A stage-structured Bayesian hierarchical model for salmon lice populations at individual salmon farms – Estimated from multiple farm data sets

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A B S T R A C T

Salmon farming has become a prosperous international industry over the last decades. Along with growth in the production farmed salmon, however, an increasing threat by pathogens has emerged. Of special concern is the propagation and spread of the salmon louse, *Lepeophtheirus salmonis*. To gain insight into this parasite's population dynamics in large scale salmon farming system, we present a fully mechanistic stage-structured population model for the salmon louse, also allowing for complexities involved in the hierarchical structure of full scale salmon farming. The model estimates parameters controlling a wide range of processes, including temperature dependent demographic rates, fish size and abundance effects on louse transmission rates, effect sizes of various salmon louse control measures, and distance based between farm transmission rates. Model parameters were estimated from data including 32 salmon farms, except the last production months for five farms, which were used to evaluate model predictions. We used a Bayesian estimation approach, combining the prior distributions and the data likelihood into a joint posterior distribution for all model parameters. The model generated expected values that fitted the observed infection levels of the chalimus, adult female and other mobile stages of salmon lice, reasonably well. Predictions for the periods not used for fitting the model were also consistent with the observational data. We argue that the present model for the population dynamics of the salmon louse in aquaculture farm systems may contribute to resolve the complexity of processes that drive this host-parasite relationship, and hence may improve strategies to control the parasite in this production system.

1. Introduction

Salmon farming has become a large and economically prosperous international industry over the last decades. Norway holds a leading position as a producer of farmed salmonids with an annual production of about 1.2 million tonnes, which is roughly half of the worldwide production (Anonymous, 2015). Further growth in the production of salmonids is in demand (Anonymous, 2015), but this will come at the cost of increasing risks of pathogen propagation and transmission. Large-scale host density dependence acting on pathogen transmission has been demonstrated in salmon farming production systems, both for macro parasites (Aldrin et al., 2013; Jansen et al., 2012; Kristoffersen et al., 2014) and viruses (Aldrin et al., 2011, 2010; Kristoffersen et al., 2009). Of special concern, is the propagation and spread of the salmon louse, *Lepeophtheirus salmonis*, which is implicitly responsible for regulating the salmon farming industry through density dependent host parasite interactions (Frazer et al., 2012; Jansen et al., 2012; Groner et al., 2016b) Consequently, this parasite plays a dominant role in the formulation of management policies (Anonymous, 2015), dominates among salmon pathogens in the scientific literature (Murray et al., 2016) and is perceived as a major threat to wild salmon populations (Taranger et al., 2015; Vollset et al., 2015; Forseth et al., 2017), all testifying to the gravity of detrimental effects of the salmon louse on salmon farming.

Mathematical and statistical models are increasingly being used to evaluate infection pathways and risk factors for pathogen propagation and disease development, both in aquatic and terrestrial

animal farming (Aldrin et al., 2013, 2011, 2010; Salama and Murray, 2013; Murray and Salama, 2016; Jonkers et al., 2010; Diggle, 2006; Höhle, 2009; Keeling et al., 2001; Scheel et al., 2007). When such models are capable to reproduce the main patterns in the host-pathogen population dynamics, including the spread within and between farms, they can be used to predict future infection levels as well as simulate the outcomes of disease mitigation scenarios, examples being interventions to mitigate bovine tuberculosis in Great Britain (Brooks-Pollock et al., 2014) and long term effects of infection control measurements to mitigate salmonid alphavirus (SAV) incidences causing pancreas disease (PD) outbreaks (Aldrin et al., 2015). The Norwegian salmonid production system is exceptionally well suited for developing models for salmon lice infection dynamics because of the wealth of surveillance time-series that document both the spatial locations and population sizes of host populations at risk of infection, as well as salmon lice abundances in these host populations. Coupling these host and parasite population data have provided insights into e.g. how salmon lice spread between farms depending on between-farm distances, and how transmission and parasite abundances depend on local host biomasses (Jansen et al., 2012; Aldrin et al., 2013; Kristoffersen et al., 2014). However, previous models that describe both between and within farm parasite population dynamics have for simplicity typically been autoregressive statistical models focusing on single aggregated measures of parasite infection levels (Jansen et al., 2012; Aldrin et al., 2013; Kristoffersen et al., 2013, 2014). Alternatively, models have been developed for simulation purposes only (Groner et al., 2014) or focused on the population dynamics on single farms over a limited period (Krkošek et al., 2010). Most of these approaches have relied heavily on estimates of demographic rates obtained in the laboratory (Stien et al., 2005; Revie et al., 2005; Gettinby et al., 2011; Groner et al., 2013, 2016a; Rittenhouse et al., 2016).

The aim of the present paper is to formulate a fully mechanistic stage-structured population model for the salmon louse, that also allows for the complexities inherent in full scale salmon farming. Furthermore, the model accounts for the hierarchical structure of the data obtained from the production system where salmon lice are counted on subsamples of fish, the fish being aggregated into separate cages and the cages being aggregated to farm. The model estimates parameters controlling a wide range of processes, including effects of temperature on demographic rates, fish size and abundance effects on transmission rates, the different effect sizes, temporal and stage specific effects of a wide range of salmon lice control measures, and distance-based transmission rates between farms. The objectives for developing such a complex population model for the salmon louse was to cover several needs in modern salmon farming: (1) To develop a tool that keeps account of the salmon louse populations at the production unit level in salmon farms, based on the successive counting of salmon louse infections, and produce more reliable estimates of salmon louse population sizes at any point in time than the individual salmon louse counts. (2) To produce short term predictions of future salmon louse infection levels to enable proactive use of salmon louse management actions. (3) To evaluate the efficiency of different control measures. (4) To evaluate whether estimates of demographic rates obtained in the laboratory seems applicable in full scale production settings. (5) To explore importance of different sources of infection (e.g. internal versus external sources). (6) Finally, to develop a sufficiently realistic model that can be used for scenario-simulations exploring the effects of various parasite control strategies. In this paper, we describe the model in detail and discuss the results in relation to the first five objectives. Scenario simulations from the model will be the focus in later work.

2. Materials and methods

2.1. Data

Farm production of salmon comprises a freshwater juvenile phase, being followed by a marine grow out phase, the latter which is the focus of this study. The production of salmon on a Norwegian marine farm is initiated by stocking juvenile smolts to cages (or net-pens) either in spring or in autumn. Salmon are kept in the marine farms for about 1.5 years after which they are slaughtered for food consumption. In Norway, only fish of the same year class of age are kept on a given farm and we term this a cohort throughout the present paper. After slaughtering, it is mandatory to fallow the farm for a period of at least two months before stocking a new cohort of salmon.

The main body of data in the present study consist of cage-level data from 32 marine salmon farms in Norway, of which 12 farms are aggregated just north of the island Frøya in Mid-Norway (Fig. 1). For each farm, the data covers a full production cycle for farmed salmon, from stocking as smolts to slaughtering as adult Atlantic salmon (*Salmo salar* L.), including fish production data, lice counts, temperatures and louse control efforts. Salmon were stocked between 2011 and 2013 and slaughtered about 1 1/2 year after stocking, between 2012 and 2014. The number of production units (cages) per farm varied from 3 to 12, but were usually around 8 (mean 7.7). For 9 farms, the fish were moved between cages within the farm during the production period.

Seawater temperatures were measured at 3 m depth at the farms. The average temperature was 9.1 °C, and 95% of the temperatures were between 3.6 and 15.0 °C. Data on salinity were unavailable in sufficient detail and have therefore not been used.

The production data consist of daily numbers and mean weights of salmon per cage during the production period, information on movement of salmon between cages within farms and information on antiparasitic lice treatment using chemotherapeutic medicals (day of application and type of medical). Furthermore, the data contain information on stocking of cleaner fish (day and number of cleaner fish stocked), but with limited information on their mortality, and hence on the number of cleaner fish present at a given day. The cleaner fish are usually either lumpsuckers (*Cyclopterus lumpus*), ballan wrasses (*Labrus bergylta*) or goldsinny wrasses (*Ctenolabrus rupestris*) or a mix of these, but we do not distinguish between various species of cleaner fish in the model.

The production cycles lasted on average 16.5 months per cage, with on average 140 000 fish per cage, typically more in the beginning of a production cycle and less towards the end. The average minimum and maximum fish weights during a production cycle was 140 g and 5.7 kg, respectively. 89% of the cages contained cleaner fish in parts of the production period.

As a main rule, lice counts were performed on a sample of at least 10 fish every second week for each cage. The salmon lice were divided into three categories according to developmental stages, *i.e.* (i) chalimus (CH), (ii) other mobiles (OM), which consist of pre-adults of both sexes and adult males, and (iii) adult females (AF). There were on average 41 dates with lice counts per cage, with averages (abundance) of 0.23 CH, 0.76 OM and 0.18 AF per fish. Six different types of antiparasitic medicals were used (Table 1), and there were on average 4.6 events of medical treatments per cage. The medicals emamectin benzoate and diflubenzuron are given through the feed, typically over a period of around two weeks. These treatments have a relatively low daily effect, but effects last over a prolonged period. The other medicals are applied as bath treatments over a duration of a few hours, with a larger daily effect, but lasting over a shorter period (see Section 2.2.3).

In addition to the detailed cage-level data on the 32 farms, we have more aggregated data on all other Norwegian marine salmon