

Harbour seals spend a considerable amount of time hauled out on land (Stevick *et al*. 2002), for reasons such as resting, avoiding predators (Da Silva and Terhune 1988), and for important life-cycle events, such as pupping during mid summer and moulting during autumn (Everitt and Braham 1980, Jemison and Kelly 2001, Sullivan 1980, Thompson 1989, Thompson *et al*. 1994). The seals haul out on exposed rocks, sandbanks and ice, usually close to their feeding grounds (Bjørge *et al*. 1995). Fidelity to specific haul-out sites by individual seals have been observed (Pitcher and McAllister 1981, Yochem *et al*. 1987, Godsell 1988, Suryan and Harvey 1998, Dietz *et al*. 2012). The haul-out sites are usually located in isolated areas with access to deeper water to minimize potential threats (Terhune 1985) and allowing for an easy escape from terrestrial predators and human disturbance (Terhune and Almon 1983).

Understanding the haul-out behaviour of harbour seals is important for management issues. Counts of hauled out seals during aerial and visual surveys are used for population estimates and are designed to coincide with periods when the highest numbers of seals are hauled out. Large seasonal variation in the haul-out behaviour of harbour seals has been reported (Brown and Mate 1983, Schneider and Payne 1983, Terhune and Almon 1983, Thompson 1989, Harris *et al*. 2003, Cronin *et al.* 2009, Cunningham *et al.* 2009), with low numbers at haul-out sites in winter and spring, and increasing numbers through summer and fall (Brown and Mate 1983, Harris *et al*. 2003) when harbour seals give birth and moult. The annual moult is believed to be a very energy demanding process and seals haul out on land to satisfy the thermal requirements of their epidermal cells (Boily 1995). Consequently, seals haul out more frequently and for a longer duration of time during moult to increase their skin temperature (Paterson *et al*. 2012). Thompson and Harwood (1990) compared results from surveys during the pupping and the moulting periods in Orkney, Scotland and discovered twice as many seals hauled out during the moult. As a result they recommended that future estimates of population size should be based on surveys made during this period. During aerial surveys the haul-out sites are photographed and the photos analyzed in the laboratory. Surveys are usually flown at low tide (± 2 hours) during daytime and in good weather conditions without rain and preferably with sun (Nilssen *et al*. 2010). Seals are easier to count when hauled out ashore; nevertheless, at no point are all the animals in a population hauled out, and counts during aerial surveys only provide a minimum estimate of the population. As a consequence it is desirable to ensure that the timing of the monitoring period coincides with a peak in the probability of a seal being hauled out.

The literature reveals different factors that can influence seal numbers at haul-out sites; these factors can be the origin of variation in numbers at different temporal scales, such as within-day or between-day variation, and spatial scales. Spatial variation can be caused for example by differences in habitats which translate into differences in haul-out site availability (Schneider and Payne 1983, Stewart 1984, Calambokidis *et al*. 1987, Roen and Bjørge 1995), tolerance to disturbance (Suryan and Harvey 1998) or climate (Watts 1992). Within-day variation can be related to time of day (Pauli and Terhune 1987b, Frost *et al*. 1999, Cronin *et al*. 2009), the tidal cycle (Terhune and Almon 1983, Schneider and Payne 1983, Pauli and Terhune 1987b, Cronin *et al*. 2009, Cunningham *et al*. 2010) and single disturbance events (Allen *et al*. 1984). Between-days variation can be due to the timing of low tide with respect to the dial cycle (Kovacs *et al*. 1990, Fowler and Stobo 2005), weather variables like temperature (Schneider and Payne 1983), wind direction (Cronin *et al*. 2010), wind speed (Schneider and Payne 1983, Boveng *et al*. 2003), precipitation (Godsell 1988, Simpkins *et al*. 2003) and cloud cover (Reder *et al*. 2003), or behavioural differences between sexes, among age classes (Härkönen *et al*. 1999) and between individuals (Cronin *et al*. 2009). In addition to the natural sources of variability in seal numbers listed above, an extra source of variation, contributing to the uncertainty of population estimates is represented by the observation error during surveys. Several factors may add to this error, such as counting error due to observer inaccuracy (Thompson and Harwood 1990) or failure to account for all existing haul-out sites (Olesiuk *et al*. 1990).

In Norway there have been few studies regarding these different sources of variation. Roen and Bjørge (1995) studied haul-out behaviour between three different habitats and found that both the tidal cycle and the dial light cycle had an effect on the within-day variation in harbour seal numbers during summer in Kongsfjord (70°42'N, 29°20'E) and in Froan (63°57'N, 9°00'E). Both areas have large to moderate tidal amplitude, while no effect were detected at Hvaler (59°00'N, 10°50'E), an area with small tidal amplitudes. In Vesterålen (69°N, 15°E), Mogren *et al*. (2010) studied the haul-out behaviour of harbour seals and found that during the moulting period tidal cycle did not have a significant effect on the number of seals hauled out. Environmental variables like temperature and cloud cover contributed significantly to explaining the variation in numbers of seals, with more clouds and higher temperatures leading to more seals hauled out. These variations in results obtained from the different studies suggest that haul-out patterns are somehow specific to a population or area and therefore need to be studied at the local scale. In addition, more studies are needed on a fine temporal scale, investigating the fine daily development in time used by seals at haul-out sites and the factor influencing the within-day variation in seal numbers.

When determining population size from the number of harbour seals at haul-out sites, correction factors to account for seals not hauled out are needed to achieve more accurate estimates. Several studies have addressed this issue and different techniques have been used. Behavioural data from individual radio-tagged seals have been used to estimate the proportion of seals in the water to correct aerial survey counts carried out simultaneously (Huber *et al*. 2001, Gilbert *et al*. 2005, Harvey and Goley 2011). In addition, behavioural data from individual radio-tagged seals have also been used to estimate a correction factor for the re-sighting frequency of freeze-branded adult seals, used to model the true proportion of the population that was hauled out (Härkönen *et al*. 1999). Studies using covariate adjusted counts to account for the proportion of seals not hauled out have also been performed. Thompson and Harwood (1990) used observation data of harbour seals hauled out relative to time of day and data on the activity pattern of radio-tagged individual seals to provide a correction factor to compensate for seals which were at sea at the time of surveys. Understanding how the number of seals at a haul-out site develops in time according to the most influential environmental factors will provide information necessary to compute a covariate adjusted correction factor dealing with small scale temporal variation. As well as allowing for sources of variation in counts, covariate adjusted correction factors will help in understanding when the numbers of seals hauled out is less stable and therefore when corrected counts have a high uncertainty. The covariate adjusted correction factors in the present study should not be confused with correction factors used to estimate true population size, which is outside the scope of this study.

This master thesis was done in collaboration with the Institute of Marine Research, who is responsible of performing regular counts (every 5 years) and updates on the abundance of harbour seals in Norway. The study aimed to model land based counts of hauled out harbour seals at three different locations in northern Norway in order to gain a better understanding of the relationship between the fine scale haul-out behaviour of harbour seals and the environmental processes influencing it.

The objectives were:

- To investigate the fine scale development in time of the use of a haul-out site with respect to the tidal cycle and other environmental factors in order to:
  - determine the major sources of variability in the number of seals hauled out,
  - explore the shape of the temporal pattern and identify the timing of the lowest variation in numbers of seals.
- To use the results to define covariate adjusted correction factors.
- To evaluate the quality of aerial surveys by comparing visual count with photographic counts.

Material and methods

Study areas

The present study was carried out on three different harbour seal populations in eastern Finnmark, North Norway: Porsangerfjord (Valdak) (70°8'54.3"N 24°54'57.46"E), Tanafjord (Tana River estuary) (70°30'57.66"N 28°23'33.83"E) and Kongsfjord (70°40'20.42"N 29°16'8.65"E) (Figure 1). The approximate distance (by sea) between Reinøy in Porsangerfjord to the inner eastern part of Tanafjord is 230 km, while the distance from the Tana River estuary to Kongsfjord is approximately 82 km. Preliminary results indicate that the harbour seals from these areas represent genetically separated subpopulations (A.K. Frie, IMR, personal communication). A dispersal study along the Norwegian coast showed that the mean distance between tagging and recovery of harbour seals in North Norway was 54 km (Bjørge *et al*. 2002). In addition, tagging experiments from Porsangerfjord showed that harbour seals move up to 100 km (V. Ramasco, IMR, unpublished data, personal communication). As a consequence, possible exchange of animals between the Tanafjord and Kongsfjord population must be considered due to the relatively short distance between these areas.

Porsangerfjord is 123 km long with depths of 300 meters in the northern area; it is the fourth longest fjord in Norway. The harbour seals are known to haul out at different places in the fjord, along the coast and on small islands (skerries) and rocks. The fieldwork concentrated in Vesterbotn in the inner-western part of the fjord, at the haul-out site called Valdak. Throughout this thesis the Valdak haul-out site will be referred to as Porsangerfjord, although the harbour seals are known to use other haul-out sites in the fjord as well (V. Ramasco, IMR, personal communication). The Valdak haul-out area is very shallow, being 25 meters at its deepest and the harbour seals haul out on exposed rocks as they became available during low tide. In Tanafjord, the study area is in the inner eastern part of the fjord where seals haul out on exposed sandbanks that appear in the Tana River delta at low tide. Around the haul-out sites the water is not deeper than 50 meters, while the fjord is 300 meters at its deepest. The study area in Kongsfjord is located in the inner part of the fjord, where seals haul out on rocks and skerries which become available during low tide. The area is separated from the outer part of Kongsfjord by a narrow strait. The inner part is rather shallow, not deeper than 50 meters, while the rest of the fjord is 80 meters at its deepest. All the three areas in the present study experience large tidal amplitudes (up to 2.5 m).

The most recent (2008) harbour seal abundance estimates in the study areas revealed minimum population counts of 137, 95 and 135 animals in Porsangerfjord (Valdak), Tanafjord and Kongsfjord, respectively (K.T. Nilssen, IMR, personal communication).

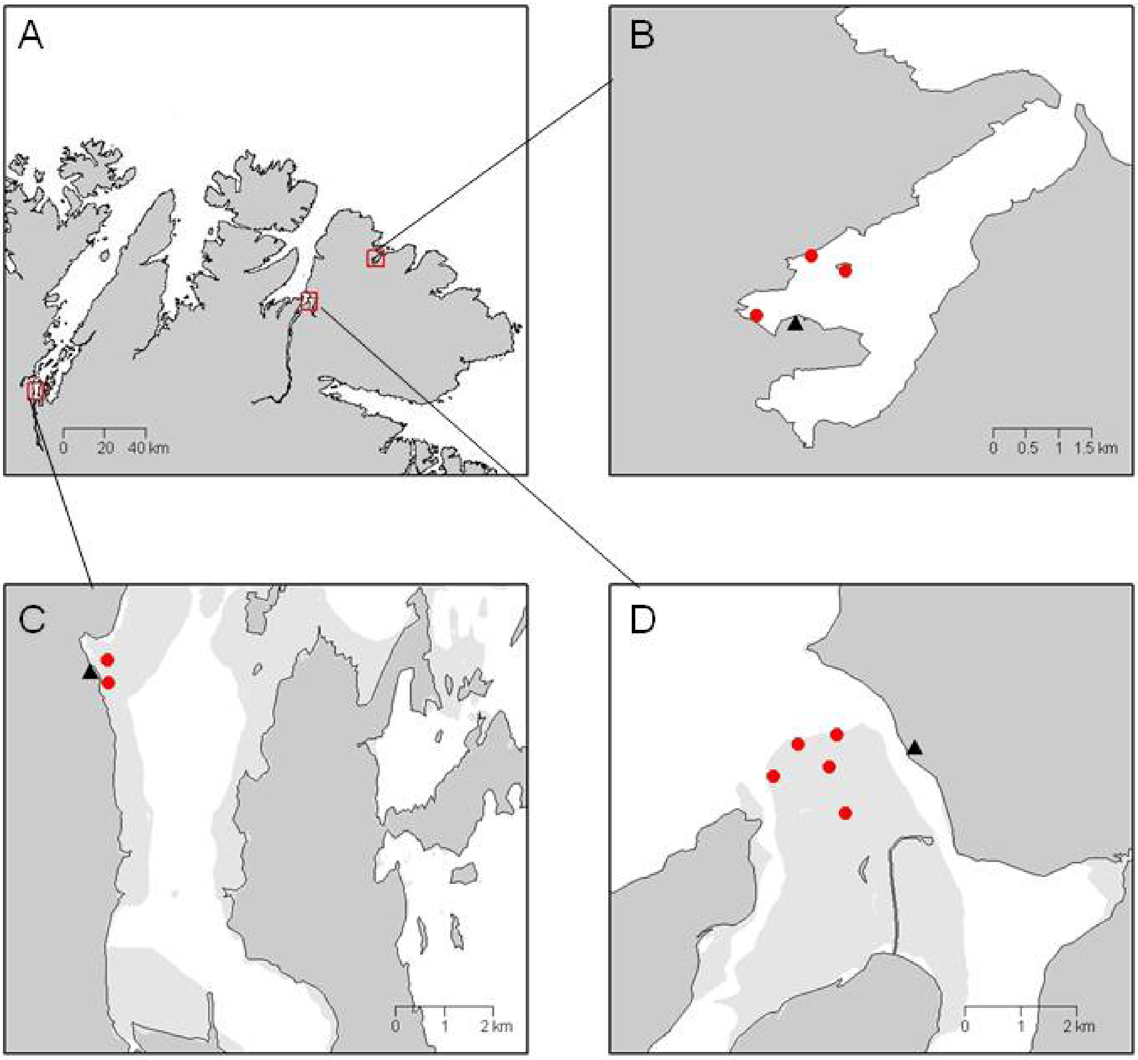

Figure 1: Study area in Finnmark, northern Norway (A): Kongsfjord (B), Porsangerfjord (C) and Tanafjord (D). The light grey polygons represent the areas that dry at the lowest low tides. The black triangles and the red circles are located at the observation site and at the different harbour seal haul-out sites in the study areas, respectively.

Data collection by ground counts

Counts of harbour seals at each haul-out site were carried out by one or two observers from a distance of 200-400, 500-2000 and 600-1000 meters, and at a height of 20, 128 and 36 meters for Porsangerfjord, Tanafjord and Kongsfjord, respectively (Figure 1). The seals were observed using a Swarovski 10x42 binocular and a Swarovski Habicht 80 spotting scope with a 30xWW lens on a tripod. Seals spread along the shoreline, and were considered to be hauled out if their body was resting on a substrate. At high densities repeated counts of the seals were performed. The possibility of seals hiding behind each other was considered and at occasions with large abundance they could be identified if they moved or raised their head or flippers. Seals in the water close to the haul-out site were counted separately.

The timing of the fieldwork were designed to coincide with the annual harbour seal moulting period (Bjørge and Øien 1999). In Tanafjord and Kongsfjord, fieldwork took place between the 10th and the 23rd of August 2012. Effort was designed to make observations from each fjord every other day. The shift in low tide by approximately one hour every day allowed observations to be performed during morning and afternoon low tide at each study area. Observations started from 6 to 3 hours before low tide and seals were counted with 15 minutes intervals until no more seals were hauling out or up to 12 hours of total observation. The Norwegian mapping authority (Kartverket) provided data on the predicted time and height of the tide. During the observation period air temperature (^{o}C), wind speed (m/s) and wind direction were measured by a wireless weather station positioned as close as possible to the haul-out site. Precipitation (absent or present), cloud coverage (percentage of covered sky) and any possible human or animal disturbance were also recorded.

Due to the geographical distance between Porsangerfjord and the two other study areas, the fieldwork in Porsangerfjord was done separately. Observations were carried out between the 22nd and 27th of September 2011, and from the 30th of August to the 4th of September 2012, and followed the same procedure as for Tanafjord and Kongsfjord.

Throughout this thesis the term ‘study area’ represents any of the three different fjords, and ‘haul-out sites’ represents the sites ashore used by the seals within each study area. Figure I.1 (Appendix I) shows as an example the distribution of the different haul-out sites in the study area of Tanafjord.

Statistical analyses of ground counts

Prior to any statistical analysis, data exploration, *i.e*. checking for outliers and collinearity (correlations between covariates) was performed. The response variable (repeated counts of seals at haul-out site) showed clear temporal correlation, and therefore statistical models taking into account auto-correlation were used. The response variable was expected to be related to time relative to low tide (Roen and Bjørge 1995) and the non monotonic pattern in time suggested the use of a non-linear model. In addition, the observed difference in seal numbers between days suggested including days as a random effect. Ignoring positive correlation among observations may increase the type I error (discovering a false covariate effect) and lead to too small p-values (Zuur *et al*. 2010). As a consequence, a Generalized Additive Mixed Model (GAMM) was used to investigate the influence of different factors potentially affecting the number of seals hauled out. GAMMs are a combination of Generalized Additive Modelling (GAMs) and Mixed Modelling (Wood 2006, Zuur *et al*. 2009). The term Generalized refers to models using distributions belonging to the exponential family, and a Poisson distribution was used since the response variable was a count result. GAMs allow for non-linear relationships between the response variable and multiple explanatory variables by using smoothing curves (Hastie and Tibshirani 1990). They do not require any prior assumptions about the underlying relationship between response and predictor variables. Mixed models allow for both random and fixed coefficients and auto-correlation structures can be included.

Over-dispersion, which occurs when the sampling variance is larger than expected by a statistical model, is often observed in count data as a result of a lack of independence between counts (Burnham and Anderson 2002). Ignoring over-dispersion leads to too high precision of model parameters and selection of overly complex models (Anderson *et al*. 1994). Quasi-Poisson (fitted using a quasi-likelihood approach) and negative binomial models have equal numbers of parameters, and either could be used for over-dispersed count data. Comparing two such models by Akaike's Information Criterion (AIC) resulted in the choice for a quasi-Poisson model.

The following explanatory variables defined the upper limit of model complexity (Table 1): time relative to low tide (TRL), precipitation (PREC), wind direction (WD), cloud coverage (CLOUD), disturbance (DIS), time of day (TIME), observation day (OD), wind strength (WIND) and temperature (TEMP) and number of seals swimming in the water close to the haul-out site (SWIM). Due to strong variation in the haul-out behaviour of harbour seals between the three different study areas, separate models were fit for each area.

Observation day (OD) was selected as the random component in the model allowing the variation between the different days, and not described by the fixed effects, to be taken into account. However, the distribution of the random component appeared to be far from normal on a log scale (as assumed by GLMM), which created a bias in the estimation of the auto-correlation. OD was therefore treated both as a fixed and a random factor, the latter to be able to include auto-correlated observations. The full model was therefore specified as following:

$$Log(E[N_{ti}]) \sim s(TRL_t) + \beta_1 PREC_t + \beta_2 WD_t + \beta_3 CLOUD_t + \beta_4 DIS_t + \beta_5 TIME_t + \beta_6 WIND_t + \beta_7 TEMP_t + \beta_8 SWIM_t + \beta_9 OD_t + r_i, \quad (1)$$

where N_{ti} is the total number of seals (on land and in the water) at haul-out site for count at time *t* on day *i*, s is the smoothing function, $r_i \sim N(0, \sigma^2_{OD})$ is the random effect for observation day *i* with variance σ^2_{OD}. $Corr(N_{ti}, N_{ti+1}) = \rho$ (*i.e.* a first-order auto-regressive model).

In the GAMMs thin plate regression splines were used to estimate the smooth function and the parameters were estimated by the method of penalized maximum likelihood. Number of knots, defining the amount of smoothing, were adjusted to avoid over-fitting (Wood 2006).

Due to the complexity of the GAMMs (hierarchical structure and auto-correlated observations), model selection with AIC (Burnham and Anderson 2004) was not used and p-values were applied instead. The best model was obtained by performing a backward stepwise selection on a model containing all the explanatory variables. Those variables not found to be significant (p-values>0.05) in explaining the variation in numbers of seals hauled out were dropped sequentially. The residuals from the best fitting model were investigated for variance homogeneity, and lack of fit (particularly outliers) and the main assumptions were met (Figure I.2-7, Appendix I).

Observer error was tested on the subset of the data where observations were fairly balanced between observers. Observer was entered as a factor in a GAMM model together with the TRL smoother and OD.

A correction factor (CF) for each study area was computed to predict the maximum number of seals at a haul-out site based on the timing of a count relative to low tide. To achieve this, the proportion of seals (P) hauled out was modelled against TRL using a GAMM with a binomial distribution. Mixed models with OD as a random factor were used to be able to implement an auto-correlation structure. Separate models were fit for each area, and the models were specified as:

$$Logit\ (P_{ti}) = s(TRL_t) + r_i, \tag{2}$$

where P_{ti} denotes the proportion of seals at time t on day i (defined as seals hauled out at time t divided by the maximum number of seals hauled out for day i), s is the smoothing function, $r_i \sim N(0, \sigma^2_{OD})$ is the random effect for observation day i, with variance σ^2_{OD}. $Corr(P_{ti}, P_{ti+1})=\rho$ (*i.e.* a first-order auto-regressive model).

The tidal cycle was expected to be the most influential variable at the origin of the non-linear patterns in seal numbers within each day and TRL (modelled as a smoother) was therefore chosen as the only explanatory variable in this model. The variation in maximum number of seals between days was eliminated from the data by using daily proportions and the other potential sources of variation (weather conditions, day time, etc.) were left unexplained and therefore contributed to the residual variation.

The CF_t at time t relative to low tide was defined as:

$$CF_t = \frac{1}{P_t} \tag{3}$$

where P_t is the proportion of seals hauled at time t as predicted from the model. P_t is a stochastic variable with standard deviation σ_{Pt}.

Normally, the covariate adjusted correction factor (CF_t) would be used to find the maximum number of seals at a haul-out site (N_{max}) based on a survey count at time t (N_t) and the associated covariate value (TRL_t). The maximum number of seals (N_{max}) and related confidence intervals (σN_{max}) would then be computed as following:

$$N_{max} = N_t CF_t = \frac{N_t}{P_t}, \tag{4}$$

$$\sigma_{Nmax} = \frac{N}{P_t^2}\, \sigma_{P_t}, \tag{5}$$

$$N_{max} \pm 1.96\, \sigma_{Nmax}. \tag{6}$$

Equation 5 is derived from the methods of propagation of errors based on the properties of the variance (see Appendix II).

However, in this study CF was used in a small simulation experiment to estimate the value of σ_{Nmax} given simulated survey counts at different times relative to low tide. A maximum number of seals (N_{max}) was set and survey counts (N) were simulated along a vector of times *t* by using equation (4). The standard deviation σ_{Nmax} and therefore the confidence intervals ($1.96*\sigma_{Nmax}$) that N_{max} would have had if was computed from a count at time *t* (N_t), were calculated using equation (5). The width of the confidence intervals obtained was used to illustrate an optimal time window relative to low tide when counting-surveys should be performed to achieve estimates with the smallest uncertainties.

All statistical analyses in this thesis were carried out in R (R Core Team 2012), using the *mgcv* package for the mixed modelling (Wood 2006).

Table 1: The explanatory variables, their acronyms, type and factor levels, defining the upper limit of the GAMM models.

Variable	Acronym	Type of variable	Factor level
Time relative to low tide	TRL	Smoother	
Precipitation	PREC	Categorical	Absent, present
Wind direction	WD	Categorical	N, S, E, W
Cloud coverage	CLOUD	Categorical	< 50%, > 50%
Disturbance	DIS	Categorical	Absent, present
Time	TIME	Categorical	Morning, afternoon
Observation day	OD	Categorical	1-25
Wind strength	WIND	Continuous	
Temperature	TEMP	Continuous	
Number of swimming seals	SWIM	Continuous	

Aerial photographic survey

The timing of the present study coincided with the aerial photographic survey of harbour seals done approximately every 5th year by the Institute of Marine Research. In order to estimate the size of the harbour seal population a fixed-wing twin engine Piper Navajo Chieftain aircraft (operated by Terratec, Norway) was used to conduct photographic surveys covering previously known harbour seal moulting haul-out sites (Øynes 1962, Bjørge 1991, Bjørge and Øien 1999, Bjørge *et al*. 2007, Nilssen *et al*. 2010). Aerial surveys were performed in the counties of Sør-Trøndelag, Nord-Trøndelag, Nordland, Troms and Finnmark between the 16th and the 24th of August 2012. The aircraft was equipped with a Vexcel Ultracam Xp digital camera, which provided multichannel images (Red-Green-Blue-Infrared). The surveys were conducted at altitudes of approximately 365 meters shooting vertical photos. GPS positions were recorded for each photo. The surveys were flown around low tide (± 2 hours) during daytime and continuing as long as possible in good weather conditions in the absence of rain and fog, preferably with sun, and moderate wind speed. Each photo session started when the aircraft entered an area containing a known haul-out site and continued until the aircraft moved out of the area. Thus, the survey tracks were predetermined and aimed at complete coverage of the haul-out areas. In high density sites, areas adjacent to the known haul-out sites were also photographed. The harbour seal haul-out sites in Tana River estuary and Kongsfjord were surveyed during the evening of the 16th of August and in the morning of the 17th of August, while Porsangerfjord was surveyed only in the morning of the 17th of August. Figure 2 shows the complete coverage of photographs obtained from the study areas. The photographs obtained from the aerial survey were double-blind counted by two readers to check for reader differences, and then compared with the visual counts from the same area.

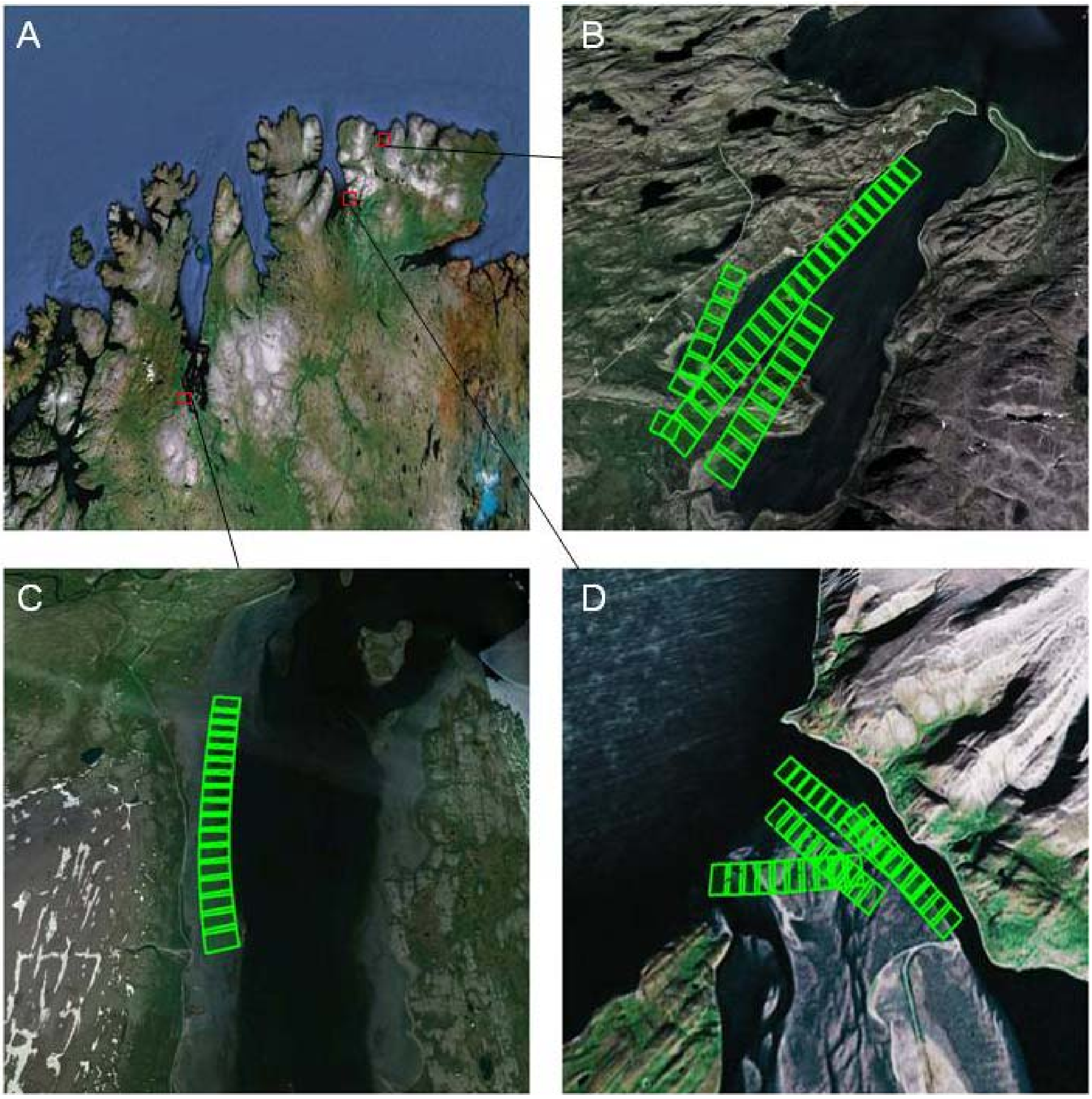

Figure 2: Map of Finnmark, northern Norway (A), showing the extent of the aerial photographic surveys in Kongsfjord (B), Porsangerfjord (C) and Tanafjord (D). The green rectangles indicate each photograph obtained.

Results

Ground counts

Visual observation data for harbour seals hauled out in Porsangerfjord, Tanafjord and Kongsfjord were collected over 5 days in 2011 and 19 days in 2012, producing a total of 590 counts. In all of the three study areas the seals use of different haul-out sites were observed. The seals shifted between these different haul-out sites, influenced by factors such as tide level and disturbance. The maximum numbers of seals observed were 110, 147 and 191 for Porsangerfjord (Valdak), Tanafjord and Kongsfjord, respectively. Details on the observation effort per site and the data obtained are presented in Table 2, and the variables recorded during the study period are presented in Table I.1 (Appendix I).

In Tanafjord and Kongsfjord, the study areas were not regularly exposed to human disturbance, because they were located at isolated sites away from roads and urban habitats. The seals in Tanafjord experienced some boat traffic at 300 to 1000 meters distance from the haul-out site, but the seals did not seem to react to it. In Kongsfjord, on the other hand, the seals experienced disturbance from a red fox (*Vulpes vulpes*) on the beach close to the rocks at one of the haul-out sites. This resulted in all the seals rushing into the water and not returning for the rest of the observation period that day. For the rest of the study period seals were rarely seen at this haul-out site again, and they chose other haul-out sites in the area. On two occasions in Kongsfjord grey seals (*Halichoerus grypus*) were seen hauling out in the same areas as the harbour seals. Four individuals were identified, but this caused little disturbance to the harbour seal group. Individual harbour seals displayed discomfort by growling and flapping their flippers, but at no point did any of the harbour seals leave the haul-out area due to the grey seal interaction. Another source of disturbance to the seals in Kongsfjord was the aerial survey aircraft. One of the two aerial survey sessions in Kongsfjord was performed during an observation period and the seals were observed responding to the approaching aircraft by rushing into the water. In Tanafjord and Porsangerfjord, aerial surveys and ground counts were not executed at the same time so no such response could be detected. However, the seals in Porsangerfjord are known to show little response to aircraft disturbance. The haul-out site at Valdak is located close to the local airport, and during the study period a reaction to this disturbance was not noticed, not even during air force training.

Due to few counts, two observations days in Porsangerfjord were removed from the analysis. In addition, the two first observation days in Kongsfjord and one additional count were also removed from the analysis, due to uncompleted visual coverage of the entire study area. At one occasion in Kongsfjord all the seals rushed to the water shortly after full low tide. No disturbance was visually identified, but these counts were removed from the statistical analysis as well because an undetected disturbance was assumed the most likely cause of it. Number of seals counted by different observers varied as one counter continuously underestimated seal numbers, but this difference was not found significant by the model testing for observer error on a subset of the data (df=1,t=-1.47, p=0.14).

Table 2: Data obtained from ground counts for each of the three study areas.

	Porsangerfjord	Tanafjord	Kongsfjord
Days observed	10	6	9
Number of counts	207	141	242
Hours observed	49.5	40	59.5
Average number of seals	45	84	75
Maximum number of seals	110	147	191

Fine scale haul-out behaviour

The estimated smoothers for time relative to low tide from the best fitted GAMMs revealed a strong tidal effect on the abundance of harbour seals at the haul-out sites in all of the three study areas (Figure 3). The number of seals hauled out increased with the decreasing tide, but there was a clear difference in haul-out behaviour between the areas. In Porsangerfjord seals were observed at haul-out site from 5 hours before low tide. The number slowly increased to a peak at full low tide, then declined steadily and slowly until 5 hours after low tide. The highest number of seals was observed from 1 hour before to 1 hour after full low tide. In the Tanafjord study area the number of hauled out seals increased rapidly from 5 hours until 1 ½ hours before low tide when numbers became rather stable, reaching a peak shortly after full low tide, and quickly decreasing from 1 ½ hours after low tide. The effect of the TRL variable in Kongsfjord revealed that the number of hauled out seals started to increase around 5 hours before full low tide, reaching a peak between 3 ½ hours before and 2 hours after low tide. The smoother revealed unstable numbers of hauled out seals until 2 hours after full low tide when seal numbers started decreasing.

The effects of the covariates on seal numbers were similar among the three study areas. The TRL smoother and the OD factor in the models were highly significant for all the three areas (Table 3). Due to the use of different haul-out sites within each of the three study areas and the observed movement of the seals between these haul-out sites, a variable indicating seals in the water was present in the model (SWIM). In Tanafjord, this had a negative effect (estimate: -0.006764, 95% CI: [-0.012,-0.0006]) on number of seals at haul-out site, indicating that a part of the variation within an observation day was due to the fact that seals in the water were more difficult to count.

In Tanafjord, time of day had an effect (estimate: 0.25, 95% CI: [0.49-0.01]) on haul-out numbers, with more seals hauling out in the morning than in the afternoon. In Porsangerfjord and Kongsfjord, no such effect was detected. Kongsfjord was the only place experiencing disturbance to the seals during the study period (estimate: -0.86, 95% CI: [-1.41,-0.32]). None of the weather variables were found significant in the models.

The fit of the models explained 85% (R^2adj), 87% and 87% of the observed variation in the response variable, for Porsangerfjord, Tanafjord and Kongsfjord, respectively. As OD was added as a fixed variable in the model, it was expected to explain most of the variation. Removing this variable from the models, gave R^2 adjusted of 1.75%, 73% and 52% for Porsangerfjord, Tanafjord and Kongsfjord, respectively.

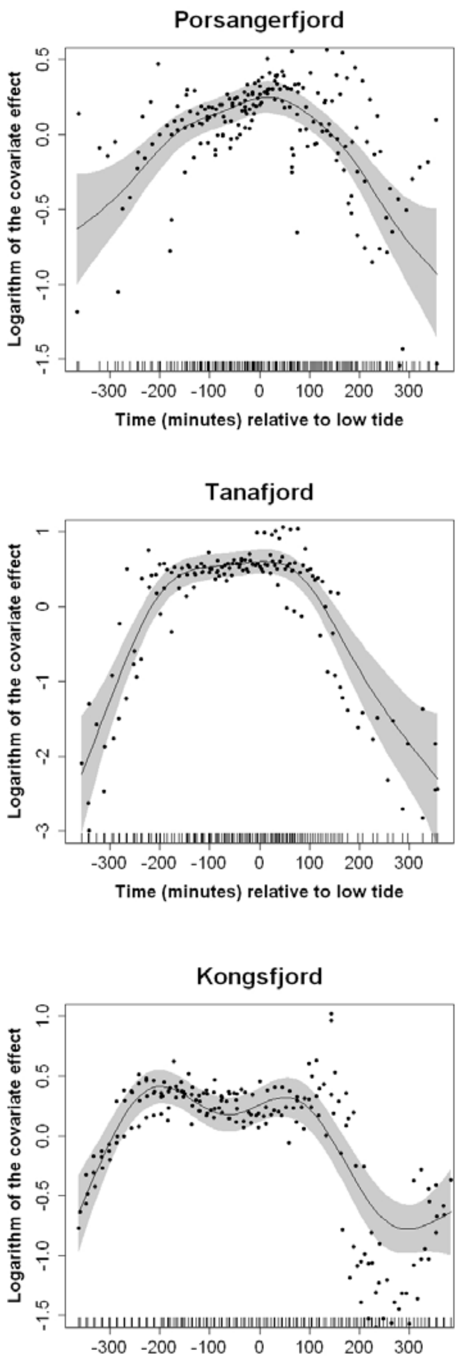

Figure 3: The panels show the estimated smoothing curves for the three best fitted GAMMs, indicating the number of harbour seals hauled out depending on tide for the study areas. The x-axis shows the time relative to low tide (0) in minutes and the y-axis the contribution of the smoother to the fitted values. The solid lines show the smoother and the shaded areas the 95% confidence bands. Partial residuals (black dots) are shown to give an indication of the scale of variability in the data. The ticks along the x-axis correspond to the timing of each observation; their distribution on the axis illustrates the concentration of the observations.

Table 3: ANOVA results from the three best fitting GAMMs showing degrees of freedom (df), F-values and p-values for the explanatory variables fitted as smooth (s) and parametric terms. TRL= time relative to low tide, OD = observation day, TIME = time of day, SWIM = seal in the water close to haul-out sites.

Study area	Coefficient	df	F	p-value
Porsangerfjord	TRL (s)	4.85	5.96	<0.0001
	OD	7	7.75	<0.0001
Tanafjord	TRL (s)	5.98	13.7	<0.0001
	SWIM	1	4.81	0.03
	TIME	1	4.39	0.0382
	OD	5	6.34	<0.0001
Kongsfjord	TRL (s)	4.77	15.2	<0.0001
	DIS	1	9.92	0.0019
	OD	5	8.55	<0.0001

Variation between days

In all of the three study areas the number of seals hauled out varied between observation days (Table I.2, Appendix I). The parameters of the best fitted models are presented in Table I.3 (Appendix I), showing the estimated variability between OD.

Figure 4 illustrates how the maximum numbers of seals varied between observation days. In Kongsfjord, the maximum number of seals increased with observation day, while in Porsangerfjord the maximum number of seals decreased with observation day. In Tanafjord, the numbers showed no such pattern. Tanafjord displayed the least amount of variation in the number of seals hauled out between observation days (mean maximum number of seals = 133.5, SD = 20.3), compared to Kongsfjord (mean maximum number of seals = 136.6, SD = 40.7) and Porsangerfjord (mean maximum number of seals = 56.9, SD=35.7). On observation day number 15 in Tanafjord (Figure 4) counts started after full low tide. Consequently, the maximum number of seals observed that day may be inaccurate due to the fact that more seals could have been hauled out before full low tide.

Due to few observation days and relatively stable weather conditions throughout the study period, the daily variation in number of harbour seals was not modelled. In Figure I.8 (Appendix I) the daily maximum number of seals observed is plotted against the average of the different weather and environmental variables for the three different sites to look for potential trends in seal numbers. Spring tides are the exceptionally high and low tides that occur at the time of the new moon or the full moon when the sun, moon, and earth are approximately aligned. Number of days before or after the timing of spring tide was also included in the plot to explore the effect of tidal amplitude on harbour seal numbers. Patterns differed between study areas. For instance, in Kongsfjord more seals hauled out with less cloud coverage, while in Tanafjord the pattern showed the opposite. In Porsangerfjord the number of seals decreased with days closer to spring tide, while in Kongsfjord the number increased. The only general pattern in all the study areas was more seal at days with afternoon low tides compared to days with morning low tides.

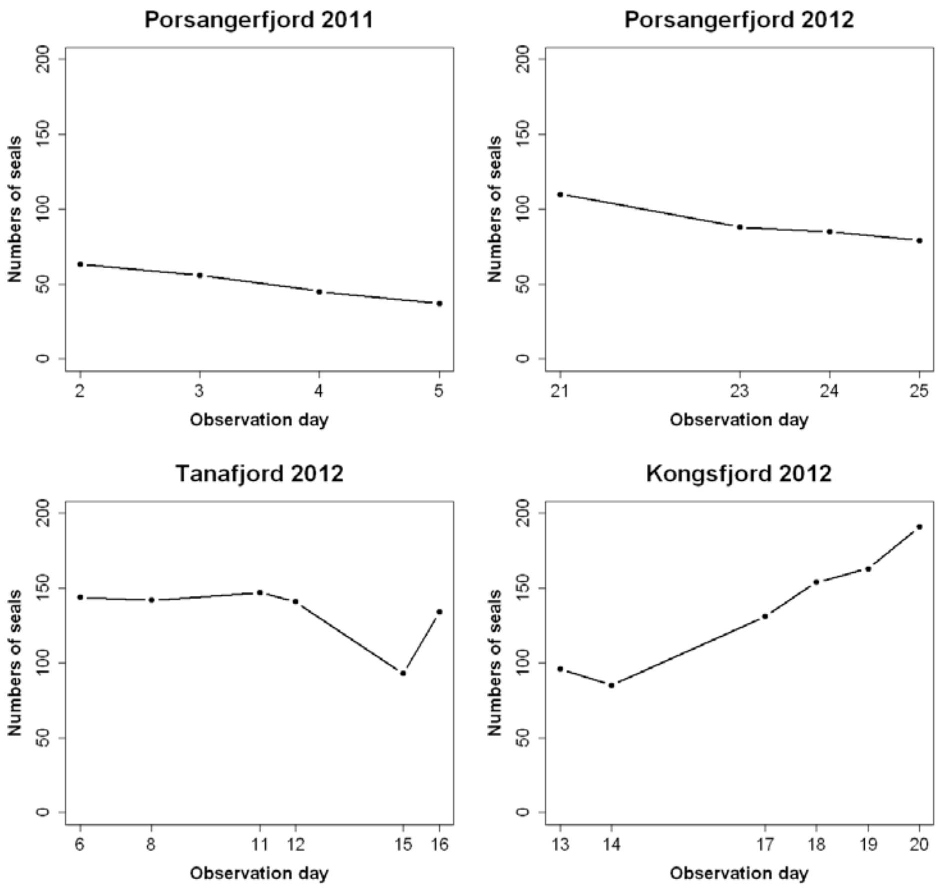

Figure 4: Plots showing the maximum number of harbour seals hauled out in the three study areas according to observation day. Observation day is represented by a number indicating the order of the observations. The observation days in Porsangerfjord lasted from the 22nd to the 27th of September 2011 and from the 30th of August to the 4th of September 2012. In Tanafjord and Kongsfjord the observations were done between the 10th to the 23rd of August 2012. Observation 1, 7, 9, 10 and 22 are removed due to few counts or bias in seal numbers.

Correction factors

Correction factors depending on the time relative to low tide (TRL) variable were calculated in order to estimate the maximum number of seals during a haul-out period based on the number of seals counted at a specific time relative to low tide. The correction factors were calculated using the proportions of seals hauled out relative to low tide as predicted from the binomial GAMM model. In Figure 5, the left panels show the proportion of seals hauled out (the inverse of the correction factor) plotted against time relative to low tide to give an indication of the development in time of the proportion of daily maximum seals hauled out.
The information used to produce these panels is presented in Table I.4, Appendix I, along with the associated correction factors.

The right panels in Figure 5 shows the width of the confidence intervals of the maximum number of hauled out seals (N_{max}) predicted from a simulated survey at different times relative to low tide. N_{max} was set to 120 seals and the width of the confidence intervals obtained is used to illustrate how the variation is smallest around low tide when the peak of number of seals at the haul-out site is reached and the variation in numbers are small, while it is highest when the number of seals is increasing or decreasing. Counting-surveys performed between 3 hour before to 2 hour after low tide, 3 hours before to 1 ½ hour after low tide and 4 ½ hours to 1 ½ before low tide, will provide estimates of maximum numbers of seals with the lowest uncertainties, for Porsangerfjord, Tanafjord and Kongsfjord, respectively.

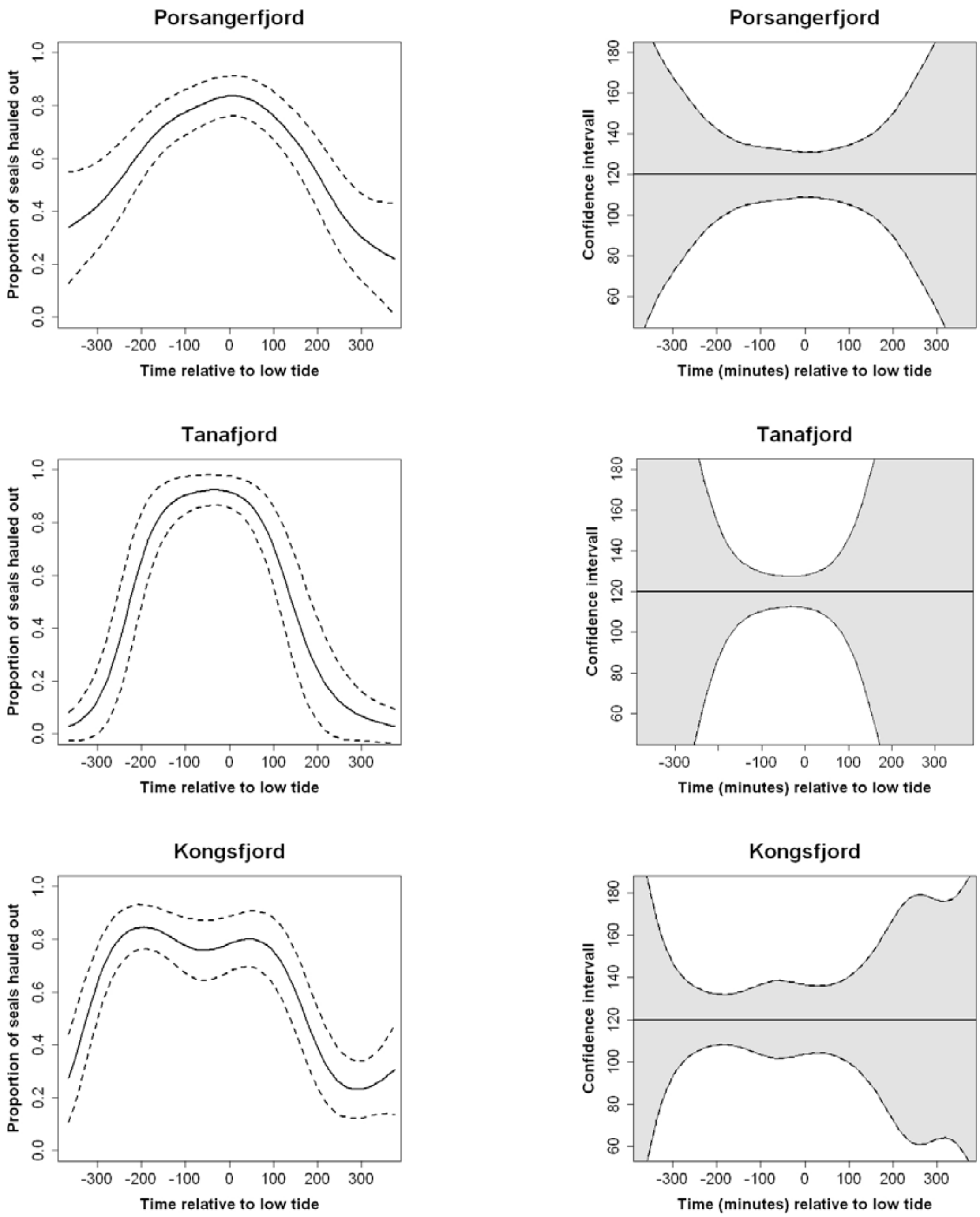

Figure 5: The three left panels' show the proportion of seals hauled out relative to low tide (0) predicted from the binomial GAMMs in Porsangerfjord, Tanafjord and Kongsfjord. The dotted lines represent the 95% confidence intervals of the predictions. The three right panels show the confidence intervals (CI) to the maximum number of seals (N_{max}) plotted against time relative to low tide (0) for Porsangerfjord, Tanafjord and Kongsfjord, illustrating when (relative to low tide) counting surveys should be performed to achieve corrected estimates with lowest uncertainty. The horizontal solid line indicates the set value for N_{max}, while the shaded area shows the width of the CI to N_{max}.

Aerial survey counts

The results from the aerial surveys conducted in the three study areas are presented in Table 4. In Tanafjord and Kongsfjord, two surveys were performed, while in Porsangerfjord only one was achieved. In Porsangerfjord, a total of 99 harbour seals were counted on the photographs from an aerial survey performed ½ hour after low tide. Ground counts from Porsangerfjord performed around the same time relative to low tide revealed a mean of 60 (SD= 22.05) seals across observation days. The two sessions for Tanafjord were performed around 2 ½ and 1 hour before low tide and photographs obtained revealed a total of 104 and 34 harbour seals, respectively. In comparison, the visual counts revealed a mean of 102 (SD= 47.90) and 125 (SD= 20.73) seals across observation days at the same time around low tide respectively. In Kongsfjord, the two sessions were performed 3 hours and 1½ hour before low tide and revealed 20 and 0 seals respectively. The ground counting session that coincided with the first aerial survey session in Kongsfjord revealed 56 seal at the haul-out sites. Due to the fact that the seals rushed to the water when the aircraft approached, not all seals were detected on the photographs. Mean ground counts from 3 and 1½ hour before low tide revealed 132 (SD= 46.86) and 116 (SD= 28.97) seals in this area, respectively.

Table 4: Results from the aerial photographic surveys in the three study areas.

Survey No.	Date	Time	Place	Time of low tide	Time (minutes) relative to low tide	Number of seals counted in photographs
6	16.08.2012	19:41	Kongsfjord	22:47	-186	20
7	16.08.2012	19:43	Kongsfjord	22:47	-184	0
8	16.08.2012	19:53	Tanafjord	22:25	-152	0
9	16.08.2012	19:55	Tanafjord	22:25	-152	104
10	17.08.2012	09:32	Kongsfjord	11:15	-103	0
11	17.08.2012	09:40	Kongsfjord	11:15	-95	0
12	17.08.2012	09:41	Kongsfjord	11:15	-94	0
13	17.08.2012	09:52	Tanafjord	10:53	-61	0
14	17.08.2012	09:55	Tanafjord	10:53	-58	34
25	17.08.2012	10:42	Porsangerfjord/Valdak	10:04	38	99

Discussion

Fine scale haul-out behaviour

Consistent with other studies from areas where haul-out sites availability is influenced by the tide (Terhune and Almon 1983, Schneider and Payne 1983, Pauli and Terhune 1987b, Boveng *et al*. 2003, Cronin *et al*. 2009, Cunningham *et al*. 2010), the GAMMs revealed that the tidal cycle explained most of the within-day variation in harbour seal numbers at haul-out sites in all of the three study areas. In contrast, hauled out harbour seals in Vesterålen, Norway (69°N,15°E) (Mogren *et al*. 2010) showed no significant response to the tidal cycle during the moulting period (see also Lonergan *et al*. 2013). Reder *et al*. (2003) found different haul-out behaviour with respect to the tidal cycle at two different sites at Prince Karls Forland, Svalbard (78°30'N). At one site, more seals were hauled out at high tide, while at the other site, time of day, rather than tide, explained most of the variation in seal numbers. The areas in the present study experience large tidal amplitudes, in contrast with that of Vesterålen (1-1.5 m) (Mogren *et al.* 2010) and Svalbard (<1.5 m) (Reder *et al*. 2003), suggesting that the difference in haul-out behaviour between areas is influenced by local habitat.

Disturbance affects haul-out behaviour of harbour seals (Schneider and Payne 1983, Allen *et al*. 1984, Henry and Hammill 2001), as was experienced in Kongsfjord, caused by the red fox and the survey aircraft. The observed behaviour reflects a high sensitivity to disturbance by the seals in this area. In fact, the seals in Kongsfjord were more alert and responsive to sudden movements, than those in Porsangerfjord and Tanafjord. Occasions where seals simultaneously rushed into the water without any visible disturbance were also observed. However, there is a possibility that an actual disturbance was not detected by the observers. Other studies experiencing the same behaviour in harbour seals (Terhune and Almon 1983, Reder *et al*. 2003) suggested that seals respond to other seals, interpreting sudden movement as a warning signal (Terhune 1985).

Total number of seals at haul-out site was used as the response variable in the model because it was suspected that some of the variation in seal numbers was due to the fact that seals entered the water to move between different haul-out sites. In Tanafjord, the variable indicating seals in the water (SWIM) were found significant revealing that seals in the water are more difficult to count, and can create bias in population estimates. The reason for the abandonment of a haul-out site may be due to the falling tide (Terhune and Almon 1983, Terhune and Brillant 1996). At sites were seals haul out on exposed rocks, leaving the haul-out site before the water becomes too low can be a strategy to avoid being trapped on the rocks that become too steep to depart from as the water level drops. The same strategy can be used by seals hauling out on sandbanks. By following the water edge they can avoid being trapped on dry land. This behaviour may be a safety strategy facilitating escape from terrestrial predators and human disturbance. During the study period the seals observed moving between different haul-out sites quickly re-hauled at the new location and were rarely seen residing in the water around the sites.

In Tanafjord, time of day influenced the haul-out behaviour of harbour seals, with more seals hauling out before midday. A similar pattern was also observed in Kongsfjord and Porsangerfjord, but this effect was not large enough to be found significant in the analysis. Roen and Bjørge (1995) found that time of day had an effect on seal numbers in Kongsfjord and Froan, with higher abundances in the morning. In Ireland the effect of time of day have been observed to change across the year and be most influential during summer, when harbour seals were spending more time ashore around midday (Cronin *et al*. 2010). Other studies have experienced more seals hauling out in the afternoon (Allen *et al*. 1984, Reder *et al*. 2003, Patterson and Acevedo-Gutiérrez 2008), and some found no correlation with seal numbers and time of day (Terhune and Almon 1983). In Tanafjord, morning counts were performed on two days, therefore the results may be influenced by low sample size.

An additional source of variation in seal numbers could be observational error due to high density of seals. The seals were typically observed clumped together facing the same direction perpendicular to the line of view and therefore often difficult to distinguish or impossible to see. Repeated counts were performed at such times, but there is still a risk that the numbers are biased due to over- but most likely underestimation. Observational error could also be related to the view of the haul-out sites. The Tanafjord study area is an open site with better possibilities of detecting all hauled out seals in the area. In Kongsfjord, the seals haul out in a larger area and other possible haul-out sites not detected from the observation site may have been missed. As the Porsangerfjord is large and seals haul out at different sites throughout the fjord, not only the one observed in this study, it is expected that the seals observed at the Valdak haul-out site only represents a fraction of the entire population in the fjord.

The result of this study indicate that the fine scale haul-out behaviour of harbour seals varies between different areas, thus supporting previous findings that haul-out behaviour is site- and condition-specific (Huber *et al*. 2001, Hayward *et al*. 2005). In other studies, factors such as environmental conditions (Simpkins *et al*. 2003) and habitat type (Thompson *et al*.

1997) have been proposed as reasons for regional variation. In this study the suggested difference between the study areas is haul-out availability. In Kongsfjord, where seals hauled out for longer duration of time, available sites could still be found along the fjord banks as the water level rose. The same was observed in Porsangerfjord, but to a lesser degree. In Tanafjord, the sandbanks were completely flooded during higher tides and the seals left the haul-out sites. Local conditions such as disturbance, exposure to wind at haul-out site, and predators presence may also affect haul-out behaviour. Variation in the haul-out behaviour between individual seals (Thompson *et al*. 1989, Cronin *et al*. 2009, Cunningham *et al*. 2009), and between age and sex classes (Härkönen *et al*. 1999, Reder *et al*. 2003) may as well contribute to the variation between sites.

The explained variation in the GAMMs are rather high (see results), but is considerably lower when removing OD from the models. This reflects that most of the variation in the models is due to large variations in harbour seal numbers between days. In the binomial GAMMs the variation in maximum number of seals between days was eliminated from the data by using daily proportions and time relative to low tide (TRL) was the only variable in the model. The fit of these models explained 39% (R^2adj), 77% and 70% of the observed variation in the response variable, for Porsangerfjord, Tanafjord and Kongsfjord, respectively. The result reveal that the daily variation in seal numbers are explained by the effect of the tide and provided information regarding when (relative to low tide) counting-surveys should be performed to achieve better population estimates. However, the variation between days is an important factor when designing counting-surveys and the results from this study revealed a central problem as the large variation increases the risk for underestimating harbour seal numbers.

Variation between days

The patterns of variation in seal numbers between days were only described qualitatively in this thesis. In Porsangerfjord, the fieldwork was performed in two consecutive years. More seals were observed in 2012 than in 2011. Reasons for the observed variation in seal numbers between years may be due to the fact that the 2012 fieldwork was performed earlier in the season than in 2011, matching the peak of the moulting period. An additional explanation can be the higher air temperatures experienced in 2012 than in 2011 (Figure I.8, Appendix I). It has been suggested that during moult, harbour seals will favour higher temperatures to satisfy the thermal requirements of their epidermal cells (Boily 1995). Figure I.8 (Appendix I) reveal no general trend with weather variables and variation in seal numbers between days among the three study areas. Heavy rain is a factor shown to depress the number of seals ashore (Godsell 1988). Few observations in this study with rain and none with heavy rain were experienced, but fewer seals were observed hauling out on days with precipitation. Wind direction (Cronin *et al*. 2010) and wind strength (Boveng *et al*. 2003) are other factors influencing abundance of seals hauling out. This is probably related to exposure of the haul-out sites. The Valdak haul-out site in Porsangerfjord is exposed to south western winds and at one occasion in 2012 no seals were observed at low tide with strong winds (13 m/s). It is possible that the seals used other, more sheltered, haul-out sites in Porsangerfjord during that day. In accordance with the trend in Kongsfjord, Reder *et al.* (2003) found that cloud cover had a negative effect on seal numbers. However, in Tanafjord more seals were observed on days when more than 50% of the sky was covered in clouds. The difference in results between sites may be due to the low sample size. Other studies experienced that none of the weather variables exerted a significant influence on the maximum numbers of seals hauled out on a daily basis (Pauli and Terhune 1987a, Kovacs *et al*. 1990). In Canada, Kovacs *et al*. (1990) found that only time of day at which low tide occurred affected total counts; low tide late in the day resulted in higher counts than did those earlier in the day. This is consistent with the trend in this study where more seals were observed to haul out on days with afternoon low tide rather than days with morning low tides in all of the three study areas.

Cronin *et al*. (2009) found a cyclic pattern with lunar periodicity in the haul-out behaviour of *Phoca vitulina vitulina* in south west Ireland. The same has been reported on *Phoca vitulina richardii* by Simpkins *et al*. (2003) and Watts (1993). Cronin *et al.* (2009) related this activity to exploitation of vertically migrating prey affected by the lunar cycle (Hays 2003), while Watts (1993) argued that the observed pattern was related to predators rather than the amplitude of the tide. The plot in Figure I.8 (Appendix I) indicates that daily maximum numbers of seals increased with days closer to spring tide in Kongsfjord and decreased in Porsangerfjord. As there was no trend in harbour seal numbers in Tanafjord, and the fact that the number of seals from Kongsfjord continued to decrease and numbers from Porsangerfjord decreased for days after spring tide, this pattern is probably site specific and related to other factors.

Härkönen *et al.* (1999) suggest that correlations (or lack of correlations) with weather variables and hauled out numbers could be attributed to changes in the age or sex structure of the hauled out population. Studies have shown that the time of moult varies between different age and sex classes of the harbour seal population, with juveniles moulting first, followed by adult females and adult males moulting last (Thompson and Rothery 1987, Härkönen *et al*. 1999, Daniel *et al*. 2003, Reder *et al*. 2003, Merkel 2012). The proportion of time harbour seals spend hauled out have also shown to vary according to sex, with females spending more time hauled out than males (Cunningham *et al*. 2009, Lonergan *et al*. 2013). If the age and sex structure of populations differed between areas, it could lead to differences in timing and duration of the moult between these areas. The increase in maximum numbers of seals throughout the study period in Kongsfjord (Figure 4) might indicate that the number of moulted seals had not reached a peak, while in Porsangerfjord this may have been reached and seals were declining during the study periods. The low variation in maximum seal number between days in Tanafjord may indicate that the study period coincided with the time when most seals were moulting. Due to the difference in moult according to age and sex classes of the population, aerial surveys conducted during the moulting period may be biased toward a certain age and sex group. Consequently, more information on the structure of a population is needed as it affects the relationship between counts of seals hauled out and the total population size (Härkönen *et al*. 1999).

The weak trend of environmental variables on the haul-out behaviour in this study may also be affected by foraging activity. If harbour seals use more time foraging they would spend less time hauling out. As foraging activity of harbour seals during the moulting season have not been extensively studied, this effect cannot be evaluated. Bjørge *et al*. (1995) discovered that a male tagged in August in Froan, Norway, mainly foraged during the day and only completed forage trips of 5-15 km. As harbour seals spend more time on land during moulting to satisfy the requirements for hair growth, they are expected to spend less time foraging during this period. Studies on seasonal variation in blubber thickness reveal that harbour seal are fatter during the winter than during the reproductive and moult period

(Pitcher 1986), indicating that these two periods may constrain feeding activity during summer (Thompson *et al*. 1989). If the seals fast during the moulting season, feeding activity would not have a great effect on the haul-out behaviour of harbour seals during this period.

Large variation in the haul-out behaviour between individual seals have been observed (Cronin *et al*. 2009). In Porsangerfjord, preliminary results of tagged harbour seals throughout the year show that individual seals do not haul out on every low tide (V. Ramasco, IMR, unpublished data, personal communication). If seals display the same behaviour during the moulting period it would have an effect on the numbers of seals at haul-out sites and create a bias in the estimated population size derived from haul-out counts.

More data is needed to investigate the effect of weather conditions, time of low tide and tidal amplitude in explaining the variation in seal numbers between days. In addition, more extensive knowledge about individual behaviour of harbour seals, as well as foraging activity and demography of the populations during the moulting period is needed to assess whether these factors may influence haul-out behaviour and explain the variability in haul-out numbers between days, thus providing valuable information for the design of counting surveys.

Correction factors

Counts of harbour seals during surveys only provide a minimum estimate of the population because the whole population is not on land simultaneously at a given time. Correction factors provide a valid multiplier, accounting for seals not hauled out during a specific survey count. Knowing the fine scale development in time of the use of a haul-out site, the proportion of the population hauled out at given time relative to low tide can be modelled, making it possible to determine the maximum number of seals expected to be hauled out at a given tidal cycle. In this study the correction factor adjusted for the effect of time relative to low tide was used in a simulation experiment predicting maximum numbers of seals and associated confidence interval. The width of this confidence interval illustrates that although correction factors are available it is more favourable to perform counts when a large proportion of the population is hauled out to reduce the uncertainties around the corrected estimates. In fact, the results demonstrate that counting-surveys performed in a time period when the number of hauled out seals is steeply increasing or decreasing will provide corrected estimates with high uncertainty due to the high variation in numbers during those periods.

The correction factors estimated can only correct counts to the time relative to low tide, as this was the only variable used in the model explaining variation in seal proportions. As other sources of variation are not accounted for (*i.e.* between-days variation), these correction factors cannot be used to correct aerial surveys counts to provide robust population estimate and associated confidence intervals. However, the correction factors can give an indication in the uncertainty in counts performed within a tidal cycle a given day and an important contribution to management issues and design of surveys.

It should also be noted that the maximum number of seals hauled out (N_{max}) in the simulation study was selected as a plausible number; it is not the true population size in the study areas. The standard deviation to the maximum number of seals (σ N_{max}) contains the variation in seal numbers not explained by the time relative to low tide (TRL) smoother in the GAMM. This variation is only representative for the study period used in this study and cannot be extrapolated outside this period when the variation may be different.

Proper correction factors adjusting for the proportion of the animals at sea to estimate population size can be calculated using the same procedure as in this study, by replacing P_{ti} in the binomial GAMM model with information on behaviour from tagged seals during moult. During the last 30 years, studies on harbour seals using radio-tracking, satellite telemetry and GSM phone tags techniques, have become more common (Pitcher and McAllister 1981, Thompson and Miller 1990, Tollit *et al*. 1998, Lowry *et al*. 2001, Simpkins *et al*. 2003, Reder *et al*. 2003, Cronin *et al*. 2009, Cunningham *et al*. 2009, London *et al*. 2012). Using a combination of both behavioural data (haul-out information from telemetry techniques) and information of the age structure of the population (such as catch data) may further improve the correction factors for population estimates (Merkel 2012), thus providing a more accurate adjustment of population size from surveys counts.

Aerial survey counts

Information about trends in population size and abundance is important for management of vulnerable species. Important concerns included impacts of human activities; such as environmental catastrophes like oil spills or unpredicted incidents like virus outbreak, the impact of predation on fisheries and fisheries resources, as well as the impact of fisheries on seals resources. It is also important to scientifically recommend quotas for harbour seal hunt. Aerial photographic surveys have proved a valid method when defining population estimates and are believed to be more accurate than ground counting techniques (Lowry 1999, Cunningham 2006, Bjørge *et al*. 2007), due to a better coverage of the study area during a short period of time (Pitcher and McAllister 1981, Yochem *et al*. 1987, Cunningham 2006).
The result from this study regarding the Kongsfjord study area contradicts these finding. The aerial survey was not able to detect all the seals in the area due to disturbance of the seals as well as uncompleted coverage of the haul-out sites, resulting in large variations between photographic counts and ground counts. The harbour seal counts obtained from the aerial survey in Porsangerfjord and the first session in Tanafjord corresponded well with the ground counts obtained in the same area and at the same time relative to low tide. The large variation in seal numbers between the second session in Tanafjord and the ground counts is possible due to partial coverage of the entire haul-out sites by the aerial photographs. None of the counts from aerial photographs revealed the maximum numbers of seals observed at ground counts in the three study areas. However, it should be noted that the timing of the two first sessions for aerial survey in Tanafjord and Kongsfjord were not optimal. They were too early relative to low tide than the general protocol recommends.

The observed daily variation in seal numbers at haul-out site and the result from the aerial surveys in Tanafjord and Kongsfjord revealed the importance of being able to estimate the uncertainty of the counts. Increased monitoring effort by performing repeated counts will help to achieve more accurate estimates of population sizes and provide a measure of uncertainty in the result; information essential for detecting changes in the population. Previous studies propose that harbour seal haul-out sites should be surveyed every year during the moult, with at least three replicate surveys (Bjørge *et al*. 2007, Teilmann *et al*. 2010). This study supports this protocol, and stresses the importance of replicate surveys to account for the potentially high measurement bias due to variation in seals numbers and the difficulty to cover the haul-out area properly.

Conclusions

Understanding the fine scale haul-out behaviour of harbour seal populations, the factors influencing it and the timing at which most of the population are likely to be on land is important to provide an improved baseline for designing aerial surveys and thus, more accurate population estimates. This study demonstrates the different sources of variation in harbour seals numbers that are important for management issues. The within-day variability in seal numbers at haul-out site was well explained in the areas studied and can be described by the tidal cycle. However, this study was not designed to model the unexpectedly high variation between days, consequently it remains unexplained. Other sources of variation influencing haul-out behaviour in harbour seals, but not investigated in this study, are factors such as timing of moult between different age- and sex-groups, individual haul-out pattern, and movement and foraging during the moult. Future studies are therefore recommended to address these sources of variation contributing to more knowledge about the haul-out behaviour in harbour seals and information needed to design surveys with less bias.

The estimated smoother from the GAMMS reveal that seal numbers at haul-out sites are most stable around low tide. The results differed between the three study areas and reflect the need for areas specific information on harbour seal populations. The results from the simulation experiment using correction factors adjusted for the effect of time relative to low tide further reveal that counting-surveys should be performed around low tide when hauled out seal numbers are stable and corrected estimates have a small uncertainty.

Aerial surveys are an efficient method to monitor harbour seal population, but the results from this study reflects the need for replicate surveys to provide a measure of uncertainty in the counts, as well as information from telemetry studies to calculate correction factors for population estimates. Although such efforts are costly they would provide a great improvement in the precision of population estimates of harbour seals in Norway.

References

Allen, S. G., D. G. Ainley, G. W. Page, and C. A. Ribic. 1984. The effect of disturbance on harbor seal haul out patterns at Bolinas Lagoon, California. *Fishery Bulletin* 82:493–500.

Anderson, D. R., K. P. Burnham, and G. C. White. 1994. AIC model selection in overdispersed capture-recapture data. *Ecology* 75:1780–1793.

Berg, I., T. Haug, and K. T. Nilssen. 2002. Harbour seal (*Phoca vitulina*) diet in Vesterålen, North Norway. *Sarsia: North Atlantic Marine Science* 87:451–461.

Bjørge, A. 1991. Status of the harbour seal *Phoca vitulina* L. in Norway. *Biological Conservation* 58:229–238.

Bjørge, A. 1992. The reproductive biology of the harbour seal, *Phoca vitulina* L., in Norwegian waters. *Sarsia* 77:47–51.

Bjørge, A., D. Thompson, P. Hammond, M. Fedak, E. Bryant, H. Aarefjord, R. Roen, and M. Olsen. 1995. Habitat use and diving behaviour of harbour seals in coastal archipelago in Norway. In: A. S. Blix, L. Walløe, and Ø. Ulltang (eds.); *Whales, seals, fish and man*. Elsevier Science B. V., Amsterdam. 211–223.

Bjørge, A., and N. Øien. 1999. Statusrapport for Havforskningsinstituttets overvåkning av kystsel (Status report for the Institute of Marine Research's monitoring of coastal seals). 35 pp.

Bjørge, A., N. Øien, and N. A. Fagerheim. 2007. Abundance of harbour seals (*Phoca vitulina*) in Norway based on aerial surveys and photographic documentation of hauled-out seals during the moulting season, 1996-1999. *Aquatic Mammals* 33:267–275.

Bjørge, A., N. Øien, S. Hartvedt, G. Bøthun, and T. Bekkby. 2002. Dispersal and bycatch mortality in gray, *Halichoerus grypus*, and harbor, *Phoca vitulina*, seals tagged at the Norwegian Coast. *Marine Mammal Science* 18:963–976.

Boily, P. 1995. Theoretical heat flux in water and habitat selection of phocid seals and beluga whales during the annual molt. *Journal of Theoretical Biology* 172:235–244.

Bonner, N. 1999. True Seals - the Northern Seals. *Seals and sea lions of the world*. Blandford. 86–111.

Boveng, 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.

Brown, E. G., and G. J. Pierce. 1998. Monthly variation in the diet of harbour seals in inshore waters along the southeast Shetland (UK) coastline. *Marine Ecology Progress Series* 167:275–289.

Brown, R. F., and B. R. Mate. 1983. Abundance, movements, and feeding habits of harbor seals, *Phoca vitulina*, at Netarts and Tillamook Bays, Oregon. *Fishery Bulletin* 81:291–301.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A practical information-theoretic approach. Second edi. Springer-Verlag, New York. 488 pp.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* 33:261–304.

Calambokidis, J., B. L. Taylor, S. D. Carter, G. H. Steiger, P. K. Dawson, and L. D. Antrim. 1987. Distribution and haul-out behavior of harbor seals in Glacier Bay, Alaska. *Canadian Journal of Zoology* 65:1391–1396.

Cronin, M. A., A. F. Zuur, S. N. Ingram, and E. Rogan. 2010. A modelling framework to optimize timing of haulout counts for estimating harbour seal (*Phoca vitulina*) abundance. In: G. Desportes, A. Bjørge, A. Rosing-Asvid, and G. T. Waring (eds.); Harbour seals in the North Atlantic and the Baltic, *NAMMCO Scientific Publications, Volume 8*. The North Atlantic Marine Mammal Commission, Tromsø. 213–226.

Cronin, M. A., A. F. Zuur, E. Rogan, and B. J. McConnell. 2009. Using mobile phone telemetry to investigate the haul-out behaviour of harbour seals *Phoca vitulina vitulina*. *Endangered Species Research* 10:255–267.

Cunningham, L. 2006. Investigating monitoring options for harbour seals in special areas of conservation in Scotland. Ph. D. Thesis. University of St Andrews, UK. 209 pp.

Cunningham, L., J. M. Baxter, and I. L. Boyd. 2010. Variation in harbour seal counts obtained using aerial surveys. *Journal of the Marine Biological Association of the United Kingdom* 90:1659–1666.

Cunningham, L., J. M. Baxter, I. L. Boyd, C. D. Duck, M. Lonergan, S. E. Moss, and B. McConnell. 2009. Harbour seal movements and haul-out patterns: implications for monitoring and management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19:398–407.

Da Silva, J., and J. M. Terhune. 1988. Harbour seal grouping as an anti-predator strategy. *Animal Behaviour* 36:1309–1316.

Daniel, R., L. A. Jemison, S. M. Crowley, and G. W. Pendleton. 2003. Molting phenology of harbor seals on Tugidak Island, Alaska. *Marine Mammal Science* 19:128–140.

Dietz, R., J. Teilmann, S. M. Andersen, F. Riget, and M. T. Olsen. 2012. Movements and site fidelity of harbour seals (*Phoca vitulina*) in Kattegat, Denmark, with implications for the epidemiology of the phocine distemper virus. *ICES Journal of Marine Science* 69:1–10.

Everitt, R. D., and H. W. Braham. 1980. Aerial survey of pacific harbor seals in the southeastern Bering Sea. *Northwest Science* 54:281–288.

Fowler, M. A., and W. T. Stobo. 2005. Source of variability in aerial survey counts of harbour seals on haul-out sites in the Bay of Fundy. *Canadian Technical Report of Fisheries and Aquatic Sciences 2611*. 26 pp.

Frost, K. J., L. F. Lowry, and J. M. Ver Hoef. 1999. Monitoring the trend of Harbor Seals in Prince William Sound, Alaska, after the Exxon Valdez oil spill. *Marine Mammal Science* 15:494–506.

Gilbert, J. R., G. T. Waring, K. M. Wynne, and N. Guldager. 2005. Changes in abundance of harbor seals in Maine, 1981-2001. *Marine Mammal Science* 21:519–535.

Godsell, J. 1988. Herd formation and haul out behaviour in harbour seals (*Phoca vitulina*). *Journal of Zoology* 215:83–98.

Harris, D. E., B. Lellim, and S. Gupta. 2003. Long-term observations of a harbor seal haul-out site in a protected cove in Casco Bay, Gulf of Maine. *Northeastern Naturalist* 10:141–148.

Harvey, J. T., and D. Goley. 2011. Determining a correction factor for aerial surveys of harbor seals in California. *Marine Mammal Science* 27:719–735.

Hastie, T. J., and R. J. Tibshirani. 1990. *Generalized Additive Models*. Chapman & Hall, London. 335 pp.

Hays, G. C. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503:163–170.

Hayward, J. L., S. M. Henson, C. J. Logan, C. R. Parris, M. W. Meyer, and B. Dennis. 2005. Predicting numbers of hauled-out harbour seals: a mathematical model. *Journal of Applied Ecology* 42:108–117.

Henriksen, G., and N. Røv. 2004. *Kystsel - havert og steinkobbe*. Tapir Akademisk Forlag, Trondheim. 131 pp.

Henry, E., and M. O. Hammill. 2001. Impact of small boats on the haulout activity of harbour seals (*Phoca vitulina*) in Métis Bay, Saint Lawrence Estuary, Québec, Canada. *Aquatic Mammals* 27:140–148.

Huber, H. R., S. J. Jeffries, R. F. Brown, R. L. Delong, and G. Vanblaricom. 2001. Correcting aerial survey counts of harbor seals (*Phoca vitulina richardsi*) in Washington and Oregon. *Marine Mammal Science* 17:276–293.

Härkönen, T., K. C. Hårding, 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.

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.

King, J. E. 1964. True seals of the north. *Seals of the world*. Trustees of the British Museum (Natural History), London. 43–66.

Kovacs, K. M., K. M. Jonas, and S. E. Welke. 1990. Sex and age segregation by *Phoca vitulina concolor* at haul-out sites during the breeding season in the Passamaquoddy Bay region, New Brunswick. *Marine Mammal Science* 6:204–214.

Kålås, J. A., Å. Viken, and T. Bakken (eds.). 2006. Norsk Rødliste 2006 (2006 Norwegian redlist). Artsdatabanken Norge (Norwegian Biodiversity Information Centre), Trondheim. 416 pp.

London, J. M., J. M. Ver Hoef, S. J. Jeffries, M. M. Lance, and P. L. Boveng. 2012. Haul-out behavior of harbor seals (*Phoca vitulina*) in Hood Canal, Washington. *PloS one* 7:1–9.

Lonergan, M., C. Duck, S. Moss, C. Morris, and D. Thompson. 2013. Rescaling of aerial survey data with information from small numbers of telemetry tags to estimate the size of a declining harbour seal population. *Aquatic Conservation: Marine and Freshwater Ecosystems* 23:135–144.

Lowry, L. F., K. J. Frost, J. M. Ver Hoef, and R. A. Delong. 2001. Movements of satellite-tagged subadult and adult harbor seals in Prince William Sound, Alaska. *Marine Mammal Science* 17:835–861.

Lowry, M. S. 1999. Counts of California sea lion (*Zalophus californianus*) pups from aerial color photographs and from the ground: a comparison of two methods. *Marine Mammal Science* 15:143–158.

Merkel, B. 2012. The world's northern most harbour seal population - How many are there? M. Sc. Thesis. University of Tromsø, Norway. 41 pp.

Mogren, H.-G., U. Lindstrøm, K. T. Nilssen, and T. Haug. 2010. Haulout behaviour of harbour seals (*Phoca vitulina*) during breeding and moult in Vesterålen, Norway. In: G. Desportes, A. Bjørge, A. Rosing-Asvid, and G. T. Waring (eds.); *Harbour seals in the North Atlantic and the Baltic, NAMMCO Scientific Publications, Volume 8.* The North Atlantic Marine Mammal Commission, Tromsø. 303–312.

Nilssen, K. T., N.-E. Skavberg, M. Poltermann, T. Haug, T. Härkönen, and G. Henriksen. 2010. Status of harbour seals (*Phoca vitulina*) in mainland Norway. In: G. Desportes, A. Bjørge, A. Rosing-Asvid, and G. T. Waring (eds.); *Harbour seals in the North Atlantic and the Baltic, NAMMCO Scientific Publications, Volume 8*. The North Atlantic Marine Mammal Commission, Tromsø. 61–70.

Olesiuk, P. F., M. A. Bigg, and G. M. Ellis. 1990. Recent trends in the abundance of harbour seals, *Phoca vitulina*, in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 47:992–1003.

Olsen, M., and A. Bjørge. 1995. Seasonal and regional variation in the diet of harbour seals in Norwegian waters. In: A. S. Blix, L. Walløe, and Ø. Ulltang (eds.); *Whales, seals, fish and man.* Elsevier Science B. V., Amsterdam. 271–285.

Paterson, W., C. E. Sparling, D. Thompson, P. P. Pomeroy, J. I. Currie, and D. J. McCafferty. 2012. Seals like it hot: Changes in surface temperature of harbour seals (*Phoca vitulina*) from late pregnancy to moult. *Journal of Thermal Biology* 37:454–461.

Patterson, J., and A. Acevedo-Gutiérrez. 2008. Tidal influence on the haul-out behavior of harbor seals (*Phoca vitulina*) at a site available at all tide levels. *Northwestern Naturalist* 89:17–23.

Pauli, B. D., and J. M. Terhune. 1987a. Meteorological influences on harbour seal haul-out. *Aquatic Mammals* 13:114–118.

Pauli, B. D., and J. M. Terhune. 1987b. Tidal and temporal interaction on harbour seal haul-out patterns. *Aquatic Mammals* 13:93–95.

Pitcher, K. W. 1986. Variation in blubber thickness of harbor seals in southern Alaska. *The Journal of Wildlife Management* 50:463–466.

Pitcher, K. W., and D. C. McAllister. 1981. Movements and haulout behaviour of radio-tagged harbor seals, *Phoca vitulina*. *The Canadian field-naturalist* 95:292–297.

Prestrud, P., and I. Gjertz. 1990. The most northerly harbor seal, *Phoca vitulina*, at Prins Karls Forland, Svalbard. *Marine Mammal Science* 6:215–220.

R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reder, S., C. Lydersen, W. Arnold, and K. M. Kovacs. 2003. Haulout behaviour of High Arctic harbour seals (*Phoca vitulina vitulina*) in Svalbard, Norway. *Polar Biology* 27:6–16.

Roen, R., and A. Bjørge. 1995. Haul-out behaviour of the Norwegian harbour seal during summer. In: A. S. Blix, L. Walløe, and Ø. Ulltang (eds.); *Whale, seal, fish and man*. Elsevier Science B. V., Amsterdam. 61–67.

Schneider, D. C., and P. M. Payne. 1983. Factors affecting haul-out of harbor seals at a site in southeastern Massachusetts. *Journal of Mammalogy* 64:518–250.

Simpkins, M. A., D. E. Withrow, J. C. Cesarone, and P. L. Boveng. 2003. Stability in the proportion of harbor seals hauled out under locally ideal conditions. *Marine Mammal Science* 19:791–805.

Stevick, P. T., B. J. McConnell, and P. S. Hammond. 2002. Patterns of movement. In: A. R. Hoelzel (ed.); *Marine Mammal Biology: an evolutionary approach*. Blackwell Science Ltd. 185–246

Stewart, B. S. 1984. Diurnal hauling patterns of harbor seals at San Miguel Island, California. *The Journal of Wildlife Management* 48:1459–1461.

Sullivan, R. M. 1980. Seasonal occurrence and haul-out use in pinnipeds along Humboldt County, California. *Journal of Mammalogy* 61:754–760.

Suryan, R. M., and J. T. Harvey. 1998. Tracking harbor seals (*Phoca vitulina richardsi*) to determine dive behavior, foraging activity, and haul-out site use. *Marine Mammal Science* 14:361–372.

Teilmann, J., F. Rigét, and T. Härkönen. 2010. Optimizing survey design for Scandinavian harbour seals: population trend as an ecological quality element. *ICES Journal of Marine Science* 67:952–958.

Terhune, J. M. 1985. Scanning behaviour of harbour seals on haul-out sites. *Journal of Mammalogy* 66:392–395.

Terhune, J. M., and M. Almon. 1983. Variability of harbour seal numbers on haul-out sites. *Aquatic Mammals* 10:71–78.

Terhune, J. M., and S. W. Brillant. 1996. Harbour seal vigilance decreases over time since haul out. *Animal behaviour* 51:757–763.

Thompson, P. M. 1989. Seasonal changes in the distribution and composition of common seal (*Phoca vitulina*) haul-out groups. *Journal of Zoology* 217:281–294.

Thompson, P. M., M. A. Fedak, B. J. McConnell, and K. S. Nicholas. 1989. Seasonal and sex related variation in the activity patterns of common seals (*Phoca vitulina*). *Journal of Applied Ecology* 26:521–535.

Thompson, P. M., and J. Harwood. 1990. Methods for estimating the population size of common seals, *Phoca vitulina*. *Journal of Applied Ecology* 27:924–938.

Thompson, P. M., and D. Miller. 1990. Summer foraging activity and movements of radio-tagged common seals (*Phoca vitulina.* L.) in Moray Firth, Scotland. *Journal of Applied Ecology* 27:492–501.

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., 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. 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.

Tollit, D. J., A. D. Black, P. M. Thompson, A. Mackay, H. M. Corpe, B. Wilson, S. M. Van Parijs, K. Grellier, and S. Parlane. 1998. Variations in harbour seal *Phoca vitulina* diet and dive-depths in relation to foraging habitat. *Journal of Zoology* 244:209–222.

Watts, P. 1992. Thermal constraints on hauling out by harbour seals (*Phoca vitulina*). *Canadian Journal of Zoology* 70:553–560.

Watts, P. 1993. Possible lunar influence on hauling-out behavior by the pacific harbor seal (*Phoca vitulina richardsi*). *Marine Mammal Science* 9:68–76.

Wood, S. 2006. *Generalized additive models: an introduction with R*. Chapman & Hall/CRC, Boca Raton, Florida. 410 pp.

Yochem, P. K., B. S. Stewart, R. L. DeLong, and D. P. DeMaster. 1987. Diel haul-out patterns and site fidelity of harbor seals (*Phoca vitulina richardsi*) on San Miguel Island, California, in autumn. *Marine Mammal Science* 3:323–332.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:3–14.

Zuur, A. F., E. N. Ieno, N. Walker, A. a. Saveliev, and G. M. Smith. 2009. *Mixed Effect Models and Extensions in Ecology with R*. Springer, New York. 574 pp.

Zyryanov, S. V., and S. A. Egorov. 2010. Status of the harbour seal (*Phoca vitulina*) along the Murman coast of Russia. In: G. Desportes, A. Bjørge, A. Rosing-Asvid, and G. T. Waring (eds.); *Harbour seals in the North Atlantic and the Baltic, NAMMCO Scientific Publications, Volume 8*. The North Atlantic Marine Mammal Commission, Tromsø. 37–46

Øynes, P. 1962. Sel på norskekysten fra Finnmark til Møre. *Fiskets Gang* 48:694–707.

Appendix I: Additional figures and tables

Figure I.1: The study area in the Tana River estuary with H1-H5 showing the different haul-out sites used by the harbour seals.

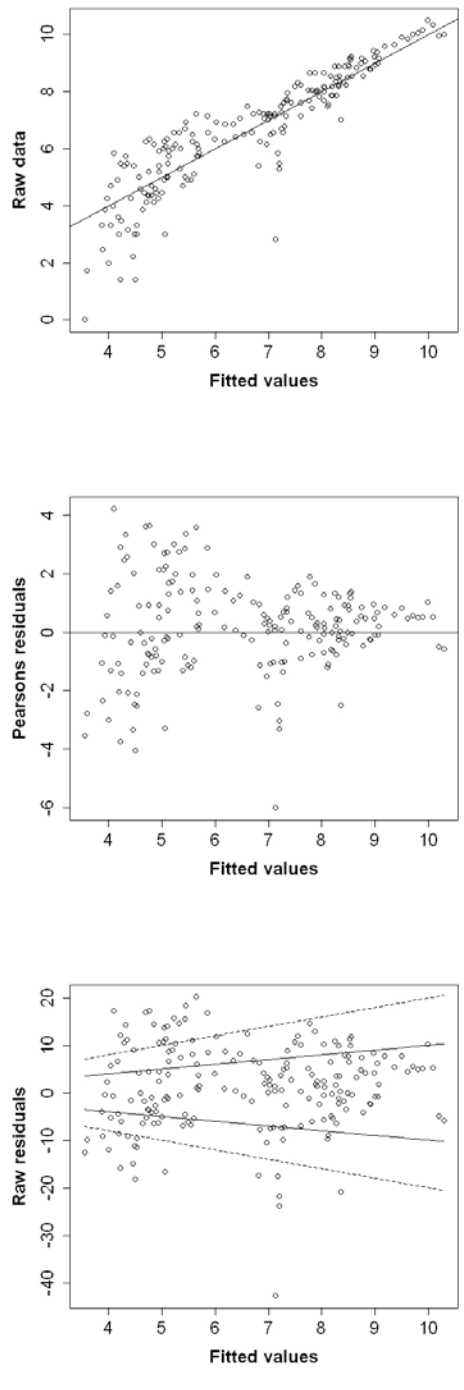

Figure I.2: Model validation plots for the best fitted GAMM of the Porsangerfjord harbour seal ground counts data. The upper panel shows the relationship between raw data and fitted values. The middle panel plots Pearson residuals against fitted values. The lower panel shows raw residuals against fitted values, with reference lines illustrating where 1 residual standard deviation and 2 residual standard deviations from the residual mean should lie, for each fitted value.

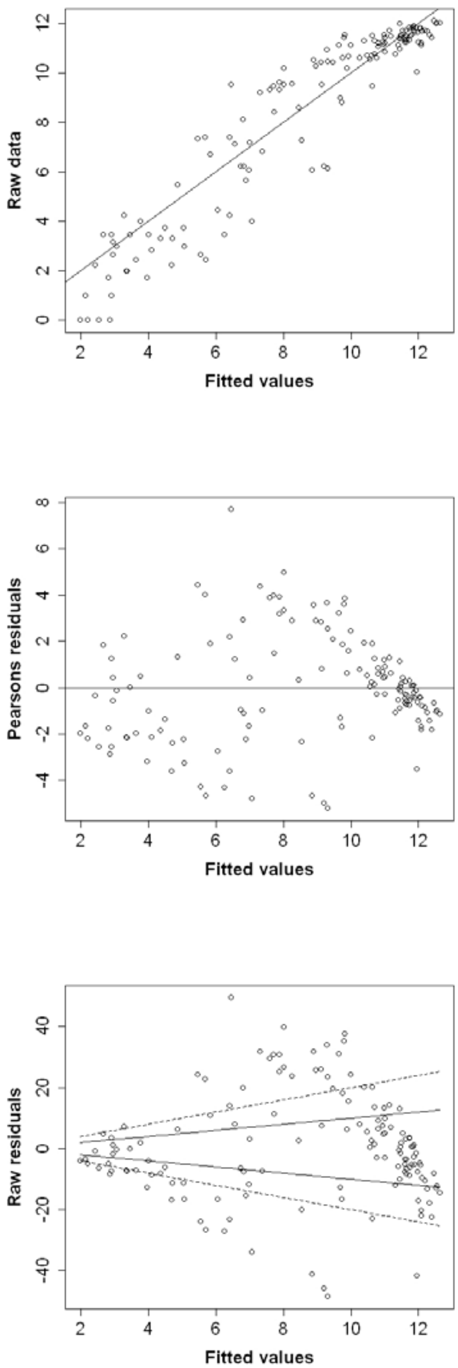

Figure I.3: Model validation plots for the best fitted GAMM of the Tanafjord harbour seal ground counts data. The upper panel shows the relationship between raw data and fitted values. The middle panel plots Pearson residuals against fitted values. The lower panel shows raw residuals against fitted values, with reference lines illustrating where 1 residual standard deviation and 2 residual standard deviations from the residual mean should lie, for each fitted value.

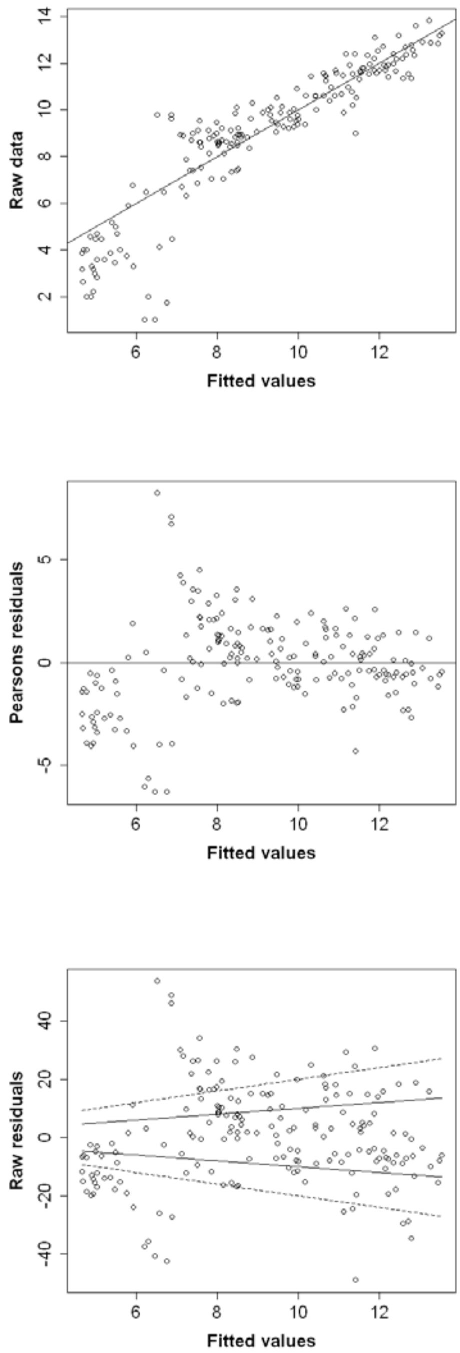

Figure I.4: Model validation plots for the best fitted GAMM of the Kongsfjord harbour seal ground counts data. The upper panel shows the relationship between raw data and fitted values. The middle panel plots Pearson residuals against fitted values. The lower panel shows raw residuals against fitted values, with reference lines illustrating where 1 residual standard deviation and 2 residual standard deviations from the residual mean should lie, for each fitted value.

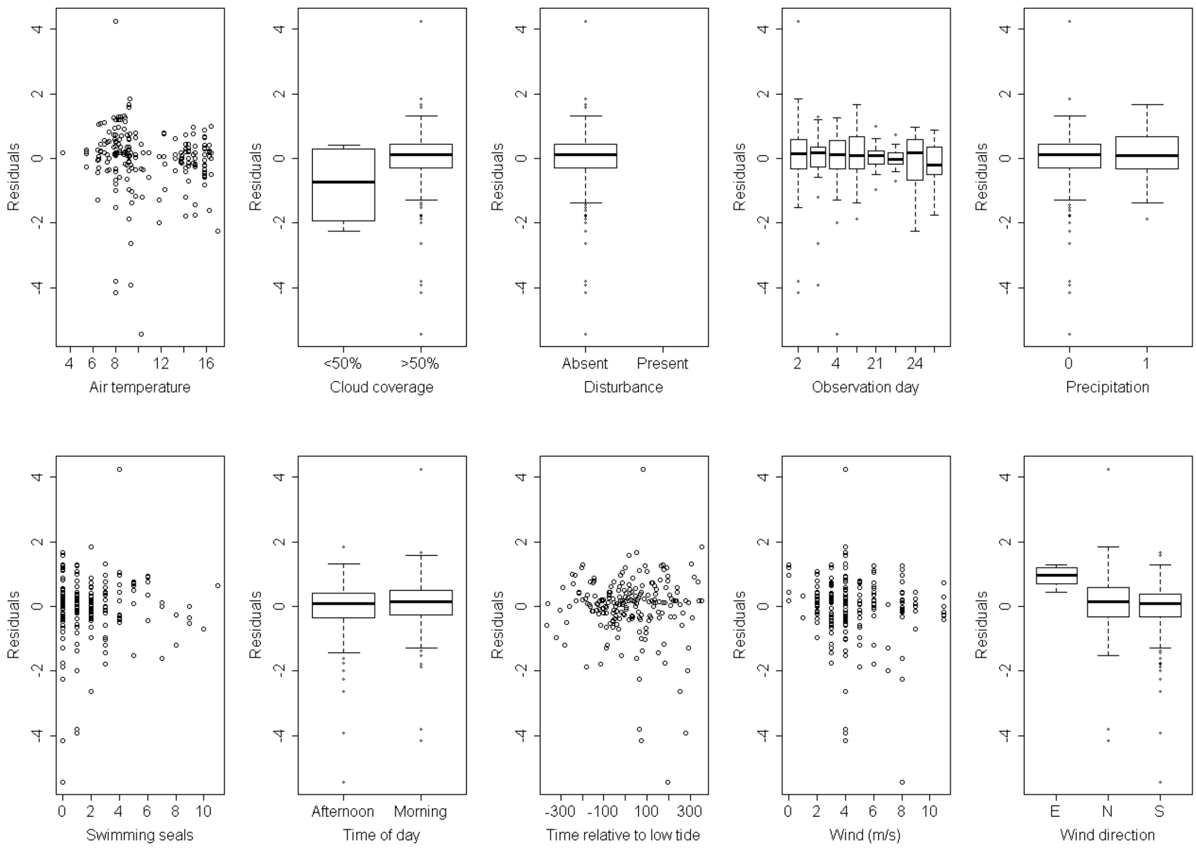

Figure I.5: Model validation plots: the residuals from the best fitted GAMM from Porsangerfjord plotted against all the different explanatory variables, those used in the final model (time relative to low tide and observation day) as well as the ones dropped during model selection procedure. In the box plots the median is indicated by the black horizontal line and the 25% and 75% quartiles forms a box around the median that contains half of the observations.

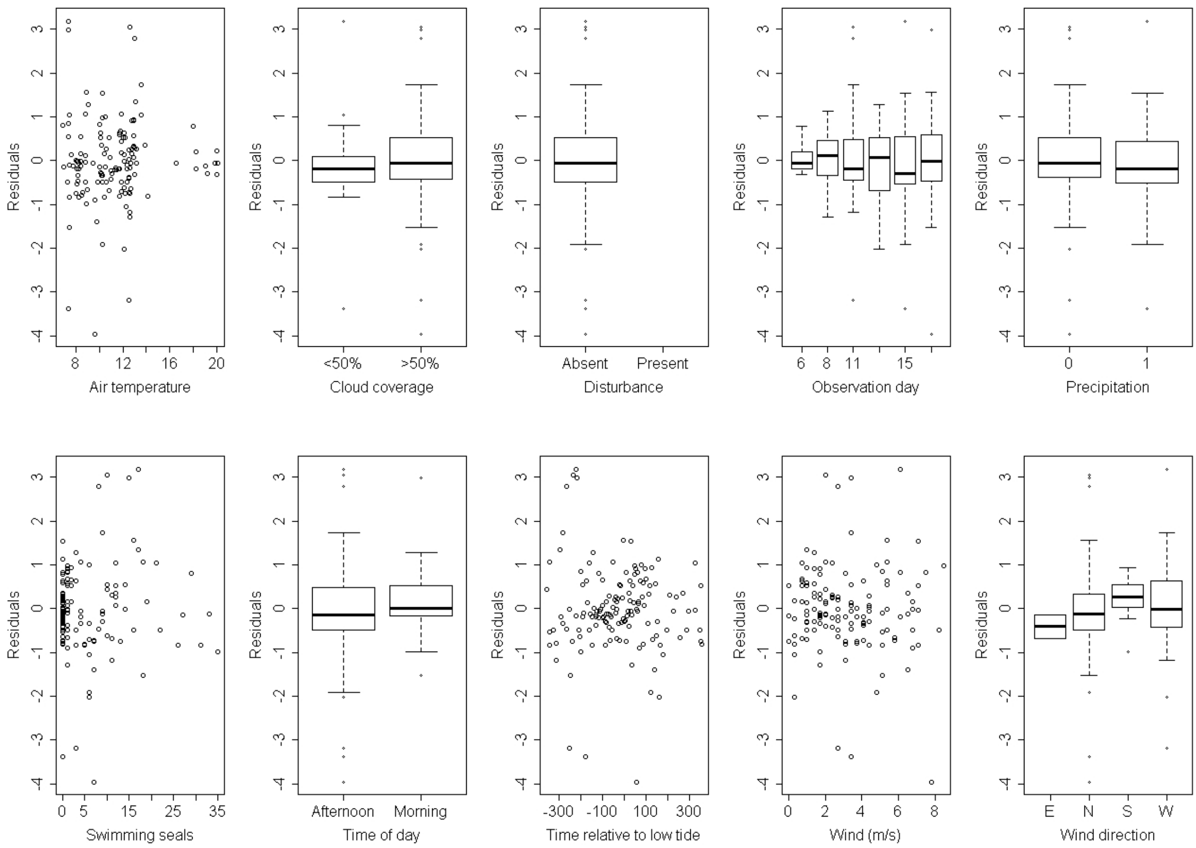

Figure I.6: Model validation plots: the residuals from the best fitted GAMM from Tanafjord plotted against all the different explanatory variables, those used in the final model (time relative to low tide, observation day, swimming seals and time of day) as well as the ones dropped during model selection procedure. In the box plots the median is indicated by the black horizontal line and the 25% and 75% quartiles forms a box around the median that contains half of the observations.

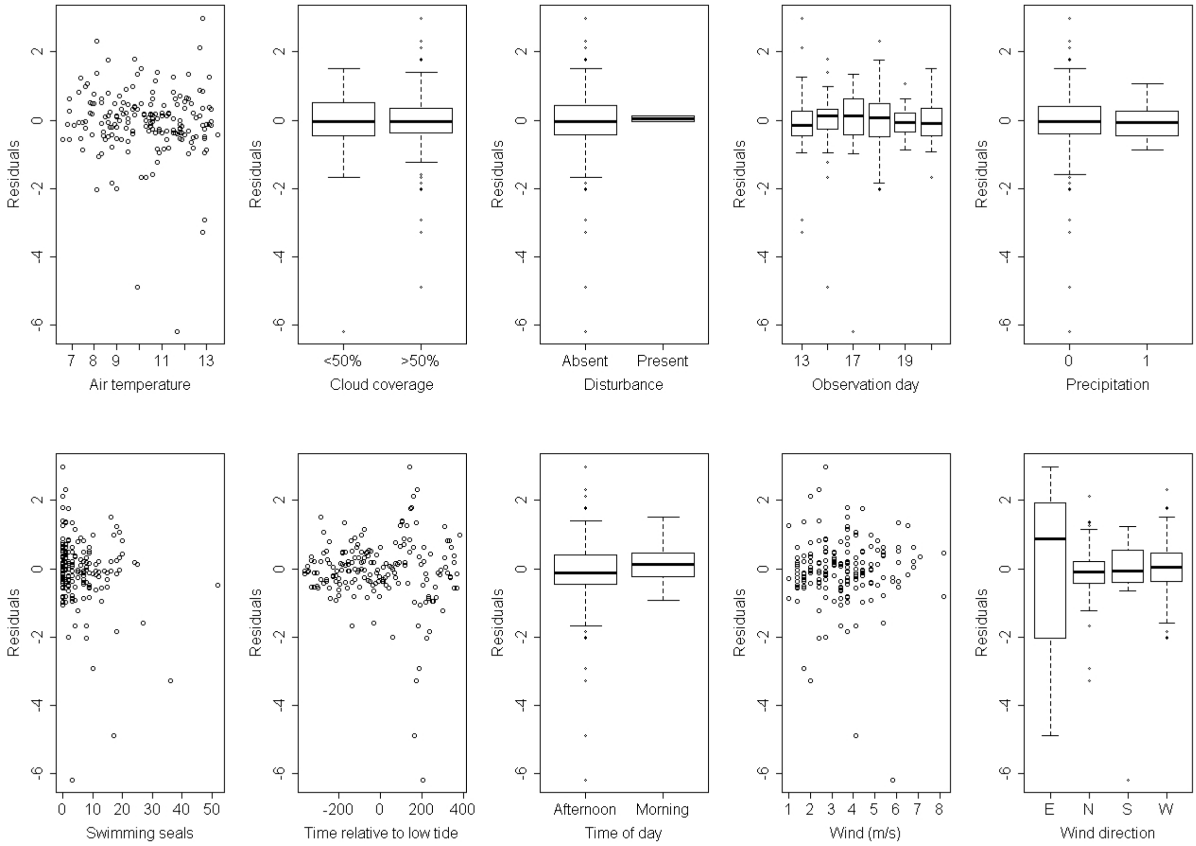

Figure I.7: Model validation plots: the residuals from the best fitted GAMM from Kongsfjord plotted against all the different explanatory variables, those used in the final model (time relative to low tide, observation day and disturbance) as well as the ones dropped during model selection procedure. In the box plots the median is indicated by the black horizontal line and the 25% and 75% quartiles forms a box around the median that contains half of the observations.

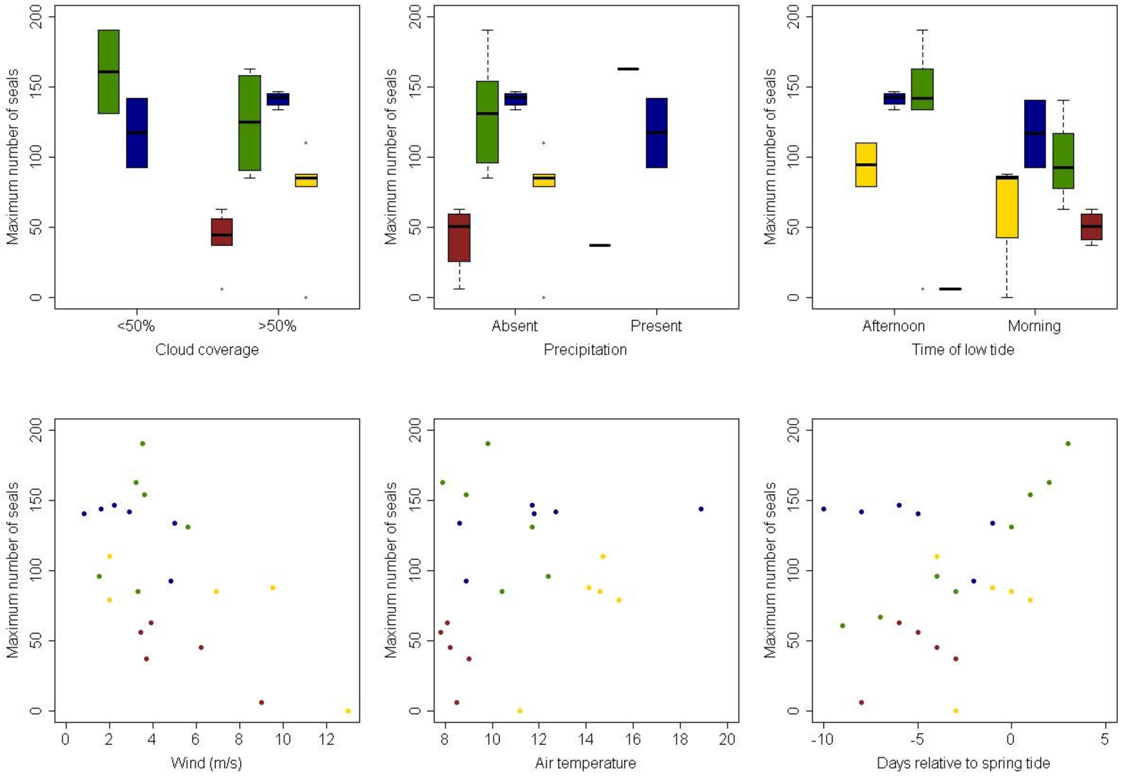

Figure I.8: The lower plots shows the variation in the daily maximum number of harbour seals hauled out in relations to weather variables averaged per day. In the three upper box plot panels the median is indicated by the black horizontal line and the 25% and 75% quartiles forms a box around the median that contains half of the observations. The yellow, brown, blue and green colours indicate data from Porsangerfjord 2011, Porsangerfjord 2012, Tanafjord 2012 and Kongsfjord 2012, respectively.

Table I.1: The table present details regarding variables recorded during the study period at the different study areas. The factor variables are presented in times observed and the continuous variables are average, minimum and maximum observed during the study period.

Weather variables	Levels	Porsangerfjord			Tanafjord			Kongsfjord		
		Number of times observed								
Precipitation	Absent	175			106			218		
	Present	32			35			24		
Wind direction	North	41			86			93		
	South	160			11			21		
	West	0			38			117		
	East	5			2			5		
Cloud cover	<50% of covered sky	4			28			24		
	>50% of covered sky	203			113			218		
Time of day	Afternoon	84			107			168		
	Morning	123			34			74		
Disturbance	Absent	207			141			225		
	Present	0			0			17		
		Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Wind (m/s)		4.7	0	13	3.1	0	8.5	3.6	1	9.2
Temperature (°C)		10.7	3.3	17	11.2	6.9	20.1	11	6.6	17.4

Table I.2: Observed variability in harbour seal numbers between observation days. Observation day is represented by a number indicating the order of the observations. The shaded rows indicate the observations removed from the statistical analysis due to few or bias observations (see material and methods for details).

Study area	Observation day	Average number of harbour seals	Maximum number of harbour seals
Porsangerfjord	1	3	6
	2	39	63
	3	37	56
	4	27	45
	5	21	37
	21	88	110
	22	0	0
	23	75	88
	24	70	85
	25	62	79
Tanafjord	6	130	144
	8	123	142
	11	94	147
	12	80	141
	15	32	93
	16	99	134
Kongsfjord	7	35	61
	9	45	67
	10	10	10
	13	30	96
	14	53	85
	17	87	131
	18	113	154
	19	109	163
	20	132	191

Table I.3: The parameters of the best fitted GAMM models (with quasipoisson error structure and log link function) predicting the number of hauled out seals. OD = Observation day, TRL = time relative to low tide, SWIM = Number of swimming seals, TIME = time of day, DIS = Disturbance.

Study area	Coefficient	Estimate	St. Error	t-value	p-value
Porsangerfjord	Intercept	3.7427	0.1362	27.481	<0.0001
	OD3	-0.0947	0.2178	-0.435	0.6642
	OD4	-0.5124	0.2486	-2.061	0.0407
	OD5	-0.7243	0.2483	-2.917	0.0039
	OD21	0.6924	0.1877	3.689	0.0002
	OD23	0.4165	0.1939	2.148	0.0331
	OD24	0.3002	0.2028	1.48	0.1406
	OD25	0.2477	0.1961	1.263	0.2082
	Approximate significance of smooth terms				
		edf	Ref.df	F	
	s(TRL)	4.847	4.847	5.958	<0.0001
Tanafjord	Intercept	4.30645	0.140631	30.622	<0.0001
	OD8	0.075844	0.159982	0.474	0.6363
	OD11	0.162959	0.163282	0.998	0.3202
	OD12	-0.213312	0.205214	-1.039	0.3006
	OD15	-0.73621	0.195351	-3.769	0.0002
	OD16	-0.341967	0.185551	-1.843	0.0677
	SWIM	-0.006764	0.003083	-2.194	0.0301
	TIME (morning)	0.253305	0.120931	2.095	0.0382
	Approximate significance of smooth terms				
		edf	Ref.df	F	
	s(TRL)	5.977	5.977	13.72	<0.0001
Kongsfjord	Intercept	3.8593	0.1596	24.175	<0.0001
	DIS	-0.8641	0.2744	-3.149	0.0019
	OD14	0.1075	0.2153	0.499	0.6181
	OD17	0.4198	0.2016	2.082	0.0388
	OD18	0.6764	0.1878	3.602	0.0004
	OD19	0.836	0.1965	4.255	<0.0001
	OD20	0.9343	0.1882	4.965	<0.0001
	Approximate significance of smooth terms				
		edf	Ref.df	F	
	s(TRL)	4.769	4.769	15.24	<0.0001

Table I. 4: The proportion of seals hauled out (P_t) and its standard errors (SE_{Pt}) as predicted from the binomial GAMMs, together with the correction factors calculated (CF_t), spanning from 4.5 hours before low tide to 4.5 hours after low tide at 30 minute intervals, for Porsangerfjord, Tanafjord and Kongsfjord.

	Porsangerfjord			Tanafjord			Kongsfjord		
Time (hours) relative to low tide	P_t	SE_{Pt}	CF_t	P_t	SE_{Pt}	CF_t	P_t	SE_{Pt}	CF_t
-4.5	0.46	0.07	2.17	0.21	0.08	4.76	0.73	0.06	1.37
-4	0.52	0.07	1.92	0.36	0.09	2.78	0.8	0.05	1.25
-3.5	0.59	0.06	1.69	0.55	0.09	1.82	0.84	0.04	1.19
-3	0.66	0.05	1.52	0.71	0.07	1.41	0.84	0.04	1.19
-2.5	0.71	0.04	1.41	0.80	0.05	1.25	0.82	0.04	1.22
-2	0.75	0.04	1.33	0.87	0.04	1.15	0.8	0.04	1.25
-1.5	0.77	0.04	1.30	0.90	0.03	1.11	0.77	0.05	1.30
-1	0.80	0.04	1.25	0.91	0.03	1.10	0.75	0.05	1.33
-0.5	0.82	0.04	1.22	0.91	0.03	1.10	0.76	0.05	1.32
0	0.83	0.03	1.20	0.90	0.03	1.11	0.78	0.05	1.28
0.5	0.83	0.03	1.20	0.87	0.04	1.15	0.79	0.05	1.27
1	0.80	0.04	1.25	0.81	0.05	1.23	0.79	0.05	1.27
1.5	0.76	0.04	1.32	0.71	0.07	1.41	0.76	0.06	1.32
2	0.71	0.05	1.41	0.58	0.09	1.72	0.69	0.07	1.45
2.5	0.65	0.05	1.54	0.43	0.1	2.33	0.57	0.07	1.75
3	0.58	0.06	1.72	0.30	0.1	3.33	0.44	0.07	2.27
3.5	0.49	0.07	2.04	0.20	0.09	5.00	0.33	0.07	3.03
4	0.41	0.07	2.44	0.14	0.08	7.14	0.23	0.05	4.35
4.5	0.34	0.08	2.94	0.09	0.06	11.11	0.23	0.05	4.35

Appendix II: The method of propagation of errors (Delta method)

If Y is a function of the stochastic variable X, $Y = g(X)$, and the expected value of X is $E\{X\} = \mu$, then the variance of Y, calculated through the delta method, is defined as (Casella and Berger 1990):

$$\text{Var}\,(Y) \approx \left(g'(\mu)\right)^2 \text{Var}\,(X)$$

The confidence interval of the maximum number of seals is defined as:

$$N_{max} \pm 1.96\,\sigma_{Nmax}$$

Given that

$$N_{max} = N_t\,CF_t = \frac{N_t}{P_t},$$

The delta method was used to find the standard deviation, σ_{Nmax}, of the maximum number of seals, N_{max} from the variance of the stochastic variable P_t as following:

$$\sigma^2_{Nmax} = \text{Var}\,(N_{max}) \approx \left(\frac{\partial N_{max}}{\partial P_t}\right)^2 \text{Var}(P_t),$$

$$= \left(\frac{\partial}{\partial P_t}\frac{N}{P_t}\right)^2 \sigma^2_{P_t},$$

$$= \left(-\frac{N_t}{P_t^2}\right)^2 \sigma^2_{P_t},$$

$$= \left(\frac{N_t^2}{P_t^4}\right)\sigma^2_{P_t},$$

and from this we get

$$\sigma_{Nmax} = \frac{N_t}{P_t^2}\,\sigma_{P_t},$$

where N_t is the count at time *t*, P_t is the estimated proportion of seals hauled out at time *t* and σ_{Pt} is the standard deviation of the estimated proportion of seals hauled out at time *t*.

References

Casella, G., and Berger, R. L. (1990). *Statistical Inference*. Duxbury Press, Belmont, California. 650 pp.

Appendix III: R-script generating statistical models and associated figures

```
load("Data")
library(mgcv)

#The full GAMM model (with poisson distribution).  Separate models were produced for each
study area.
M1<-gamm(N~s(TRL)+PRED+WD+CLOUD+DIS+TIME+WIND+TEMP+SWIM+OD,
random=list(OD=~1),family=quasipoisson,data=Data,na.action=na.omit,correlation=corAR1(
form=~1|OD))

#Model validation plots:
fv<- exp(fitted(M1$lme))
resid <- Data$N-fv
plot(fv^0.5,Data$N^0.5)  # The relationship between raw data and fitted values.
abline(0,1)
plot(fv^.5,resid/fv^.5) # Pearson residuals against fitted values.
abline(0,0)
plot(fv^.5,resid) #Raw residuals against fitted values.
fl<-sort(fv^.5)
lines(fl,fl);lines(fl,-fl);lines(fl,2*fl)
lines(fl,-2*fl)
plot(resid(M1$lme,type="normalized")~Data$TRL)
plot(resid(M1$lme,type="normalized")~Data$PRED)
plot(resid(M1$lme,type="normalized")~Data$WD)
plot(resid(M1$lme,type="normalized")~Data$CLOUD)
plot(resid(M1$lme,type="normalized")~Data$DIS)
plot(resid(M1$lme,type="normalized")~Data$TIME)
plot(resid(M1$lme,type="normalized")~Data$WIND)
plot(resid(M1$lme,type="normalized")~Data$TEMP)
plot(resid(M1$lme,type="normalized")~Data$SWIM)
plot(resid(M1$lme,type="normalized")~Data$OD)
```

```
#GAMM with binomial distribution
Data$number.of.failures<-Data$Max-Data$N
M2<-gamm(cbind(N,number.of.failures)~s(TRL),data=Data,na.action=na.omit,
family=quasibinomial,correlation=corAR1(form=~1|OD),random=list(OD=~1))
newdata<-data.frame(TRL = seq(from = min(Data$TRL), to = max(Data$TRL), by = 10))
P1<-predict(M2$gam,newdata,se=TRUE,type="response")
plot(newdata$TRL, P1$fit, type = "l", ylim = c(0, 1)) # Predicted proportion of seals (the inverse of the correction factor) hauled out relative to low tide.
lines(newdata$TRL,P1$fit+1.96*P1$se.fit)
lines(newdata$TRL,P1$fit-1.96*P1$se.fit)
Pred<-data.frame(Time=newdata$TRL, Abundance=P1$fit, SE=P1$se)

MaxN<-120 # Selecting a number for max seals.
FindCI<-function(t1,MaxN){
temp<-matrix(0,nrow=length(t1),ncol=2)
for(n in 1:length(t1)){
CF1<-PredP$Abundance[PredP$Time==t1[n]]
Nt1<- MaxN* CF1
SeCF1<-(Nt1/(CF1^2))
SeCFest<-PredP$SE[PredP$Time==t1[n]]*SeCF1 # Corrected standard error at time t
uprCFest<-MaxN+1.96*SeCFest   # uper CI
lwrCFest<-MaxN-1.96*SeCFest  #lower CI
temp[n,1]<-uprCFest
temp[n,2]<-lwrCFest
}
return(temp)
}
Table<-FindCI(PredP$Time,MaxN)

plot(Table[,1]~PredP$Time,type='l') # The confidence interval to the maximum number of seals plotted against time relative to low tide.
lines(Table[,2]~PredP$Time)
abline(h=120)
```