Investigating Seal Depredation at Scottish Salmon Farms

KATHERINE FAE WHYTE

16 August 2015

BL5199 Marine Mammal Science Research Project

This thesis is submitted in partial fulfilment for the degree of
MSc Marine Mammal Science at the University of St Andrews.

Declaration

I hereby certify that this dissertation, which is approximately 9,924 words in length, has been composed by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree. This project was conducted by me at the University of St Andrews from January 2015 to August 2015 towards fulfilment of the requirements of the University of St Andrews for the degree of Master of Science under the supervision of Dr Simon Northridge.

_____

Katherine Fae Whyte

Date: _____

Contents

Abstract

Seal depredation is a common problem on Scottish salmon farms, causing an average loss of £26,000 per year on each site. Economic losses are incurred principally from physical damage to fish but also from the necessary repair of damaged equipment. Acoustic deterrent devices (ADDs) are widely used in Scotland as a means of reducing depredation, as the sounds emitted by these devices are designed to deter seals from feeding at sites. Despite this, little is known on how effective these devices are as their performance varies widely with respect to deployment technique, target population and environmental conditions. This study aims to inform aquaculture businesses in Scotland about the efficacy of the common types of ADDs and provide an insight into seal behaviour around fish farms so as to inform and improve deterrence strategies. Using records of seal-attributed mortalities from fish farms across Scotland, hidden Markov modelling is used to investigate factors influencing the occurrence and severity of seal depredation events. The number of expected salmon mortalities is found to be dependent on both season and region. The use of an Ace Aquatec ADD reduced mortalities by an average of 70% whereas the Airmar device caused only a 50% reduction. No significant reduction in mortalities was detected from using a Terecos device. We further discuss the possible effects of seal abundance, distribution and life history, prey availability and environmental conditions on regional and seasonal variation in seal feeding behaviour. Secondary to this, we also conduct a case study on a site where ADDs and a new electric net deterrent device are installed for the first time. We find the combination of both the devices significantly reduces mortalities but further studies are required to determine whether the electric net provides any added benefit.

Acknowledgements

First and foremost, I am grateful to my supervisor Simon Northridge for his support and guidance throughout all stages of the project. In particular, I would like to thank him for his insightful comments on both my project proposal and an earlier draft of this thesis. I would also like to thank Alex Coram for his advice throughout and for taking the trip up to Orkney with me to visit the case study site.

I am also very grateful to the aquaculture company that provided the fish mortality data and site information which enabled me to conduct a large-scale investigation into seal depredation across Scotland.

I extend my thanks to Nathan Pyne-Carter (Managing Director at Ace Aquatec) for inviting us to conduct the case study on Orkney and assess the new electric net deterrent device the company have produced. He was also essential in liaising with various contacts at the field site to make this possible.

Finally, I must thank the aquaculture company that allowed us to conduct the case study in Orkney (in particular the site manager, the dive team and everyone else involved with the case study site). We are grateful for the provision of mortality data and for allowing us to visit the site multiple times throughout the study period.

DISCLAIMER: In the interests of confidentiality and security, details regarding the identity and location of fish farm sites and companies has not been disclosed in this report.

1   Introduction

Salmon farms in Scotland are frequently faced with economic losses caused by seal predation. An average of 264 fish per site per stocked month, the equivalent of £26,000 per site per year (Northridge et al., 2013; Coram et al., 2014), is estimated to be lost due to predation. Seals not only consume stock, but damage equipment and remaining fish, further accentuating the costs. Thus, reducing seal attacks is a priority for the aquaculture industry. Deterrent devices are employed on over 52% of sites in Scotland (Quick et al., 2004) and range over a wide variety of kinds. Yet, despite their widespread use, little is known about the efficacy of deterrent devices or how they can be best put to use. In this study, we aim to quantify the effect of popular deterrents on predation and investigate how deterrents could be used to better match the dynamics of how seals feed.

The aquaculture industry in Scotland, including both finfish and shellfish, is of great economic importance and was worth over £560 million (at farm gate value) in 2012 (Scottish Government, 2014). The salmon farm industry itself was worth £536 million in 2012 (Scottish Government, 2014), with Atlantic salmon (*Salmo salar*) accounting for over 98% of all marine finfish produced in Scotland (Marine Scotland Science, 2013). In 2013, 163,234 tonnes of salmon were produced from across 257 active sites in Scotland, all of which were located on the western and northern islands and coastlines (Marine Scotland Science, 2013). Sites were owned by a total of 21 different companies, but production was dominated by seven main companies who collectively accounted for 98% of salmon farm production (Marine Scotland Science, 2013). The industry directly employs 1,086 staff, with numerous other jobs provided indirectly in downstream processing and marketing (Marine Scotland Science, 2013; Coram et al., 2014). Furthermore, the aquaculture industry has plans for expansion and aims to reach a sustainable growth target of 210,000 tonnes of marine finfish production by 2020 (Scottish Government, 2014). It is the will to sustain and grow this industry that makes further study of seal predation and deterrence vital.

The costs incurred by seal predation stem from three principal sources. First, there is the consumption of stock by seals and the incidental escape of captive fish (Northridge et al., 2013). Second, the repairs necessary for damaged fishing gear and, third, the potential reduced growth (Schotte and Pemberton, 2002) and increased disease susceptibility (Nash et al., 2000; Northridge et al., 2010) of fish stressed by continual seal presence. All three causes contribute to the economic losses experienced across the industry. Seal depredation is reported as a serious issue on at least an occasional basis by 23% of all sites and as a minor issue by a further 49% of sites (Northridge et al., 2010). Furthermore, here we consider only grey (*Halichoerus grypus*) and harbour (*Phoca vitulina*) seals, but depre-

dation (the damage or removal of captive fish) is a prevalent problem with many marine mammals worldwide including California sea lions (*Zalophus californianus*), South American sea lions (*Otaria flavescens*), Cape fur seals (*Arctocephalus pusillus*), killer whales (*Orcinus orca*), false killer whales (*Pseudorca crassidens*), sperm whales (*Physeter macrocephalus*) and bottlenose dolphins (*Tursiops truncatus*) (Shaughnessy et al., 1981; Yano and Dahlheim, 1995; Beeson and Hanan, 1996; Sepúlveda and Oliva, 2005; Sigler et al., 2008; Rabearisoa et al., 2015). The range of marine mammals involved reveals why depredation must be considered on both a focal and global scale: deterrent strategies must target each perpetrator singly, but also be aware of its effect on the surrounding ecosystem. Additionally, the depredation is widespread geographically (e.g. California, Chile, southern Africa, Ireland and the Bering Sea) and occurs in a variety of fishery types (Read, 2008; Schakner and Blumstein, 2013) where deterrent strategies necessarily differ.

The prevention of seal predation usually involves the improvement of either net design or acoustic deterrent devices (ADDs). Nets made with tailored materials and with smaller mesh sizes have been essential in improving depredation by reducing the ability of marine predators to access fish (Nash et al., 2000; Schotte and Pemberton, 2002; Königson et al., 2007). Nevertheless, the economic losses can still be profound. Hence, since the 1970's, acoustic deterrent devices (ADDs) have been considered as an additional method of reducing marine mammal depredation (e.g. Anderson and Hawkins (1978)). These devices operate on the principle of producing an aversive or threatening stimulus, with the aim of inducing an avoidance response in the animal (Götz and Janik, 2010). They produce loud sounds underwater which are unpleasant or uncomfortable at close ranges (Reeves et al., 1996), or mimic predator sounds such as those of killer whales (Jefferson and Curry, 1996). ADDs are currently widely used but can have highly variable success (Götz and Janik, 2013). The main problem is that the efficiency of these devices is thought to reduce over time as animals habituate to the signal, especially when strong motivation (such as food presence) to tolerate the signal exists (Kastelein et al., 2006; Graham et al., 2009). ADDs may also produce a "dinner bell" effect and attract predators to a potential food source (Jefferson and Curry, 1996). Additionally, these devices will be less effective for animals with poor hearing or hearing damage caused by exposure to ADDs or other sound sources. There is also serious concern over the long-ranging impacts of ADDs on non-target species, in particular cetaceans (Gordon and Northridge, 2002). Harbour porpoises (*Phocoena phocoena*) seem to be highly sensitive to ADDs and so can face habitat exclusion when ADDs are active (Johnston, 2002; Olesiuk et al., 2002). In one case porpoises have been observed to exhibit avoidance behaviour up to 7.5 km from the ADD source (Brandt et al., 2013). ADD devices must therefore be used with regard to the ecosystem as a whole so as to maximise the benefits of these devices whilst minimising the potential drawbacks.

Improving net design and ADD performance is a primary focus of developers; however, it raises the question of whether other possible deterrent devices could be implemented. For decades, electric fences have been used in terrestrial ecosystems for the control of both livestock and wildlife (Karhu and Anderson, 2006). In wildlife management they have been used to control the movement of animals by excluding the target animals from particular regions. These have been applied in cases where the grazing (Porter, 1983; Reidy et al., 2008) or predation (LaGrange et al., 1995) of wild animals have been successfully controlled. Electric fences have also been recommended as the best method for reducing otter depredation at fish farms in Finland and France (Skaren, 1990; Leblanc, 2003). As electric fields are a form of tactile deterrent device, they would be expected to be more effective than acoustic deterrents and be more difficult to habituate to (Schakner and Blumstein, 2013). The development of a similar deterrent system for use in marine ecosystems could present a major step forward in predator control. Forrest et al. (2009) developed and tested the use of electric fields to deter harbour seals in salmon gill-net fisheries. Both captive and wild seals exhibited strong avoidance of a low-voltage pulsed electric gradient when placed across a pool or river. The electric gradient was also integrated into an experimental drift net where half of the net was electrified. Significantly higher salmon catches were recorded in the electrified portion of the net and net damage rates were also lower. It is notable that behavioural responses to electric fields in seals were recorded at substantially lower voltages than that thought to cause a response in salmonid fish (Lines and Kestin, 2004; Forrest et al., 2009; Milne et al., 2013). Given that the conductivity of sea water is higher than for the freshwater system investigated by Forrest et al. (2009), the power required to run a similar system in seawater is a major challenge. Pool trials by Milne et al. (2013) review the testing of a similar device for seawater which generates a pulsed, low-voltage electric field within a localised area around a feeding station. Both grey and harbour seals were able to detect electric fields, with the level of response varying according to voltage (signal amplitude), pulse duration and pulse length. At low levels, seals refrained from entering the feeding station until food was present and exhibited muscle tremors when reaching in for food. All animals showed strong aversion to high level electric fields with refusal to enter the feeding station when food was presented. Thus, electric fields may be a welcome addition to the current deterrent strategies employed in marine mammal and fishery interactions.

Sites in Scotland apply a variable deterrent regime comprising many parts. Foremost is the good husbandry practices such as the regular removal of dead fish from pens and the maintenance of good net tension in different tidal states (to reduce the ability of seals to push on nets to access fish) (Northridge et al., 2013). Coupled with this upkeep is the sporadic use of ADDs. The majority of devices in use are from three manufacturers (Ace Aquatec, Airmar and Terecos) (Lepper et al., 2014) but the true extent and distribution

of devices in Scotland is currently unknown. Sites are also allowed to carry out lethal removal of seals through licensed shooting (under the Marine (Scotland) Act (2010)) to protect fish and fish farms during periods of high depredation. Although this may remove 'problem individuals' (Königson, 2007; Graham et al., 2011), it contradicts conservation efforts and is not a long-term solution. Overall, the Scottish aquaculture industry can clearly benefit from improved knowledge of how deterrents could be managed so as to minimise economic loss and seal shootings.

To quantify the effect of deterrents and capture the dynamics of feeding cycles is a challenging task for two reasons. First, available data is collected by sites during operation rather than from a designed experiment. Second, the processes generating the data are often temporally correlated and require sophisticated statistical techniques. For example, data supplied by sites usually comprises a long list of predation counts over time. These counts are often highly variable (over-dispersed) which immediately prohibits the application of basic statistical tools such as generalised additive models (Zuur et al., 2009). Furthermore, seal presence at a site is unknown so zero mortalities may indicate seal absence or satiation; a complication that most popular statistical methods cannot accommodate. State-space models (SSMs), however, are ideal for such data. These models are often used in ecology to study the (unknown) condition or state of ecosystems or individual animals. They are built up from two parts: a state process which describes how the hidden state changes over time, and an observation process which describes the link between the state and what we observe (Zucchini and MacDonald, 2009). In marine mammal science for example, they have been used to estimate grey seal population sizes from survey data (Thomas and Harwood, 2003), infer health from observations of body condition in North Atlantic right whales (*Eubalaena glacialis*) (Schick et al., 2013a) and study the body condition of elephant seals (*Mirounga spp.*) using measurements of drift dive behaviour (Schick et al., 2013b). Hidden Markov models (HMMs) have the same structure as state-space models but they assume there are a finite number of states (Schliehe-Diecks et al., 2012). These finite models are therefore much easier to fit and present a reasonable alternative when the system studied can be divided into a finite number of behavioural or ecological states. One of the most common applications of HMMs in ecology is to animal movement and behaviour data. By extracting measurements (e.g. travel speed, turn angle) from telemetry data on animal movement, HMMs can be used to infer the behavioural state (travelling, resting, foraging) of tagged animals (Franke et al., 2004; Patterson et al., 2009). One study (Franke et al., 2006) used telemetry data to estimate behavioural states and prey kill sites in wolves (*Canis lupus*). Schliehe-Diecks et al. (2012) used observations on the feeding behaviour of grey mouse lemurs (*Microcebus murinus*) to investigate changes in the underlying motivational state (hungry, satiated) of animals. Modelling of the feeding and foraging behaviour of animals such as this can be used to gain important

information on predation rates. HMMs are therefore a powerful tool for studying changes in animal feeding behaviour. Here, we aim to apply hidden Markov modelling to the feeding behaviour of seals at fish farms and infer what, if any, effect deterrents may have and how feeding changes temporally and spatially.

This research project aims to inform aquaculture businesses about the economic efficacy of ADDs and provide a summary of seal behaviour around fish farms so as to improve deterrent strategies. In Section 2.1, we introduce our study of seal depredation across Scotland and develop the statistical methods used. Additionally, in Section 2.2, we focus on a case study of a salmon farm site where ADDs and a new electric net device were recently installed. We present the results of both studies in Section 3 and discuss how our findings impact upon the aquaculture industry at large in Section 4.

2 Methods

2.1 Seal Depredation Across Scotland

2.1.1 Data Collection

Under the SSPO Code of Good Practice (Scottish Salmon Producers Organisation, 2015), Scottish salmon farmers are recommended to inspect pens and stock frequently for signs of damage. They are also required to regularly remove dead fish and record the likely cause of death in each instance.

Fish mortality data was provided from a fish farm company for a number of salmon aquaculture sites on the west coast of Scotland. Mortality data was collected by each site on a weekly basis and classified into 21 causes of death (e.g. due to different aspects of production, types of disease, environmental causes and predation). Predation mortalities, attributed to both grey (*Halichoerus grypus*) and harbour (*Phoca vitulina*) seals, are typically identified by puncture wounds, flank gashes and missing flesh of collected fish (Northridge et al., 2013). Also provided were site-specific details such as the location and number of pens on each site. If sites used an acoustic deterrent device (ADD), the type of ADD used was also given. The data used here were collected between January 2007 and June 2013.

2.1.2 Data Preparation

There was a difference in the temporal resolution of mortality data provided by different sites, with some showing weekly counts and others showing data aggregated by month. Given that the interest here was to investigate long-term patterns, we reduced the temporal resolution to increase the number of sites in the analysis. Mortalities attributed to predation were extracted and summed for each month where required. Salmon farm sites were located in distinct geographic clusters, each experiencing different ecological and environmental dynamics. The sites were therefore grouped into three regions: South-West Scotland (comprising all sites south of Oban), North-West Scotland (comprising all mainland sites north of Oban and the islands of Mull and Skye) and the Outer Hebrides. Finally, continuous covariates were standardised (i.e. to have zero mean and a standard deviation of one).
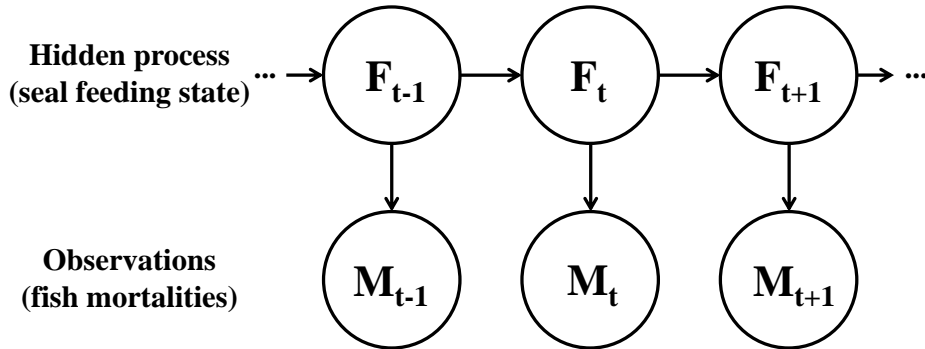
Figure 1. Dependence structure of the hidden Markov model (HMM). For each time step t, seal behaviour F_t around salmon farms is either in a "feeding" or "non-feeding" state and this is only dependent on the state in the previous time step. Observations of fish mortalities M_t are made where each observation depends on the current hidden state.

2.1.3 Constructing a Hidden Markov Model (HMM)

Seal predation mortality counts typically take the form of long periods of no mortalities interspersed with sharp peaks when seal attacks occur. Hence, a model which can distinguish between these two distinct states of predation is critical. During these attacks, mortality levels are variable and can occasionally reach extremely high levels (e.g. due to catastrophic events such as severe net damage). Attack length can also vary highly. This type of data is therefore a challenge for statistical modelling: mortality counts are often zero-inflated and overdispersed. Zero-inflated models, which are designed to cope with an excessive number of zeros (Agarwal et al., 2002), do not account for the temporal correlation in predation counts and so cannot be applied here.

A hidden Markov model (HMM) is a type of state-space model with two components (Cappé et al., 2005; Zucchini and MacDonald, 2009). First, there is a state process representing the unknown condition of a system that can switch between a number of different states over time. In this application, we considered this to be the presence of seals around a fish farm or their motivational state to feed at a farm. Second, there is an observation process whereby observations made at each time depend on the hidden state of the system. Here, we observed the number of fish mortalities attributed to seals. Given that the hidden state is dependent on the state in the previous time step and each observation is dependent on the current state (Cappé et al., 2005), the HMM was constructed using the dependence structure illustrated in Figure 1. These models can accommodate both overdispersion and temporal dependence (appropriate for coping with long time series containing mostly zeros) and so they are ideal for applying to seal depredation data (Zucchini and MacDonald, 2009).

The hidden feeding process is here represented as a Markov process. For each discrete time step t, the current state (F_t) of the system is only dependent on the state in the previous time step (F_{t-1}) (and not on any earlier time steps) (Zucchini and MacDonald, 2009). Hence, the probability of the system being in a particular state at time t $(F_t = f_t)$ is conditional on the value of the previous state:

$$Pr(F_t = f_t | F_{t-1} = f_{t-1}, F_{t-2} = f_{t-2}, \ldots F_0 = f_0)$$

$$= Pr(F_t = f_t | F_{t-1} = f_{t-1})$$

This is known as a first order Markov chain (Zucchini and MacDonald, 2009) as the current state is only dependent on the previous state. Here, we consider two states: a "non-feeding state" (state 1) where seals are absent from the site and a "feeding state" (state 2) where seals are considered to be present locally and actively feeding at the site. Each time unit t is one month in duration.

A key component of the Markov chain is the transition probability matrix. The transition probability matrix $\boldsymbol{\Gamma}$ is a square matrix of probabilities (Zucchini and MacDonald, 2009):

$$\boldsymbol{\Gamma} = \begin{pmatrix} 1 - \gamma_{in} & \gamma_{in} \\ \gamma_{out} & 1 - \gamma_{out} \end{pmatrix}$$

where γ_{in} is the probability of moving into a feeding state and γ_{out} is the probability of moving out of a feeding state. For example, $\gamma_{in} = Pr(F_{t+1} = 2 | F_t = 1)$ is the probability of entering a feeding state at the next time step given that the current state is non-feeding. The matrix is characterised by two parameters because any system which is in state i at time t must either stay in state i or switch to state j at time $t+1$. Therefore, the rows of $\boldsymbol{\Gamma}$ sum to one (Zucchini and MacDonald, 2009; Schliehe-Diecks et al., 2012).

The Markov chain is also characterised by an initial distribution $\boldsymbol{\delta} = (\delta_1, \delta_2)$, where $\boldsymbol{\delta}$ is a row vector containing the probability of a system starting in either state (Zucchini and MacDonald, 2009). To deduce the distribution of F_1 we simply multiply $\boldsymbol{\delta}$ by the transition probability matrix $\boldsymbol{\Gamma}$ (Zucchini and MacDonald, 2009). Hence, at any time t (from $t = 0$ onwards) the distribution of F_t can be given by $\boldsymbol{\delta}\boldsymbol{\Gamma}^t$. In theory, if the chain is run forever (as $t \to \infty$) the distribution approaches a dynamic equilibrium state $(\boldsymbol{\delta}\boldsymbol{\Gamma}^t \to \boldsymbol{\delta}^*)$ where the proportion of time spent in each state remains the same (Zucchini and MacDonald, 2009). $\boldsymbol{\delta}$ (or $\boldsymbol{\delta}^*$) is sometimes also called the equilibrium distribution since $\boldsymbol{\delta}^*\boldsymbol{\Gamma} = \boldsymbol{\delta}^*$.

The observed fish mortalities attributed to seals are dependent on the underlying state (Figure 1) (Schliehe-Diecks et al., 2012). If the system is in a non-feeding state $(F_t = 1)$, seal-attributed mortalities at this time (M_t) must be equal to zero as there are no seals

present to attack fish ($Pr(M_t = 0|F_t = 1) = 1$). In a feeding state ($F_t = 2$), we assume the mortalities follow a negative binomial distribution with size parameter r and success probability p. The flexibility of the negative binomial allows for possible overdispersion to be accommodated (Ver Hoef and Boveng, 2007; Zuur et al., 2007). The model assumes that the distribution of mortalities given the current feeding state is independent of all previous states and observations (Schliehe-Diecks et al., 2012).

There are therefore four different parameters to estimate: the probability of switching into a feeding state (γ_{in}), the probability of switching out of a feeding state (γ_{out}) and the two parameters of the negative binomial distribution (r, p) which relate to the number of fish mortalities within a feeding state. We estimate these parameters by maximum likelihood estimation (MLE), where the likelihood L is constructed as follows (Zucchini and MacDonald, 2009). For each observation m_t,

$$\mathbf{P}(m_t) = \begin{pmatrix} Pr(m_t|F = 1) & 0 \\ 0 & Pr(m_t|F = 2) \end{pmatrix}$$

which is a diagonal matrix with the diagonal elements being the probability of the observation for each of the hidden states (Zucchini and MacDonald, 2009). To construct the likelihood we take the product of the equilibrium distribution $\boldsymbol{\delta}$ and $\boldsymbol{\Gamma}\mathbf{P}(m_t)$ for times $t = 0, 1, 2, \ldots T$ and so

$$L = \boldsymbol{\delta}\mathbf{P}(m_0)\boldsymbol{\Gamma}\mathbf{P}(m_1)\boldsymbol{\Gamma}\mathbf{P}(m_2)...\boldsymbol{\Gamma}\mathbf{P}(m_T)\mathbf{1}$$

where $\mathbf{1}$ is a 2×1 column vector of ones (Zucchini and MacDonald, 2009). This matrix product is an efficient algorithm (known as the forward algorithm) and is equivalent to summing over all possible sequences of hidden states whilst weighting them by their likelihood (Zucchini and MacDonald, 2009).

Within biological data such as that analysed here, there are often gaps in the time series where we do not make an observation M_t at time t. We do not gain any information about the hidden state in these time steps but we know that the system will still follow the same transition probability matrix $\boldsymbol{\Gamma}$. Hence, we simply replace $\mathbf{P}(m_t)$ with the identity matrix for each missing observation.

2.1.4   Including Covariates

The parameters γ_{in}, γ_{out} and r can all depend on other variables (Zucchini and MacDonald, 2009; Schliehe-Diecks et al., 2012), allowing us to examine the factors influencing the transitions between states and the number of mortalities per month of a feeding state.

We use a generalised linear modelling (GLM) framework:

$$g(x_i) = \beta_0 + \beta_1 X_1 + \ldots + \beta_k X_k$$

where g is a link function, β_0 is the intercept term and $\beta_1 \ldots \beta_k$ are the estimates for the effect of explanatory covariates $X_1 \ldots X_k$ (Zuur et al., 2007, 2009). We use a logit link to ensure that the values of γ_{in} and γ_{out} remain between zero and one, and a log link for the count data r:

$$logit(\gamma_{in}) = \eta_{\gamma_{in}}$$

$$logit(\gamma_{out}) = \eta_{\gamma_{out}}$$

$$log(r) = \eta_r$$

where $\eta_{\gamma_{in}}$, $\eta_{\gamma_{out}}$ and η_r are the linear predictors. We consider several linear predictors for each of the parameters, using combinations of the explanatory variables described in Table 1. Factor variables only were considered in the linear predictors for the transition probabilities as these could be easily estimated for all possible combinations of the factors. Models requiring estimation of transition probabilities for all combinations of factor and continuous variables were not computationally feasible.

Table 1. Description of covariates (continuous (C) and factor (F)) considered in models and the range of values they could take. Shown also are the parameters they were each considered for.

Covariate	Description	C/F	r	γ_{in}	γ_{out}
Month	Month of the year (Jan-Dec)	F	✓	✓	✓
Region	Region of Scotland (NW, Outer Hebrides, SW)	F	✓	✓	✓
ADD Type	ADD used (none, Ace Aquatec, Airmar, Terecos)	F	✓	✓	✓
Year	2007-2013	C	✓		
Pen Number	Number of pens on site (4-16)	C	✓		

In addition to the fixed effects of covariates on predation mortalities, there is likely to be further heterogeneity in mortalities due to unmodelled differences between sites. Mixed effects models handle such a situation by combining linear effects with individualistic variation (Zuur et al., 2007, 2009). We add a random effect $u_i \sim N(0, \sigma^2)$ that adds additional variation to the intercept for each site (Zuur et al., 2007). This random effect is assumed to be normally distributed with a mean of zero and variance σ^2. Essentially we consider all sites as being similar on average, but estimate an adjustment factor for each site from the main estimate. For a given set of known random effects $(u_1, \ldots, u_s)$ where parameters can be calculated from GLMs, the likelihood for the HMM is the same

as that described in Section 2.1.3:

$$L_f(u_1, \ldots, u_s) = \boldsymbol{\delta} \mathbf{P}_0 \boldsymbol{\Gamma} \mathbf{P}_1 \boldsymbol{\Gamma} \mathbf{P}_2 ... \boldsymbol{\Gamma} \mathbf{P}_T \mathbf{1}$$

However, these random effects are unobserved and so must be averaged over. Hence, the likelihood for the mixed model (MHMM) (Altman, 2007) is given by

$$L_m = \int \ldots \int L_f(u_1, \ldots, u_s) \phi(u_1, \ldots, u_s) du_1 \ldots du_s$$

where ϕ is the standard normal density. This multidimensional integral was numerically approximated using a discrete grid across the integration interval in the same manner as Schliehe-Diecks et al. (2012).

2.1.5   Model Fitting and Parameter Estimation

Maximum likelihood estimates for models were obtained using a Newton-Raphson type optimisation procedure (Ch. 3, Zucchini and MacDonald (2009)) using the 'nlm' function in R (Dennis and Schnabel, 1983; Schnabel et al., 1985). Asymptotic variance estimates were obtained using the negative inverse Hessian (Ch. 3, Zucchini and MacDonald (2009)).

All analysis was conducted in R (R Core Team, 2014) using code adapted from the sample code provided by Zucchini and MacDonald (2009).

2.1.6   Model Selection and Evaluation

A maximal model containing all candidate explanatory variables (Table 1) was constructed and backward elimination was used to select the best fitting model. Variables were removed from the model in order of significance, with the least significant terms removed first. At each stage, models were compared by Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002), with the aim of finding the model with the lowest AIC value. We also consider including a random effect for site to see if this improves the model. The complexity of these models means there are no standard tests to check the goodness-of-fit. Thus, we simply compared the model predictions with the original data to confirm they were reasonable.

The best model was then used for two purposes. First, to infer the significant factors that determine when seals are likely to feed and how likely seal predation is to subside when present. Second, to determine the significant factors affecting the mean number of mortalities during a feeding event and whether ADDs in particular affect this.

2.2   Case Study: Installing Deterrents to a Site in Orkney

2.2.1   Field Site and Setup

A case study was conducted on a salmon farm situated in the Orkney islands off the north coast of Scotland. The farm consists of twelve circular pens arranged in two rows of six (Figure 2). Each pen is 90 metres in diameter and is fitted with an anti-predator net.

This site experienced high levels of seal-related mortalities in early May 2015 immediately after an extended fallow period. The company Ace Aquatec therefore installed six of their ADDs (Universal Scrammer 3 (US3)) across the site on 13th May to combat this issue (Figure 2). The US3 produces sounds in the range of 10-20 kHz and is reported by the manufacturer to have a source level of 195 dB re 1 μPa at 1 m (rms).

Ace Aquatec also installed a new marine mammal deterrent device on one of the pens on 13th May 2015 (Figure 2). The device consists of a net which can be attached to a pre-existing salmon pen and generates a pulsed, low-voltage electric field within a localised area (a few centimetres) around the net. The net has a series of strings running out from the base of the pen, as this is considered to be the direction from which most seal attacks occur. In principle, the net was designed to provide a tactile response to enforce the deterrence of marine mammal predators when paired with the acoustic system. For details of captive trials of a preliminary version of the device, see Milne et al. (2013).

It is important to note that, prior to these installations, the site has not used any deterrent systems before. In order to minimise losses, deterrents were installed on the pens with the highest levels of fish mortalities.
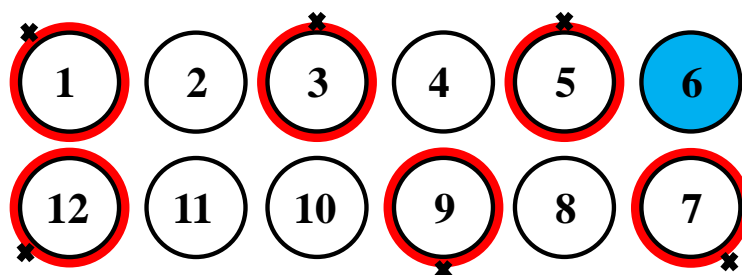

Figure 2. Layout of case study salmon farm in Orkney. Six pens were fitted with ADDs (shown by the red circles, with crosses indicating the approximate location of the transducer) and one pen was fitted with a new electric net device (highlighted in blue).

2.2.2   Data Collection

As part of good practice, dead salmon in pens at the Orkney site are collected weekly, counted, classified and recorded (similarly to that described for previous sites in Section 2.1.1). The company provided us with data on seal attack mortality numbers for the period of July 2012 to July 2015. This included counts of the number of mortalities per pen per week.

2.2.3   Using a HMM to Study Changes in Seal Depredation

In a similar method to that described in Section 2.1.3, a hidden Markov model (HMM) (recall Figure 1) was constructed to investigate the changes in seal-attributed fish mortalities and assess whether the addition of the new deterrent devices reduced the number of mortalities. The new model had the same hidden states and state process as the previous model. Differing from the previous model, here, a time step was of duration one week. Another difference was that the state switching probabilities ($\gamma_{in}, \gamma_{out}$) were not considered as GLMs and so did not depend on any covariates. This was due to the lack of data limiting the complexity of the model.

For this site, each observation $\boldsymbol{M}_t$ is a vector of twelve elements

$$\boldsymbol{M}_t = (M_{t,1}, \ldots, M_{t,12})$$

where $M_{t,i}$ is the number of seal-attributed mortalities in pen i at time t. As before, mortalities at pen i must be equal to zero if the system is in a non-feeding state ($Pr(M_{t,i} = 0|F_t = 1) = 1$). If the system is in a feeding state, we assume the mortalities in each pen ($M_{t,i}$) follow a negative binomial distribution with size parameter r and success probability p. We use the GLM structure with a log link function to include covariates as explanatory variables for the number of fish killed in a feeding state (Table 2). We included covariates to investigate whether there was an effect on a particular pen to which a deterrent device (ADD, electric net) was attached as well as a covariate for the site-wide (or 'global') effect of installing the deterrent systems.

Table 2. Description of covariates considered as explanatory variables for the number of fish killed in a feeding state. All were factor variables.

Covariate	Description
Month	Month of the year (Jan-Dec)
ADD Pen	ADD active on a specific pen (Y/N)
Net Pen	Electric net active on a specific pen (Y/N)
ADD & Net Overall	ADDs and electric net active anywhere on the site (Y/N)

The number of mortalities within individual pens may not be independent of each other and so a random effect (Zuur et al., 2007, 2009) was included to account for this. A random effect u_t for each week t was included in the linear predictor for the number of fish mortalities:

$$log(r) = \eta_r + u_t, \text{ where } u_t \sim N(0, \sigma^2)$$

where η_r is the linear predictor for the fixed effects, similar to Section 2.1.4. Here, u_t represents the correlation between pens. For example, in some weeks the mortalities will be high in one pen and so you might expect them to be high in the other pens as well. For any given week, there is a mean number of mortalities and the random effect describes how each pen varies around this. Given u_t is known, this now captures all of the pen correlation and so the pens can then be considered as independent negative binomial responses.

A mixed HMM was constructed using all of the explanatory covariates described, with the aim of determining what factors were significant in affecting the number of mortalities during a feeding event. As in Section 2.1, analysis was conducted in R (R Core Team, 2014) using code adapted from Zucchini and MacDonald (2009).

Given that this is a small dataset, one might suggest using a simpler modelling approach instead. However, a simpler model would not be sufficient in this case as it could produce a spurious significant result where a more complex model (capturing the temporal dependence, overdispersion, zero-inflation and seasonality in the data) would conclude there were no significant results.

3 Results

3.1 Seal Depredation Across Scotland

In total, data were collected from 40 sites across the west coast of Scotland, 27 of which used ADDs. Salmon mortality records for each site typically spanned the entire study period of 78 months (with the exception of occasional missing data points), resulting in a total of 2126 observations. When fish mortalities due to seals occurred, the mean number recorded per month was 462 (SD $= 1007, \min = 1, \max = 10460$).

Table 3. Summary of top three models for seal depredation ranked by AIC. Shown are models where the number of mortalities in a feeding state (r), probability of switching into a feeding state (γ_{in}) and probability of switching out of a feeding state (γ_{out}) are influenced by combinations of month (Mon), region (Reg), ADD type (ADD) and number of pens (PenNo). Also shown is a model containing a random effect (RE) for site variability.

Model specification			AIC	ΔAIC
r	γ_{in}	γ_{out}		
Reg + ADD + PenNo + RE(Site)	Mon + Reg	Mon	11571.94	0.00
Reg + ADD + PenNo	Mon + Reg	Mon	11589.96	18.02
Reg + ADD + PenNo	Mon + Reg	Mon + ADD	11590.88	18.94

The best fitting model for seal depredation included combinations of region, ADD type, pen number and month as explanatory variables of the three different parameters as well as a random effect for site (Table 3). In this model, the probability of switching into a feeding state (γ_{in}, $p < 0.05$) and the probability of switching out of a feeding state (γ_{out}, $p < 0.01$) were both significantly different from that expected by chance. The probability of moving into a feeding state (γ_{in}) was dependent on both month and region (Figure 3). There was not a significant difference in γ_{in} between the North-West and the Outer Hebrides ($p = 0.239$), but it was significantly lower in the South-West compared to the other two regions ($p < 0.001$). There were seasonal changes in γ_{in} where there was a higher chance of switching into a feeding state in the autumn or winter months (Figure 3). The probability of switching into a feeding state was significantly lower ($p < 0.05$) in April, May, June and July compared to January. The probability of moving out of a feeding state (γ_{out}) was dependent only on month, with this probability being highest in the summer months (Figure 3). Out probabilities were significantly lower in May ($p < 0.05$) and significantly higher in July ($p < 0.05$) compared to January.

The mean number of fish killed in a feeding state (r) was dependent on region, ADD type and pen number (Table 3). The number of pens on a site had a significant effect on the
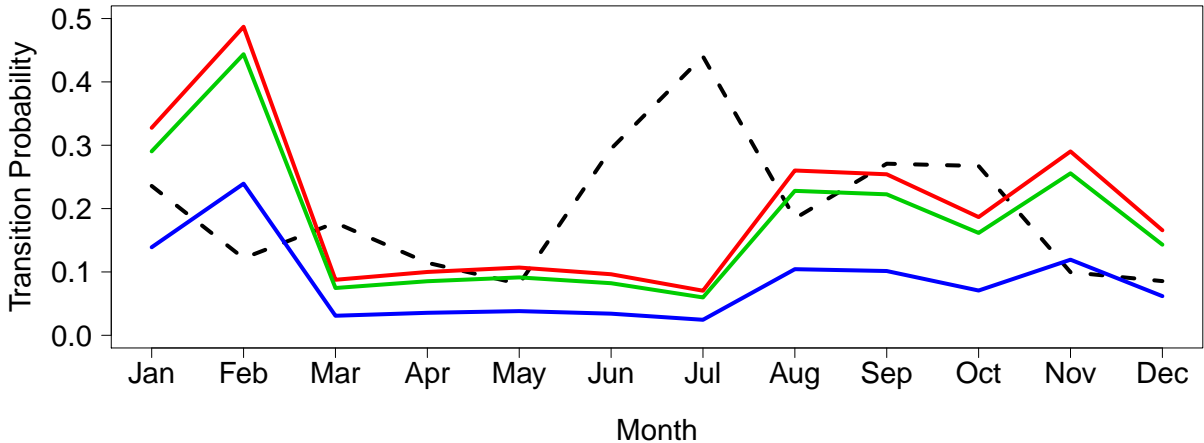
Figure 3. Estimated transition probabilities from the best fitting model for seal depredation in Scotland. The probability of moving into a feeding state (γ_{in}) depended on both month and region (solid lines): North-West (red), Outer Hebrides (green), South-West (blue). The probability of moving out of a feeding state (γ_{out}) depended only on month (black dashed line).

number of mortalities ($p < 0.001$) where the number of expected mortalities increased with pen number. Adding an extra pen to a site increased the number of fish mortalities by 13%. The number of fish killed was also dependent on region, with mortalities being highest in the North-West, moderate in the Outer Hebrides (an average of 70% lower) and lowest in the South-West (a further 15% lower) (Figure 4). Both the Outer Hebrides and the South-West had mortalities which were significantly lower ($p < 0.001$) than in the North-West. ADD type used on a site also affected the number of mortalities. Compared to sites using no deterrent devices (Figure 4- shown in black), using an Ace Aquatec ADD reduced the number of mortalities significantly ($p < 0.001$) with an average reduction of 70% (Figure 4- shown in red). Using an Airmar ADD (Figure 4- shown in green) also made a significant difference ($p < 0.01$), with an average reduction in mortalities of 50%. Sites which used a Terecos ADD experienced no reduction in mortalities, with mortalities being insignificantly different ($p = 0.497$) from when no deterrent device was used. Expected mortalities per month for Figure 4 were calculated by multiplying estimates for the number of fish killed in a feeding state by the proportion of time expected to be spent in a feeding state each month (using the equilibrium distribution $\boldsymbol{\delta}$). These were calculated for an average site with eleven pens and so estimates would need to be adjusted to obtain expectations for larger or smaller sites. The final model also contained a random effect for site individuality with a standard deviation $\sigma = 0.565$.

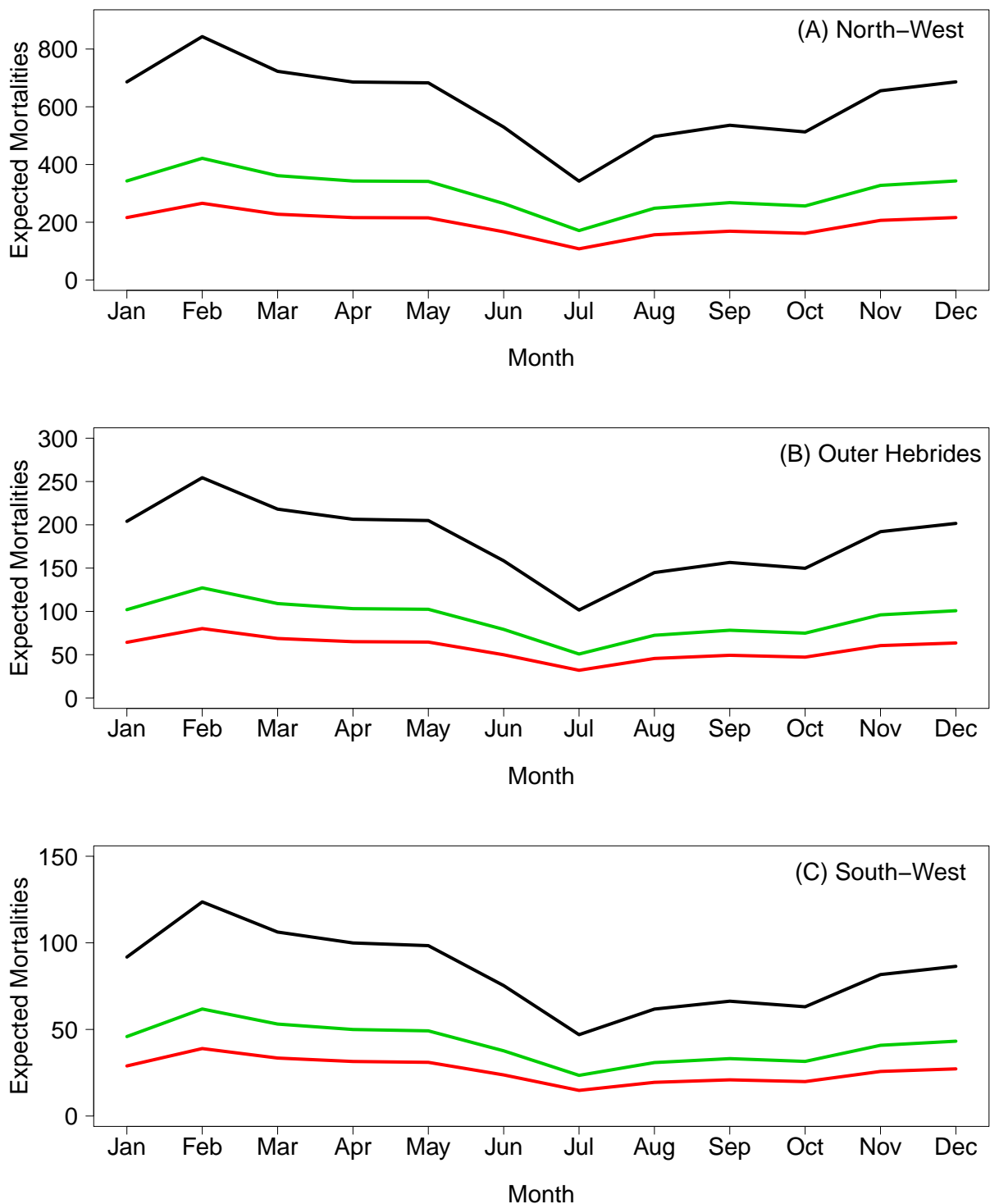**Figure 4.** Expected salmon farm mortalities across Scotland for different regions, months and deterrent systems. Shown are the estimated number of mortalities per month for each ADD type used: none or Terecos (black), Ace Aquatec (red) and Airmar (green). Expected mortalities were calculated for an average site size of 11 pens. Note the differences in the axis scale used for mortalities in the different regions (A, B, C).

3.2 Case Study: Installing Deterrents to a Site in Orkney

For the salmon farm site in Orkney there were 108 data points of mortality observations, only 9 of which occurred after the installation date of the deterrent systems. When seal-attributed fish mortalities did occur on site, the mean number recorded on the site per week was 189 (SD $= 153.9, \min = 7, \max = 728$) with a mean of 15 per pen (min $= 0, \max = 639$).

Table 4. Summary of parameter estimates, standard errors and p-values for the mixed HMM for seal depredation at the case study site in Orkney. Parameters which were significant at the $p < 0.05$ level are highlighted by an asterisk. The parameters r to γ_{out} are presented on the natural scale and the remainder of the parameters are on the scale of the linear predictor (as they were all considered as covariates for r).

Parameter Name	Estimate	SE	P-value
r	-1.215	0.189	<0.001*
p	0.025	0.002	<0.001*
γ_{in}	0.325	0.126	0.082
γ_{out}	0.059	0.024	<0.001*
Global ADD effect	-0.508	0.266	0.028*
Pen ADD effect	-0.247	0.244	0.156
Pen Net effect	0.277	0.390	0.239
Month: February	0.087	0.271	0.374
Month: March	0.522	0.324	0.054
Month: April	0.451	0.301	0.067
Month: May	0.523	0.234	0.013*
Month: June	0.653	0.279	0.010*
Month: July	0.427	0.287	0.068
Month: August	1.023	0.516	0.024*
Month: September	0.452	0.416	0.139
Month: October	0.282	0.256	0.136
Month: November	-0.263	0.330	0.213
Month: December	-0.107	0.287	0.354

The model parameter estimates as well as their significance are summarised in Table 4. The probability of switching into a feeding state (γ_{in}) was not significantly different from random ($p = 0.082$) and so a system which is in a non-feeding state is equally likely to switch or stay in the same state. The probability of switching out of a feeding state (γ_{out}) was significantly different from that expected by randomness. There was a seasonal effect

detected where some of the summer months had significantly higher mortalities than in January (Table 4). Having an active ADD on a particular pen did not affect the number of mortalities in that pen during a feeding state ($p = 0.156$). Similarly, there was no effect detected from having the electric net on a particular pen ($p = 0.239$). However, there were significantly less mortalities ($p = 0.028$) across the site (a global effect) when the six ADDs and the electric net were all active. Due to the setup of this case study it is not possible to isolate the effect of the ADDs from the electric net or estimate which contributed more to this result. The model also contained a random effect for week with a standard deviation $\sigma = 0.850$.

4   Discussion

4.1   Seal Depredation Across Scotland

The occurrence and severity of seal predation attacks on Scottish salmon farms was found to be dependent on a number of different factors. There was a clear seasonal trend detected (Figure 3), with seals more likely to abandon feeding at a site in the summer than the winter. They were also more likely to feed at farms in the autumn and winter months. This means that during the summer seal attacks will generally be less common. When they do occur there is a high chance of them ending and so they are likely to be short in duration. In contrast, depredation events in autumn and winter are more likely to occur and are likely to last for months at a time as there is a low probability that the attack will end. This trend is consistent with the general perception within the industry, where seal depredation is commonly reported to be worst in winter (Northridge et al., 2013). The peak of depredation occurrence appears to be around January and February, coinciding with the end of the grey seal breeding season (Cronin et al., 2013). As breeding seals tend to fast during this time (Harris, 2007), individuals will have to find food fast to build up energy stores again. Fish farms could therefore be seen as a quick and easy food source for seals during this time, where their presence is generally reliable (with the exception of fallow periods) and fish can be found in high quantities. The occurrence of depredation events increases from summer to autumn, coinciding with the end of the breeding season of the harbour seal (Cunningham et al., 2010) which also fasts during this period. Alternatively, this increase could be caused by grey seals increasing their food intake to stock up for the breeding season ahead. Therefore, monthly changes in depredation rates can be explained by important changes in life history stages and energy requirements of seals.

Seasonal changes in depredation are also likely to be dependent on changes in prey availability. Seals are generalist predators and so feed opportunistically on whatever prey is abundant at the time (Brown et al., 2012). This results in large variations in UK seal diet between different times of year (Hall et al., 1998; Hammond and Grellier, 2005; Harris, 2007; Brown et al., 2012). During winter, there is thought to be less prey available for seals in coastal Atlantic waters. Prey patches become more scattered and unpredictable and so seals often have to travel further offshore to feed (Breed et al., 2009). A study by Cronin et al. (2013) found that grey seals in the northwest Atlantic travelled significantly longer distances on foraging trips during the winter months, suggesting that prey is not locally abundant at this time of year. Hence, the use of fish farms as a local resource for seals during the winter could have substantial benefits for their energy budgets.

In addition to seasonal trends, there were clear regional differences in seal depredation observed. Both the probability of a seal beginning to feed at a site (Figure 3) and the number of fish eaten (Figure 4) depended on region. Seal-attributed mortalities are generally highest in the North-West of Scotland, moderate in the Outer Hebrides (an average of 70% lower) and lowest in the South-West (a further 15% lower). There is also a lower chance of a seal beginning to feed in the South-West. Northridge et al. (2013) additionally confirm depredation rates to be lower in the Outer Hebrides than in the North-West. Our analysis has furthered our knowledge by providing an additional comparison to sites in the South-West of Scotland. Regional differences are likely to be the result of a combination of different factors. First, the number of seals present in an area could influence the number of mortalities. The estimated density of both grey and harbour seals is lower in the South-West than in the other two regions (Jones et al., 2013). It could be speculated that where more seals are present, more competition exists between seals for food and so more seal attacks on fish farms might be expected. However, a comparison by Northridge et al. (2013) found that fish farm sites closer to seal haulout sites did not experience an increased frequency or intensity of depredation. The second factor that may determine regional differences is prey availability. The regional differences in seal diet in the UK are well-documented (Hammond and Grellier, 2005; Brown et al., 2012), with animals in different regions consuming different quantities of each prey species in order to make up their nutritional requirements. Regional depredation differences may be a result of diet differences based on present or historical availability of prey. Third, and finally, the geographical and biological differences inherent in each site are a key factor in determining whether depredation will be a problem. For example, the low levels of depredation observed in the South-West may be because many sites are located in relatively more isolated (inland) sea lochs where seals are less likely to frequent. We discuss further unmodelled heterogeneity in predation counts in Section 4.3.

Along with the previous natural variations in fish mortalities, this study shows that the application of ADDs can significantly reduce depredation (Figure 4). Mortalities for sites using the Ace Aquatec device showed, on average, a 70% reduction in mortalities, while those employing the Airmar ADD showed a 50% reduction. Notably, applying the Terecos ADD on sites had no significant effect on mortalities. The difference between the efficacy of these devices could be related to the characteristics of the different sounds produced. The Ace Aquatec device (Universal Scrammer) produces sounds in a range of frequencies (approximately 5–20 kHz) with a maximum observed source level of 193 dB re 1μPa at 1 m (rms) around 10 kHz (Lepper et al., 2004). The Airmar device (dB Plus II) has a peak frequency of 10.3 kHz with a source level of 192 dB re 1μPa at 1 m (rms) (Lepper et al., 2004). In contrast, the Terecos produces sounds of a lower frequency and source level, with a range of peak frequencies from 2–7 kHz and peak source level of 178 dB re 1μPa

at 1 m (rms) at 4.9 kHz (Lepper et al., 2004). This suggests that a higher source level or higher frequency is sufficient to deter seals. Other studies (Kastelein et al., 2006; Graham et al., 2009; Harris et al., 2014) that have tested ADDs of a similar or higher frequency to that of the Airmar and Ace Aquatec devices have found that these sounds can be effective in displacing seals. However, efficacy seems to vary according to the situation (i.e. environmental conditions, target population and species, deployment technique) (Götz and Janik, 2013) and so is not necessarily comparable between all studies. From our project, we can conclude that the ADDs examined here provide the observed effects for the conditions typically present in Scottish fish farms. We do not know how many sites used their ADDs continuously and how many used them intermittently (e.g. during periods of worse depredation). Therefore, we observe the effect of the common practice used on sites that have ADDs.

Finally, the model further revealed that the average number of fish mortalities increased with the number of pens on site. This can be interpreted as seals consuming a certain percentage of the fish in each pen. However, the cause of this is probably related to the attractive potential of sites. Sites with many pens and many fish present a larger potential feeding resource for seals and so seals are more likely to visit. The model also included a random effect for site variability. The multiple causes which will interact to influence seal attacks are complex, and so it is realistic that the constructed model will not capture all the variation in the data. Some sites seem to experience particular problems with seal depredation, whereas other sites experience very few problems.

4.2   Case Study: Installing Deterrents to a Site in Orkney

The more detailed data available in the case study enabled a site on Orkney to be investigated on a pen-by-pen basis (Table 4). The addition of a new electric net deterrent device on one of the pens had no observable effect on the number of mortalities within that pen. Similarly, the addition of ADDs to six of the pens did not reduce depredation within those particular pens compared to the others. However, the addition of both the ADDs and the electric net produced a significant decrease in the overall number of mortalities on the site. As ADD locations are spread throughout the site and pens are situated close together, it is likely that ADDs provide equal protection to all the pens on the site. Additionally, if seals are startled by the electric net on pen six whilst trying to feed they may be less likely to take the risk of feeding from any of the other pens. Thus, both ADDs and the electric net could provide a global deterrent effect across the site. To detect a significant result for this global effect from such a small number of data points after installation suggests a rapid deterrent ability of these systems.

Temporal variation in mortalities was also considered in this case study. Contrary to the findings presented on the west coast of Scotland (Section 3.1), significantly higher mortalities occurred in the summer months. This could be a result of regional differences in environment, ecosystems or fish farm practices. For example, a photo-ID study (Northridge et al., 2013) found that seals which visited fish farms on the west coast were a mixture of both grey and harbour seals, whereas on Orkney sites were visited exclusively by grey seals. However, it seems more likely that this result is simply due to the limited sample size available for each month.

As no pen-specific deterrence effects were significant and both the electric net and the ADDs were installed at the same time, it is impossible to isolate the individual effect of each of these deterrent systems. This is unfortunate as it could benefit the aquaculture industry to know whether electric nets are an effective deterrent device. In Section 3.1 we found that the Ace Aquatec ADD significantly reduces fish mortalities on the west coast of Scotland and so the question remains on whether the electric net has any additional benefit. Here, the deterrent devices were installed on pens with the highest levels of mortalities and so these pens are likely to always have the largest observed mortalities, even if the device begins to work.

This case study raises some important considerations in relation to the effective testing of deterrent devices. Devices should be added to sites individually so that their effects can be isolated. Pens and sites should be picked at random to test devices so as to remove potential biases on average. Devices should be left on sites for a considerable length of time in order to be sure seals do not habituate. During these trials a range of techniques (e.g. mortality records, underwater cameras, visual observations at the surface) should be carried out concurrently to fully understand how the new device is working. These observations should be carried out before, during and after the new device is implemented.

4.3   Review of Methodology

There are a number of possible shortcomings in the methods used that need to be considered. In particular, we must address the assumptions made about the mortality data used. First, it is assumed that fish mortalities are correctly classified by salmon farm workers. It is possible that, on occasion, fish that died from other causes such as physical storm-related damage or disease may be incorrectly classified as seal-attributed mortalities and vice versa. However, seal-attributed mortalities are generally quite distinctive. Most commonly the fish have a clear bite mark taken from the abdomen, with puncture wounds and missing flesh (Northridge et al., 2013). In other cases fish have multiple gashes along the flank (presumably caused by the seals using their fore-flippers) or half or more of the

fish has been bitten off. This misclassification is therefore likely to be negligible. Another assumption is that seals predate only on live fish and do not feed opportunistically on dead fish lying at the bottom of the pen. However, other studies of wild seals have shown that seals will feed on dead fish presented as bait. Fjälling et al. (2007) observed grey seals taking herring (*Clupea harengus*) bait which was attached to the anchor lines of fishing buoys. Harbour seals have also been found to take bait of several different species from net cages (Lunneryd, 2001). Notably in this study seals only visited sites at 30% of opportunities, despite seals being present in the area the entire time. This suggests that only some seals used the baited cages or that seals prefer to feed on live fish and only supplement their diet with dead fish when required. This has important implications as it reveals that seals may also, to some extent, feed on fish that are already dead in pens, leading to a potential overestimation of the problem. One final limitation of fish mortality data is that it does not account for hidden losses. As well as the observed mortalities, fish may be eaten whole or escape from holes in damaged nets. Catastrophic escape events are generally reported. For example, in 2013 there were four incidents across Scotland involving the total loss of 9,709 Atlantic salmon (Marine Scotland Science, 2013). The escape of individual fish from small net holes is less conspicuous and so may not be noticed or recorded. Similarly, seals that leave no fish remains will result in mortalities going unrecorded. Fjälling (2006) found that using fish mortalities to calculate catch losses to grey seals in salmon set traps tended to underestimate losses by 37%. Hidden mortalities will inevitably occur in salmon aquaculture also but are kept to a minimum by the fine mesh size of nets (reducing the ability of seals to pull fish through the nets) and the repair of holes by divers that regularly inspect the nets for damage.

Mortality data were collected as part of normal fish farm operation and not as part of a designed experiment. Hence, the conditions under which data were collected and the methods used could not be controlled. Given that UK fish farms must follow strict recommendations and regulations relating to all aspects of production (RSPCA, 2012; Aquaculture and Fisheries (Scotland) Act, 2013; Scottish Salmon Producers Organisation, 2015), all sites will use broadly similar equipment and protocols. This will be especially true for the sites analysed in Section 2.1 which were all owned by the same aquaculture company. Despite their potential caveats, mortality records present a large resource of data which can provide important insight into the issues occurring at aquaculture sites. These records represent some of the most long-term and geographically widespread data we have. Ideally, investigations into seal depredation would be conducted in well-designed and controlled experiments on fish farms. However, this is often not possible as many companies and workers cannot put their livelihood at risk by experimenting with changing practices.

The hidden Markov model (HMM), implemented in this project, was constructed with the assumption that the sites are stocked at all times. Yet, this may not be the case in reality as sites are regularly left fallow for the purposes of cleaning and recovery. The model was constructed under this assumption as no data were available on the stocking density of pens. Thus, it was not possible to separate periods of zero mortality from fallow periods with absolute certainty. However, it was interpreted that zeros in the data probably related to periods of zero mortality, and the missing data points related to fallow periods. It therefore made sense to model the sites as being stocked permanently, with "missing observations" during fallow periods. During fallow periods, it is likely that seals will still be present and visit sites to check if fish are present. This means that our model is a good representation of the expected mortalities during periods when sites are stocked and estimates are not biased by zeros recorded during fallow periods.

Our model for seal depredation across Scotland (constructed in Section 2.1) considers site to be the basic experimental unit. Data was not available at a more detailed resolution and so variability between specific pens could not be investigated. It is possible that the most serious issues of depredation result from 'problem pens' that have a particular weakness or are more attractive to seals. Even though it is unclear why seals pick particular pens to attack intensely, given that mortalities still occur across most pens during feeding, selecting site as the unit of interest still seems reasonable. It is also more informative for site managers as they can gain information on how the total number of mortalities is expected to vary across region and season.

In addition to the explanatory variables investigated here, there are a number of other factors that could potentially have influenced the feeding dynamics of seals at farms. We do not have information on the numbers of seals shot at each of the locations throughout the study period. Seal shootings are most likely to occur during severe mortality events as a means of ending the problem and reducing economic losses. Hence, it is possible that this influenced the number of mortalities or the probability of a feeding ending. On the other hand, the number of seals currently shot in Scotland is quite low and continues to decrease each year as other methods of deterrence improve. For example, the numbers of grey seals shot each year were 366 in 2011, 359 in 2012 and 238 in 2013 (Scottish Government, 2015). Similarly, the numbers of harbour seals shot were 93, 74 and 36 (for the years 2011, 2012 and 2013 respectively) (Scottish Government, 2015). Therefore, the total number of seals shot across Scotland during 2013 was 274, the equivalent of approximately one seal for each stocked salmon farm site in that year. Therefore it seems unlikely that failing to account for possible seal shootings in modelling will constitute a serious problem.

Similarly, aspects of site design ignored in this study may also influence depredation (e.g. pen size, pen shape, net mesh size and pen arrangement). Most common are circular pens

(Northridge et al., 2013), with pens typically arranged in parallel rows, but there will likely be some variation between sites. Sites vary in stocking density (i.e. the number of fish per volume of pen). It is believed that sites which have a high stocking density are likely to experience more depredation Northridge et al. (2013); however there is currently no evidence to support this. Environmental and ecological differences between sites such as weather, seal haulout site distance and seal prey availability may also influence mortalities. Sites may also differ slightly in their everyday practices. Despite these potential differences, our model has been able to identify consistent trends in mortalities across regions and seasons. Furthermore, the random effect included for site should capture the individualistic variations of fish farms to some extent.

4.4   Suggestions for Further Research

This research project has highlighted a number of knowledge gaps that require further study. If more fish farm data were available, the modelling framework presented here can be expanded to investigate other explanatory variables. For example, it would be interesting to test whether aspects of pen structure and design, such as the use of anti-predator nets, reduces mortalities. Measures of the environmental (e.g. sea surface temperature) and ecological (e.g. local prey availability) setting of fish farm sites should also be made and compared to mortality rates. If further data on stocking biomass were provided, the model could be used to investigate whether pens containing a higher density of fish are more likely to be predated. They could also be used to investigate how depredation changes with each stage of the production cycle. It is thought that depredation is dependent on the number of months after the site was previously fallow (Northridge et al., 2013), possibly due to seals becoming increasingly reliant on the site as a food source.

Some pens on fish farm sites appear to experience more severe depredation than others. It is unknown whether this is due to location of these particular pens within the site (e.g. end pens), maintenance of pen equipment (e.g. poor condition, degraded) or the disturbance level of pens (i.e. how close are they to regular human activity). It could be that when seals first visit the site they feed from the first pen they encounter, and so keep returning to this one pen as they know they can get food there. Any further information on why particular pens are targeted would enable fish farm managers to identify vulnerable pens and adopt appropriate prevention strategies.

The new electric net device assessed here could present a feasible alternative deterrent device which does not produce the noise pollution that ADDs do. It should be installed in a range of different sites and regions in order to gain reliable information on how effective it is at reducing depredation. All trials should be careful to follow some of the advice on experimental design in Section 4.2.

4.5   Overall Conclusions and Recommendations

To conclude, we review the main findings of this study in relation to recommendations for salmon farm management. The number of seal-attributed mortalities is seasonally dependent, with the highest numbers expected during the winter months. Hence, the use of deterrent systems (such as ADDs) should be highest during this period. At other times of the year, when fish mortalities are expected to be low, ADD use can be decreased to minimise energetic running costs and noise pollution. There are also pronounced regional differences in mortalities. For regions with higher expected mortalities, companies should be investing more in appropriate deterrent and defence mechanisms and extra efforts should be made to monitor the condition of pens. Both the Ace Aquatec and Airmar ADDs were found to significantly reduce seal depredation and use of either device is recommended. Sites with particularly high depredation should use the Ace Aquatec device as this appears to have a bigger reductive effect on fish mortalities. A summary of expected mortalities for each month, region and ADD combination is provided in Figure 4 and can be used in the planning of predator control strategies for sites across Scotland. Additionally, the number mortalities increases with site size (number of pens) and so expected mortalities should be adjusted for smaller or larger than average sites.

The installation of a new electric net deterrent was observed, but from this case study it could not be concluded whether the net reduced mortalities. A combination of the net and ADDs appeared to reduce mortalities but further studies are required before this can be recommended as a viable alternative to ADDs.

5   References

Agarwal, D. K., Gelfand, A. E., and Citron-Pousty, S. (2002). Zero-inflated models with application to spatial count data. *Environmental and Ecological Statistics*, 9:341–355.

Altman, R. M. (2007). Mixed Hidden Markov Models: An Extension of the Hidden Markov Model to the Longitudinal Data Setting. *Journal of the American Statistical Association*, 102(477):201–210.

Anderson, S. S. and Hawkins, A. D. (1978). Scaring seals by sound. *Mammal Review*, 8:19–24.

Aquaculture and Fisheries (Scotland) Act (2013). Regulations on fish farm management and equipment. *The Scottish Government.*

Beeson, M. J. and Hanan, D. A. (1996). An Evaluation of Pinniped-Fishery Interactions in California. *A Report to the Pacific States Marine Fisheries Commission (PSMFC). Prepared by the Marine Resources Division, California Department of Fish and Game (CDFG).*

Brandt, M. J., Höschle, C., Diederichs, A., Betke, K., Matuschek, R., Witte, S., and Nehls, G. (2013). Far-reaching effects of a seal scarer on harbour porpoises, Phocoena phocoena. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 23(2):222–232.

Breed, G. A., Jonsen, I. D., Myers, R. A., Don Bowen, W., and Leonard, M. L. (2009). Sex-specific, seasonal foraging tactics of adult grey seals (Halichoerus grypus) revealed by state-space analysis. *Ecology*, 90(11):3209–3221.

Brown, S. L., Bearhop, S., Harrod, C., and McDonald, R. A. (2012). A review of spatial and temporal variation in grey and common seal diet in the United Kingdom and Ireland. *Journal of the Marine Biological Association of the United Kingdom*, 92(8):1–12.

Burnham, K. P. and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach.* Springer-Verlag, New York, 2nd edition.

Cappé, O., Moulines, E., and Ryden, T. (2005). *Inference in Hidden Markov Models.* Springer, New York; London.

Coram, A., Gordon, J., Thompson, D., and Northridge, S. (2014). Evaluating and Assessing the Relative Effectiveness of Acoustic Deterrent Devices and other Non-Lethal Measures on Marine Mammals. *Scottish Government.*

Cronin, M., Pomeroy, P., and Jessopp, M. (2013). Size and seasonal influences on the foraging range of female grey seals in the northeast Atlantic. *Marine Biology*, 160(3):531–539.

Cunningham, L., Baxter, J. M., and Boyd, I. L. (2010). Variation in harbour seal counts obtained using aerial surveys. *Journal of the Marine Biological Association of the United Kingdom*, 90(8):1659–1666.

Dennis, J. E. and Schnabel, R. B. (1983). *Numerical Methods for Unconstrained Optimization and Nonlinear Equations*. Prentice-Hall, Englewood Cliffs, NJ.

Fjälling, A. (2006). The conflict between grey seals (Halichoerus grypus) and the Baltic coastal fisheries - new methods for the assessment and reduction of catch losses and gear damage. *Linköping Studies in Science and Technology, Dissertation No. 1006*.

Fjälling, A., Kleiner, J., and Beszczyska, M. (2007). Evidence that grey seals (Halichoerus grypus) use above-water vision to locate baited buoys. *NAMMCO Scientific Publications*, 6:215–227.

Forrest, K. W., Cave, J. D., Michielsens, C. G. J., Haulena, M., and Smith, D. V. (2009). Evaluation of an Electric Gradient to Deter Seal Predation on Salmon Caught in Gill-Net Test Fisheries. *North American Journal of Fisheries Management*, 29:885–894.

Franke, A., Caelli, T., and Hudson, R. J. (2004). Analysis of movements and behavior of caribou (Rangifer tarandus) using hidden Markov models. *Ecological Modelling*, 173(2):259–270.

Franke, A., Caelli, T., Kuzyk, G., and Hudson, R. J. (2006). Prediction of wolf (Canis lupus) kill-sites using hidden Markov models. *Ecological Modelling*, 197(1):237–246.

Gordon, J. and Northridge, S. (2002). Potential Impacts of Acoustic Deterrent Devices on Scottish Marine Wildlife. *Scottish Natural Heritage Commissioned Report F01AA404*.

Götz, T. and Janik, V. M. (2010). Aversiveness of sounds in phocid seals: psychophysiological factors, learning processes and motivation. *The Journal of Experimental Biology*, 213(9):1536–1548.

Götz, T. and Janik, V. M. (2013). Acoustic deterrent devices to prevent pinniped depredation: efficiency, conservation concerns and possible solutions. *Marine Ecology Progress Series*, 492:285–302.

Graham, I. M., Harris, R. N., Denny, B., Fowden, D., and Pullan, D. (2009). Testing the effectiveness of an acoustic deterrent device for excluding seals from Atlantic salmon rivers in Scotland. *ICES Journal of Marine Science*, 66(5):860–864.

Graham, I. M., Harris, R. N., Matejusová, I., and Middlemas, S. J. (2011). Do rogue seals exist? Implications for seal conservation in the UK. *Animal Conservation*, 14:587–598.

Hall, A., Watkins, J., and Hammond, P. (1998). Seasonal variation in the diet of harbour seals in the south-western North Sea. *Marine Ecology Progress Series*, 170:269–281.

Hammond, P. S. and Grellier, K. (2005). Grey Seal Diet Composition and Fish Consumption in the North Sea. *Department for Environment, Food and Rural Affairs*, pages 1–54.

Harris, R. (2007). Assessing grey seal (Halichoerus grypus) diet in western Scotland. *A Thesis Submitted for the Degree of MPhil at the University of St Andrews*.

Harris, R. N., Harris, C. M., Duck, C. D., and Boyd, I. L. (2014). The effectiveness of a seal scarer at a wild salmon net fishery. *ICES Journal of Marine Science*, 71(7):1913–1920.

Jefferson, T. A. and Curry, B. E. (1996). Acoustic methods of reducing or eliminating marine mammal-fishery interactions: do they work? *Ocean & Coastal Management*, 31(1):41–70.

Johnston, D. W. (2002). The effect of acoustic harassment devices on harbour porpoises (Phocoena phocoena) in the Bay of Fundy, Canada. *Biological Conservation*, 108:113–118.

Jones, E., Mcconnell, B., Sparling, C., and Matthiopoulos, J. (2013). Grey and harbour seal density maps, Marine Mammal Scientific Support Research Programme MMSS/001/11. *Sea Mammal Research Unit Report to Scottish Government*, pages 1–35.

Karhu, R. R. and Anderson, S. H. (2006). The Effect of High-Tensile Electric Fence Designs on Big-Game and Livestock Movements. *Wildlife Society Bulletin*, 34(2):293–299.

Kastelein, R. A., van der Heul, S., Terhune, J. M., Verboom, W. C., and Triesscheijn, R. J. V. (2006). Deterring effects of 8-45 kHz tone pulses on harbour seals (Phoca vitulina) in a large pool. *Marine Environmental Research*, 62:356–373.

Königson, S. (2007). Seal behaviour around fishing gear and its impact on Swedish fisheries. *Licentiat thesis. Department of Marine Ecology, University of Goteborg*.

Königson, S., Hemmingsson, M., Lunneryd, S.-G., and Lundström, K. (2007). Seals and fyke nets: An investigation of the problem and its possible solution. *Marine Biology Research*, 3(1):29–36.

LaGrange, T. G., Hansen, J. L., Andrews, R. D., Hancock, A. W., and Kienzler, J. M. (1995). Electric fence predator exclosure to enhance duck nesting: a long- term case study in Iowa. *Wildlife Society Bulletin*, 23(2):261–266.

Leblanc, F. (2003). Protecting Fish Farms from Predation By the Eurasian Otter (Lutra Lutra) in the Limousin Region of Central France: First Results. *IUCN Otter Specialist Group Bulletin*, 20(1):45–48.

Lepper, P. A., Goodson, A. D., and Black, K. D. (2004). Source levels and spectra emitted by three commercial aquaculture anti-predation devices. *Proceedings of the 7th European Conference on Underwater Acoustics, ECUA 5-8 July 2004*, 7:6.

Lepper, P. A., Gordon, J., Booth, C., Theobald, P., Robinson, S. P., Northridge, S., and Wang, L. (2014). Establishing the sensitivity of cetaceans and seals to acoustic deterrent devices in Scotland. *Scottish Natural Heritage Commissioned Report No. 517*.

Lines, J. and Kestin, S. (2004). Electrical stunning of fish: the relationship between the electric field strength and water conductivity. *Aquaculture*, 241(1):219–234.

Lunneryd, S. (2001). Fish preference by the harbour seal (Phoca vitulina), with implications for the control of damage to fishing gear. *ICES Journal of Marine Science*, 58(4):824–829.

Marine (Scotland) Act (2010). Section 110: Seal licences. Part 6: Conservation of Seals. *The Scottish Government*.

Marine Scotland Science (2013). Scottish Fish Farm Production Survey 2013. *Scottish Government: An Official Statistics Publication for Scotland*, pages 1–54.

Milne, R., Lines, J., Moss, S., and Thompson, D. (2013). Behavioural responses of seals to pulsed, low-voltage electric fields in sea water (preliminary tests). *A report commissioned by Scottish Aquaculture Research Forum (SARF) and prepared by Sea Mammal Research Unit (SMRU), University of St Andrews (SARF071)*.

Nash, C. E., Iwamoto, R. N., and Mahnken, C. V. (2000). Aquaculture risk management and marine mammal interactions in the Pacific Northwest. *Aquaculture*, 183(3):307–323.

Northridge, S., Coram, A., and Gordon, J. (2013). Investigations on seal depredation at Scottish fish farms. *Report to Marine Scotland. Edinburgh: Scottish Government*.

Northridge, S. P., Gordon, J. G., Booth, C., Calderan, S., Cargill, A., Coram, A., Gillespie, D., Lonergan, M., and Webb, A. (2010). Assessment of the impacts and utility of acoustic deterrent devices. *Final Report to the Scottish Aquaculture Research Forum, Project Code SARF044*.

Olesiuk, P. F., Nichol, L., Sowden, M., and Ford, J. K. B. (2002). Effect of the sound generated by an acoustic harassment device on the relative abundance and distribution of harbor porpoises (Phocoena phocoena) in Retreat Passage, British Columbia. *Marine Mammal Science*, 18(4):843–862.

Patterson, T. A., Basson, M., Bravington, M. V., and Gunn, J. S. (2009). Classifying movement behaviour in relation to environmental conditions using hidden Markov models. *Journal of Animal Ecology*, 78(6):1113–1123.

Porter, W. F. (1983). A Baited Electric Fence for Controlling Deer Damage To Orchard Seedlings. *Wildlife Society Bulletin*, 11(4):325–327.

Quick, N. J., Middlemas, S. J., and Armstrong, J. D. (2004). A survey of antipredator controls at marine salmon farms in Scotland. *Aquaculture*, 230:169–180.

R Core Team (2014). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.*

Rabearisoa, N., Bach, P., and Marsac, F. (2015). Assessing interactions between dolphins and small pelagic fish on branchline to design a depredation mitigation device in pelagic longline fisheries. *ICES Journal of Marine Science*, -:–.

Read, A. J. (2008). The looming crisis: interactions between marine mammals and fisheries. *Journal of Mammalogy*, 89(3):541–548.

Reeves, R. R., Hofman, R. J., Silber, G. K., and Wilkinson, D. (1996). Acoustic deterrence of harmful marine mammal-fishery interactions: proceedings of a Workshop held in Seattle, Washington, 20-22 March 1996. *U.S. Dep. Commer., NOAA Tech. Memo. NMFS-OPR-10.*

Reidy, M. M., Campbell, T. A., and Hewitt, D. G. (2008). Evaluation of Electric Fencing to Inhibit Feral Pig Movements. *The Journal of Wildlife Management*, 72(4):1012–1018.

RSPCA (2012). RSPCA welfare standards for farmed Atlantic salmon.

Schakner, Z. A. and Blumstein, D. T. (2013). Behavioral biology of marine mammal deterrents: A review and prospectus. *Biological Conservation*, 167:380–389.

Schick, R. S., Kraus, S. D., Rolland, R. M., Knowlton, A. R., Hamilton, P. K., Pettis, H. M., Kenney, R. D., and Clark, J. S. (2013a). Using Hierarchical Bayes to Understand Movement, Health, and Survival in the Endangered North Atlantic Right Whale. *PLoS ONE*, 8(6):e64166.

Schick, R. S., New, L. F., Thomas, L., Costa, D. P., Hindell, M. A., Mcmahon, C. R., Robinson, P. W., Simmons, S. E., Thums, M., Harwood, J., and Clark, J. S. (2013b). Estimating resource acquisition and at-sea body condition of a marine predator. *Journal of Animal Ecology*, 82(6):1300–1315.

Schliehe-Diecks, S., Kappeler, P. M., and Langrock, R. (2012). On the application of mixed hidden Markov models to multiple behavioural time series. *Interface Focus*, 2(2):180–189.

Schnabel, R. B., Koontz, J. E., and Weiss, B. E. (1985). A modular system of algorithms for unconstrained minimization. *ACM Trans. Math. Software*, 11:419–440.

Schotte, R. and Pemberton, D. (2002). Development of a Stock Protection System for Flexible Oceanic Pens Containing Finfish. *Fisheries Research and Development Corporation*, pages 1–85.

Scottish Government (2014). Fisheries: Aquaculture Statistics. *Agricultural, Fisheries and Rural Statistics from the Scottish Government. Available at: http://www.gov.scot/Topics/Statistics/Browse/Agriculture-Fisheries/TrendAquaculture [Accessed 01 Aug 2015]*.

Scottish Government (2015). Seal Licensing: Statistics. *Marine Scotland: Marine and Fisheries Licensing from the Scottish Government. Available at: http://www.gov.scot/Topics/marine/Licensing/SealLicensing [Accessed 10 Aug 2015]*.

Scottish Salmon Producers Organisation (2015). SSPO Code of Good Practice for Scottish Finfish Aquaculture. *Chapters 4 & 5*.

Sepúlveda, M. and Oliva, D. (2005). Interactions between South American sea lions Otaria flavescens (Shaw) and salmon farms in southern Chile. *Aquaculture Research*, 36(11):1062–1068.

Shaughnessy, P. D., Semmelink, A., Cooper, J., and Frost, P. G. H. (1981). Attempts to develop acoustic methods of keeping Cape fur seals Arctocephalus pusillus from fishing nets. *Biological Conservation*, 21:141–158.

Sigler, M. F., Lunsford, C. R., Straley, J. M., and Liddle, J. B. (2008). Sperm whale depredation of sablefish longline gear in the northeast Pacific Ocean. *Marine Mammal Science*, 24(1):16–27.

Skaren, U. (1990). Fish farming and otters in Finland. *IUCN Otter Specialist Group Bulletin*, 5:28–34.

Thomas, L. and Harwood, J. (2003). Estimating Grey Seal Population Size using a Bayesian State-Space Model. *NERC Special Committee on Seals (SCOS) Briefing Paper 03/3*, pages 1–8.

Ver Hoef, J. M. and Boveng, P. L. (2007). Quasi-poisson vs. negative binomial regression: How should we model overdispersed count data? *Ecology*, 88(11):2766–2772.

Yano, K. and Dahlheim, M. E. (1995). Killer whale, Orcinus orca, depredation on longline catches of bottomfish in the southeastern Bering Sea and adjacent waters. *Fishery Bulletin*, 93(2):355–372.

Zucchini, W. and MacDonald, I. L. (2009). *Hidden Markov Models for Time Series: An Introduction Using R*. CRC Press, Boca Raton, FL.

Zuur, A. F., Ieno, E. N., and Smith, G. M. (2007). *Analysing Ecological Data*. Springer, New York; London.

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., and Smith, G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York; London.

A   Appendix: R Code for Seal Depredation Model

```r
1  #################### Fish Mort Analysis #################################
2  ## Description: to fit a hidden Markov model to morts in fish farms around
3  ##              Scotland.
4  ##              Model includes predictors for mean of negative binomial
5  ##              (size predictor), probability of leaving a feeding state
6  ##              ('out' predictor) and probability of entering a feeding
7  ##              state ('in predictor'). A random effect for site is
8  ##              included.
9  ## Author: Katherine Whyte
10 ## Last Edited: 09 Aug 2015
11 ### Function Declarations
12 N2W <- function(nat,n.size=0,n.in=0,n.out=0,n.states=2) {
13    # Transforms natural parameter list to working vector
14    # Args: nat = list of natural parameters
15    #       n.size = number of covariates in size predictor
16    #       n.out = number of covariates in 'out' probability predictor
17    #       n.in = number of covariates in 'in' probability predictor
18    #       n.states = number of hidden feeding states
19    # Returns: the working vector
20    work <- numeric(4+n.size+n.in+n.out)
21    # probability parameter of negative binomial
22    work[1] <- log(nat$prob/(1-nat$prob))
23    # mean predictor
24    work[2] <- nat$size
25    if (n.size>0) {for (i in seq(n.size)) {work[2+i] <- nat$sizecov[i]}}
26    # in predictor
27    work[3+n.size] <- nat$gamma0
28    if (n.in>0) {for (i in seq(n.in)) {work[3+n.size+i] <- nat$incov[i]}}
29    # out predictor
30    work[4+n.size+n.in] <- nat$gamma1
31    if (n.out>0) {for (i in seq(n.out)) {work[4+n.size+n.in+i] <- nat$
          outcov[i]}}
32    # random effect variance
33    work[5+n.size+n.in+n.out] <- nat$sizestd
34    return(work)
35 }
36 W2N <- function(work,n.size=0,n.in=0,n.out=0,n.states=2) {
37    # Transforms working vector to natural parameter list
38    # Args: work = working vector
39    #       n.size = number of covariates in size predictor
40    #       n.out = number of covariates in 'out' probability predictor
41    #       n.in = number of covariates in 'in' probability predictor
42    #       n.states = number of hidden feeding states
43    # Returns: the working vector
```

```
44        prob <- exp(work[1])/(1+exp(work[1]))
45        # mean predictor
46        size <- work[2]
47        sizecov <- NULL
48        if (n.size>0){for (i in seq(n.size)) {sizecov <- c(sizecov,work[2+i])}}
49        # in predictor
50        gamma0 <- work[2+n.size+1]
51        incov <- NULL
52        if (n.in>0){for (i in seq(n.in)) {incov <- c(incov,work[3+n.size+i])}}
53        # out predictor
54        gamma1 <- work[4+n.size+n.in]
55        outcov <- NULL
56        if (n.out>0){for (i in seq(n.out)) {outcov <- c(outcov,work[4+n.size+n.
              in+i])}}
57        # random effect variance
58        sizestd <- work[5+n.size+n.in+n.out]
59        return(list(prob=prob,size=size,sizestd=sizestd,sizecov=sizecov,gamma0=
              gamma0,incov=incov,gamma1=gamma1,outcov=outcov))
60          }
61  NegLlk <- function(w.par,obs,size.covdat,in.covdat,out.covdat,n.states=2) {
62        # Calculates the negative log-likelihood of the HMM with random effects
63        # Args: w.par = working vector of parameters
64        #        obs = data frame of mort data
65        #        size.covdat = data frame of covariate values in mean predictor
66        #        in.covdat = data frame of covariate values in in predictor
67        #        out.covdat = data frame of covariate values in out predictor
68        #        n.states = number of hidden feeding states
69        # Returns: value of the negative log-likelihood
70        par <- W2N(w.par,ncol(size.covdat),ncol(in.covdat),ncol(out.covdat),n.
              states)
71        # calculate probability of observed under each hidden state
72        n <- nrow(obs)
73        probs <- matrix(1,nrow=n,ncol=n.states)
74        for (s in seq(n.states)) {
75            lsize <- par$size
76            if (!is.null(par$sizecov)) {for (i in seq(length(par$sizecov))) {
                  lsize <- lsize+par$sizecov[i]*size.covdat[,i]}}
77            size <- exp(lsize)
78            probs[,s] <- dnbinom(obs$predation,size*(s-1),par$prob)
79        }
80        # calculate transition probability matrix for each factor variable
              combination
81        gamma.list <- list()
82        gamma <- diag(n.states)
83        gamma[1,2] <- par$gamma0
84        gamma[2,1] <- par$gamma1
```

```
85      for (m in seq(1,12)) {
86          gamma.list[[m]] <- list()
87          for (a in seq(1,4)) {
88              gamma.list[[m]][[a]] <- list()
89              for (r in seq(1,3)) {
90                  sgamma <- gamma
91                  # commenting out lines below excludes that factor's effect
92                  # this MUST match the choices for in.covdat and out.covdat
93                  if (m>1) {gamma[1,2] <- gamma[1,2]+par$incov[m-1]}
94                  #if (a>1) {gamma[1,2] <- gamma[1,2]+par$incov[11+a-1]}
95                  if (m>1) {gamma[2,1] <- gamma[2,1]+par$outcov[m-1]}
96                  #if (a>1) {gamma[2,1] <- gamma[2,1]+par$outcov[11+a-1]}
97                  if (r>1) {
98                      #gamma[1,2] <- gamma[1,2]+par$incov[14+r-1]
99                      gamma[1,2] <- gamma[1,2]+par$incov[11+r-1]
100                 }
101                 #if (r>1) {
102                 #    gamma[2,1] <- gamma[2,1]+par$outcov[14+r-1]
103                 #    gamma[1,2] <- gamma[1,2]+par$incov[11+r-1]
104                 #}
105                 gamma[!diag(2)] <- exp(gamma[!diag(2)])
106                 gamma <- gamma/apply(gamma,1,sum)
107                 gamma.list[[m]][[a]][[r]] <- gamma
108                 gamma <- sgamma
109             }
110         }
111     }
112     # calculate likelihood for each site individually
113     llk <- 0
114     site.names <- unique(obs$site)
115     n.site <- length(site.names)
116     # iobs is the index of the current observation being processed
117     iobs <- 1
118     for (i in seq(n.site)) {
119         # slk is the likelihood of the site averaged over the random effect
                 u
120         slk <- 0
121         # discretise random effect space and calculate probability of each
                 possible
122         # value of the random effect
123         size.sd <- exp(par$sizestd)
124         lsize.list <- seq(par$size-size.sd,par$size+size.sd,length=100)
125         diff <- 0.5*(lsize.list[2]-lsize.list[1])
126         pr <- pnorm(lsize.list+diff,par$size,size.sd)-pnorm(lsize.list-diff
                 ,par$size,size.sd); pr <- pr/sum(pr)
127         # idea is to calculate the likelihood for this site for each
```

```
                    possible value
128         # of the random effect u and then weight by how likely that value
                    is
129         uobs <- iobs # need to reset back to uobs after each cycle through
                    lsize.list
130         for (u in seq(lsize.list)) {
131             iobs <- uobs
132             # ullk is the likelihood for a specific value of u
133             ullk <- 0
134             for (s in seq(n.states)) {
135                 # calculate the mean predictor for this value of u
136                 lsize <- lsize.list[u]
137                 for (c in seq(length(par$sizecov))) {lsize <- lsize+par$
                        sizecov[c]*size.covdat[,c]}
138                 size <- exp(lsize)
139                 probs[,s] <- dnbinom(obs$predation,size*(s-1),par$prob)
140             }
141             phi <- c(0.5,0.5)
142             # look only at data for this site
143             subobs <- obs[obs$site==site.names[i],]
144             subn <- nrow(subobs)
145             years <- seq(min(subobs$year),max(subobs$year))
146             months <- seq(1,12)
147             for (y in years) {
148                 for (m in months) {
149                     # select correct transition matrix
150                     gamma <- gamma.list[[m]][[as.numeric(obs$addtype[iobs])
                            ]][[as.numeric(obs$region[iobs])]]
151                     # if an observation exists for (m,y) do HMM step,
                            otherwise just
152                     # do Markov chain step (multiply by gamma)
153                     if (obs$year[iobs]==y & obs$month[iobs]==m) {
154                         phi <- phi%*%gamma*probs[iobs,]
155                         sumphi <- sum(phi)
156                         ullk <- ullk+log(sumphi)
157                         phi <- phi/sumphi
158                         iobs <- iobs+1
159                         # to stop errors when reading past the end of the
                                dataframe
160                         if (iobs>nrow(obs)) {iobs <- nrow(obs)}
161                     }
162                     else {
163                         phi <- phi%*%gamma
164                     }
165                 }
166             }
```

```
167              # multiply ullk by probability of u, then add to averaged
                    likelihood sllk
168              # for this site
169              slk <- slk + exp(ullk)*pr[u]
170          }
171          # add site averaged likelihood sllk to overall likelihood
172          llk <- llk+log(slk)
173      }
174      cat("llk =", llk, "\n")
175      return(-llk)
176  }
177
178  MLE <- function(obs, par0, size.covdat, in.covdat, out.covdat, n.states=2) {
179      # Performs maxmimum likelihood estimation
180      # Args: obs = data frame of mort data
181      #       par0 = starting values for parameters
182      #       size.covdat = data frame of covariate values in mean predictor
183      #       in.covdat = data frame of covariate values in in predictor
184      #       out.covdat = data frame of covariate values in out predictor
185      #       n.states = number of hidden feeding states
186      # Returns: list of maximum likelihood estimates, standard errors and
             AIC
187      w.par <- N2W(par0, ncol(size.covdat), ncol(in.covdat), ncol(out.covdat), n.
             states)
188      # numerical optimiser
189      mod <- nlm(NegLlk, w.par, obs, size.covdat, in.covdat, out.covdat, n.states,
             hessian=TRUE)
190      par <- W2N(mod$estimate, ncol(size.covdat), ncol(in.covdat), ncol(out.
             covdat), n.states)
191      # variance of parameters are diagonal of inverse hessian matrix
192      # (not negative hessian since using negative likelihood here)
193      se <- sqrt(diag(solve(mod$hessian)))
194      pvals <- pnorm(-abs(w.par), 0, se)
195      AIC <- 2*(length(w.par)+mod$minimum)
196      return(list(par=par, se=se, pvalue=pvals, AIC=AIC))
197  }
198  Factor2Mat <- function(x) {
199      # Transforms factor variables into design matrices
200      # Args: x = data vector of factor variable levels
201      # Returns: the design matrix
202      levs <- levels(x)
203      mat <- matrix(0, nr=length(x), nc=length(levs))
204      for (i in seq(x)) {
205          ilev <- levs==x[i]
206          mat[i, ilev] <- 1
207      }
```

```
208        mat <- mat[,-1]
209        return(mat)
210   }
211   Stdise <- function(x) {return((x-mean(x))/sd(x))}
212   ### Executed Statements
213   obs <- read.table ('obs.csv', header=T, sep=",")
214   obs$addtype <- relevel(obs$addtype,"none")
215
216   # transform factors into design matrices
217   month.mat <- Factor2Mat(factor(obs$month))
218   region.mat <- Factor2Mat(factor(obs$region))
219   addtype.mat <- Factor2Mat(factor(obs$addtype))
220
221   # set covariates for mean predictor
222   #size.covdat <- as.data.frame(cbind(month.mat,region.mat,addtype.mat))
223   size.covdat <- as.data.frame(cbind(region.mat,addtype.mat))
224   cts.start <- ncol(size.covdat)
225   #size.covdat$year <- Stdise(obs$year)
226   size.covdat$pen.num <- Stdise(obs$pen.num)
227   size.pars <- ncol(size.covdat)
228
229   # set covariates for 'in' and 'out' predictors
230   in.covdat <- data.frame(cbind(month.mat,region.mat))
231   out.covdat <- data.frame(cbind(month.mat))
232   in.pars <- ncol(in.covdat)
233   out.pars <- ncol(out.covdat)
234
235   # set starting parameter values
236   n.states <- 2
237   size0 <- 50
238   prob0 <- 0.01
239   par0 <- list(prob=prob0,size=-0.3,sizestd=log(0.4),sizecov=rep(0.0,size.
         pars),gamma0=log(0.1/0.9),incov=rep(0.0,in.pars),gamma1=log(0.1/0.9),
         outcov=rep(0.0,out.pars))
240
241   # fit model to data
242   mod <- MLE(obs,par0, size.covdat, in.covdat, out.covdat)
```

B   Appendix: R Code for Case Study

```r
1  ################## Orkney Site Analysis ###################################
2  ## Description: to fit a hidden Markov model to morts in fish farm on
3  ##              Orkney to determine if ADDs had any effect within 8 weeks
4  ##              activation period. Model includes predictor for mean morts
5  ##              in a pen of negative binomial and a random effect to induce
6  ##              correlation between pens.
7  ## Author: Katherine Whyte
8  ## Last Edited: 13 Aug 2015
9  ### Function Declarations
10 N2W <- function(par, n.states=2) {
11     # Transforms natural parameter list to working vector
12     # Args: par = list of natural parameters
13     #       n.states = number of hidden feeding states
14     # Returns: the working vector
15     b <- 2
16     a <- b+13
17     work <- numeric(a+3)
18     # negative binomial parameters
19     work[1] <- par$size
20     work[2] <- log(par$prob/(1-par$prob))
21     # size predictor
22     work[b+1] <- par$add
23     work[b+2] <- par$net
24     work[(b+3):(b+13)] <- par$month
25     work[(a+3)] <- par$add.overall
26     work[(a+4)] <- par$re.sd
27     # transition probabilties
28     work[(a+1):(a+2)] <- c(par$gamma0, par$gamma1)
29     return(work)
30 }
31 W2N <- function(work, n.states=2) {
32     # Transforms working vector to natural parameter list
33     # Args: work = working vector
34     #       n.states = number of hidden feeding states
35     # Returns: the working vector
36     b <- 2
37     a <- b+13
38     # negative binomial parameters
39     size <- work[1]
40     prob <- exp(work[2])/(1+exp(work[2]))
41     # size predictor
42     add <- work[b+1]
43     net <- work[b+2]
44     month <- work[(b+3):(b+13)]
```

```
45        add.overall <- work[a+3]
46        re.sd <- work[a+4]
47        # transition probabilities
48        gamma0 <- work[a+1]
49        gamma1 <- work[a+2]
50        return(list(size=size,prob=prob,add.overall=add.overall,add=add,net=net
              ,gamma0=gamma0,gamma1=gamma1,month=month,re.sd=re.sd))
51    }
52    NegLlk <- function(w.par,obs,n.states=2) {
53        # Calculates the negative log-likelihood of the HMM with random effect
54        # Args: w.par = working vector of parameters
55        #       obs = data frame of mort data
56        #        n.states = number of hidden feeding states
57        # Returns: value of the negative log-likelihood
58        par <- W2N(w.par,n.states)
59        # calculate probability of observed under each hidden state
60        # averaging over random effect for each week
61        n <- nrow(obs)
62        probs <- matrix(0,nrow=n,ncol=n.states)
63        # partition random effect space
64        re.sd <- exp(par$re.sd)
65        reffect <- seq(-re.sd,re.sd,length=100)
66        diff <- reffect[2]-reffect[1]
67        pu <- pnorm(reffect+diff*0.5,0,re.sd)-pnorm(reffect-diff*0.5,0,re.sd);
              pu <- pu/sum(pu)
68        for (s in seq(n.states)) {
69            if (s==2) {
70                not.missing <- (!is.na(obs[,3:14]))
71                for (ob in seq(n)) {
72                    for (u in seq(reffect)) {
73                        # calculate size predictor
74                        size <- rep(par$size,12)
75                        size <- size+par$net*as.numeric(obs[ob,16:27])+par$add*
                            as.numeric(obs[ob,29:40])+par$add.overall*obs$add.
                            overall[ob]+reffect[u]
76                        if (obs[ob,41]>1) {size <- size+rep(par$month[obs[ob
                            ,41]-1],12)}
77                        size <- exp(size)
78                        size <- size[not.missing[ob,]]
79                        mort <- as.numeric(obs[ob,3:14])
80                        # not.missing is used to include only data of pens in
                              use
81                        mort <- mort[not.missing[ob,]]
82                        if (length(mort)==1) {
83                            probs[ob,s] <- probs[ob,s]+dnbinom(mort[1],size=
                                  size,prob=par$prob)*pu[u]
```

47

```
84                          } else {
85                              # prod used here as pens are independent given
                                    random effect
86                              probs[ob,s] <- probs[ob,s]+prod(dnbinom(mort,size=
                                    size,prob=par$prob))*pu[u]
87                          }
88                      }
89                  }
90          }   else {
91              mort <- rowSums(obs[,3:14],na.rm=TRUE)
92              probs[,1] <- 1*(mort==0)
93          }
94      }
95      # calculate the transition probability matrix
96      gamma <- diag(n.states)
97      gamma[1,2] <- exp(par$gamma0)
98      gamma[2,1] <- exp(par$gamma1)
99      gamma <- gamma/apply(gamma,1,sum)
100     # calculate likelihood using forward algorithm
101     llk <- 0
102     iobs <- 1
103     phi <- rep(0.5,n.states)
104     years <- seq(min(obs$year),max(obs$year))
105     weeks <- seq(1,52)
106     for (y in years) {
107         for (w in weeks) {
108             # if an observation exists for (m,y) do HMM step, otherwise
                    just
109             # do Markov chain step (multiply by gamma)
110             if (obs$year[iobs]==y & obs$week[iobs]==w) {
111                 phi <- phi%*%gamma*probs[iobs,]
112                 sumphi <- sum(phi)
113                 llk <- llk+log(sumphi)
114                 phi <- phi/sumphi
115                 iobs <- iobs+1
116                 # to stop errors when reading past the end of the dataframe
117                 if (iobs>n) {iobs <- n}
118             }
119             else {
120                 phi <- phi%*%gamma
121             }
122         }
123     }
124     cat("llk=",llk,"\n")
125     cat("pars =", w.par, "\n")
126     return(-llk)
```

```
127  }
128
129  MLE <- function(obs,par0,n.states=2) {
130      # Performs maxmimum likelihood estimation
131      # Args: obs = data frame of mort data
132      #       par0 = starting values for parameters
133      #       n.states = number of hidden feeding states
134      # Returns: list of maximum likelihood estimates, standard errors and
                AIC
135      w.par <- N2W(par0,n.states)
136      # numerical optimiser
137      mod <- nlm(NegLlk,w.par,obs,n.states,hessian=TRUE)
138      par <- W2N(mod$estimate,n.states)
139      # variance of parameters are diagonal of inverse hessian matrix
140      # (not negative hessian since using negative likelihood here)
141      se <- sqrt(diag(solve(mod$hessian)))
142      pvals <- pnorm(-abs(mod$estimate),0,se)
143      AIC <- 2*(length(mod$estimate)+mod$minimum)
144      return(list(par=par,se=se,pvalue=pvals,AIC=AIC))
145  }
146  ### Executed Statements
147  obs <- read.table('obs.csv',header=T,sep=",")
148  # calculate month each week falls into
149  mon.names <- NULL
150  num <- c(4,4,4,4,5,4,5,4,4,5,4,5)
151  for (m in seq(12)) {mon.names <- c(mon.names,rep(m,num[m]))}
152  mon <- numeric(nrow(obs))
153  for (i in seq(nrow(obs))) {
154      mon[i] <- mon.names[obs$week[i]]
155  }
156  obs$month <- mon
157
158  # set starting parameters for optimiser
159  par0 <- list(size=-0.3,prob=0.0008,size.pen=rep(0,11),add.overall=0,add=0,
         net=0,gamma0=log(0.1/0.9),gamma1=log(0.1/0.9),rho=0,month=rep(0,11),re.
         sd=log(0.3))
160
161  # fit model
162  mod <- MLE(obs,par0)
```