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Using state-space models to predict the abundance of juvenile and adult sea lice on Atlantic salmon

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ABSTRACT

Sea lice are marine parasites affecting salmon farms, and are considered one of the most costly pests of the salmon aquaculture industry. Infestations of sea lice on farms significantly increase opportunities for the parasite to spread in the surrounding ecosystem, making control of this pest a challenging issue for salmon producers. The complexity of controlling sea lice on salmon farms requires frequent monitoring of the abundance of different sea lice stages over time. Industry-based data sets of counts of lice are amenable to multivariate time-series data analyses.

In this study, two sets of multivariate autoregressive state-space models were applied to Chilean sea lice data from six Atlantic salmon production cycles on five isolated farms (at least 20 km seaway distance away from other known active farms), to evaluate the utility of these models for predicting sea lice abundance over time on farms. The models were constructed with different parameter configurations, and the analysis demonstrated large heterogeneity between production cycles for the autoregressive parameter, the effects of chemotherapeutant bath treatments, and the process-error variance. A model allowing for different parameters across production cycles had the best fit and the smallest overall prediction errors. However, pooling information across cycles for the drift and observation error parameters did not substantially affect model performance, thus reducing the number of necessary parameters in the model. Bath treatments had strong but variable effects for reducing sea lice burdens, and these effects were stronger for adult lice than juvenile lice. Our multivariate state-space models were able to handle different sea lice stages and provide predictions for sea lice abundance with reasonable accuracy up to five weeks out.

1. Introduction

A major threat to salmonid aquaculture in Chile, and worldwide, is infestation with sea lice. Sea lice (*Caligus rogercresseyi* or *Lepeophtheirus salmonis*) cause stress, reduced growth, and may lead to increased mortality when fish are heavily infested (Adams et al., 2012). There are also important production costs associated with the presence and control of sea lice (Costello, 2009; González et al., 2012; Liu and Bjelland, 2014).

Infestations on farms may elevate the number of lice in surrounding waters, above what would occur naturally, increasing opportunities for sea lice to spread. Farms with heavy burdens of sea lice may infest neighboring farms (Krkošek et al., 2011; Jansen et al., 2012; Kristoffersen et al., 2013) and may also spread lice to wild salmonid populations (Krkošek et al., 2007; Rogers et al., 2013).

Infestation with sea lice on farms occurs from both internal and external farm sources (Aldrin et al., 2013; Kristoffersen et al., 2013); for example, in Norway it has been estimated that approximately 66% of

infestations are internally transmitted, 28% come from neighboring farms, and the remaining 6% come from other sources (Aldrin et al., 2013). Controlling sources of infestation is critical in the prevention of the parasite since Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) do not develop immunity to this parasite (Jones and Beamish, 2011).

Chemical bath treatments are the most common management practice for reducing sea lice abundance and spread of the parasite. However, the effectiveness of this control strategy depends on the timing of the application, and the life stage (juvenile or adult) of the parasite. Despite all the efforts put into controlling sea lice infestations on farms, they continue to be problematic for the aquaculture industry. Understanding the dynamics between sea lice populations on and among farms, and being able to predict lice burdens from different sources is critical to the management of this parasite, especially as the net-pen aquaculture industries around the world continue to grow and intensify.

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The parasite's complex life cycle, results in different age structures of sea lice on individual fish (González and Carvajal, 2003; Bravo, 2010). In Chile, the different juvenile life stages are aggregated into one juvenile stage for reporting purposes, which is differentiated from the mobile adult male and non-gravid female lice stages. These life stages subdivide the sea lice populations into correlated subpopulations, resulting in complex population structures. The subpopulations have different characteristics and managerial factors may affect juvenile and adult lice differently. Also, fluctuations in seawater temperature and salinity that influence the growth of sea lice may vary over time and between geographic regions where salmon farms are located. All these factors need to be taken into consideration when modeling sea lice abundance on farms.

Many prior research studies have been undertaken to better understand the transmission of sea lice within and between farms in Norway and Chile. To this end, a variety of analytic approaches for estimating and predicting transmission patterns of the parasite have been published. Jansen et al. (2012) applied a two-component mixture model with negative binomial and Bernoulli response variables to assess the farm-to-farm infestation pressure for *Lepeophtheirus salmonis* in the Norwegian aquaculture industry. A space-time modeling approach was used by Aldrin et al. (2013) for analyzing the spread of sea lice within and between salmon farms in Norway, using a zero-inflated negative-binomial response variable. Recently, Aldrin et al. (2017) formulated the life stages of sea lice in a stage-structured hierarchical model and used Markov Chain Monte Carlo (MCMC) for parameter estimation. In Canada, Rittenhouse et al. (2016) applied a delay differential equation model to sea lice data from British Columbia and southern Newfoundland; their deterministic model incorporated temperature and salinity as seasonally varying factors. In Chile, Kristoffersen et al. (2013) analyzed juvenile *C. rogercresseyi* using a two-part random effects model; they modeled the odds of the non-zero mean abundance using a random-effects logistic model, and the non-zero mean juvenile abundance by a random-effects gamma regression model. Also, a linear mixed-effects model was used by Arriagada et al. (2014, 2017) to model sea lice mean abundance in Chile. Even though many statistical models have been used to describe sea lice abundance and treatment, most have failed to consider unmeasured variable effects, measurement errors, and maybe imperfect data (e.g. due to missing values).

State-space models have advantages over the aforementioned statistical models because they account better for multiple sources of uncertainty, and therefore, may provide more accurate predictions than traditional models. These types of models are intensively used in econometrics (Tsay, 2005; Durbin and Koopman, 2012) and ecology (Cantrell et al., 2010; Newman et al., 2014). In veterinary epidemiology, many ecological models have been used for infectious diseases, when the environment plays an important role in pathogen spread (e.g. Escobar et al., 2015). For example, they allow modellers to separate the variation in the observed data, due to measurement error, from the variation due to true population fluctuations. The process error is different than the measurement error, in that the latter does not influence current or future outcome levels; it only affects the estimation of the outcome.

The specific objectives of this study were threefold. The first was to demonstrate the use of state-space models in modeling sea lice data and explore the feasibility of multivariate time-series analysis of data from multiple farms. The second was to gain understanding of heterogeneity between production cycles and how to best incorporate data that comprise multiple cycles into state-space models. The third was to simultaneously analyze data from isolated farms with relatively few neighbors (and hence likely not receiving large parasite burdens from outside their own farm), using multivariate state-space models to estimate parameters related to sea lice abundance in this population. To our knowledge, this is the first reported use of state-space models for modeling Chilean sea lice data.

2. Materials and methods

2.1. Sea lice data

Data were extracted from the sea lice monitoring program database of the Chilean salmon farming association (INTESAL-SalmonChile), collected from 2009 to 2015. Details of the monitoring program and data collection have been described elsewhere (Kristoffersen et al., 2013; Arriagada et al., 2014; Arriagada et al., 2017). Briefly, farms of either Atlantic salmon or rainbow trout, located in different geographic regions of Chile, participated in the monitoring program; most of these farms had multiple production cycles separated by fallow periods. On each participating farm, sea lice counts were performed on a weekly basis, on a sample of 40 fish from four pens (10 fish per pen), and reported to INTESAL-SalmonChile. The lice counts included attached juvenile (chalmus I to IV), and mobile adult (including gravid female) stages.

To focus on internal farm transmission of sea lice, we restricted our analyses to data from six Atlantic salmon production cycles from five of the most isolated farms in the region; these farms were at least 20 km seaway distance away from other known active farms in our database during their production cycles. Fish in these six production cycles were followed for their cycle duration (between 42 and 72 weeks), for a total of 373 farm-weeks. The production cycles were temporally unrelated and only roughly temporally aligned by the sea lice monitoring period, which commences when salmon are stocked on marine farms. The duration of the six time series (one per production cycle) were based on their production cycles (i.e., started at stocking and ended at harvest). Bath treatments (pyrethroids and azamethiphos) were applied to fish in all production cycles except cycle 5, and in-feed treatments (emamectin benzoate) were applied in three production cycles (cycles 1, 3, and 4; Fig. 1). Other investigated covariates (explanatory variables) included water temperature (mean: $11.3^{\circ}\text{C} \pm 1.6$), stocking density ($805,595 \pm 215,243$), and salinity ($29.2 \text{ ppt} \pm 5.0$).

2.2. Statistical modeling and analysis

2.2.1. State-space models

State-space models consist of two models to simultaneously account for two distinct sources of variation: a state model (latent process) deals with process uncertainty caused by unobserved factors, e.g., the fluctuations of environment, and an observation model which incorporates the effect of error caused by mismeasurement of outcomes (Durbin and Koopman, 2012; Newman et al., 2014). For n observations of m states ($n \geq m$) at each time step, the general form of a multivariate autoregressive state-space (MARSS) model as described in Holmes et al. (2012) is given by

$$\mathbf{X}_t = \mathbf{B}_t \mathbf{X}_{t-1} + \mathbf{u}_t + \mathbf{C}_t \mathbf{c}_t + \mathbf{W}_t \quad (1)$$

$$\mathbf{Y}_t = \mathbf{Z}_t \mathbf{X}_t + \mathbf{D}_t \mathbf{d}_t + \mathbf{V}_t, \quad (2)$$

where Eqs. (1) and (2) are the state and observation equations, respectively.

This model describes the development of lice abundance (on natural logarithmic scale) through the latent process \mathbf{X}_t , which is an $m \times 1$ vector of the multiple autoregressive (of order one, AR-1) processes at time t ; \mathbf{B}_t is an $m \times m$ transition matrix for the first order autoregressive processes; \mathbf{u}_t is an $m \times 1$ vector of growth rates (drift); \mathbf{c}_t is an $p \times 1$ vector of inputs (state covariates); is an $m \times p$ matrix of state-covariate effects; \mathbf{W}_t is an $m \times 1$ vector of process errors. Furthermore, \mathbf{Y}_t is an $n \times 1$ vector based on the process \mathbf{X}_t and represents the observed lice abundances (on natural logarithmic scale) at time t ; \mathbf{Z}_t is an $n \times m$ matrix to connect observed time series with corresponding processes; \mathbf{d}_t is an $q \times 1$ vector of inputs (observation-model covariates); \mathbf{D}_t is an $n \times q$ matrix of observation-model covariate effects; \mathbf{V}_t is an $n \times 1$ vector of measurement errors. The process error \mathbf{W}_t and observation

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