



Estimating sea lice infestation pressure on salmon farms: Comparing different methods using multivariate state-space models

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ABSTRACT

Sea lice are ectoparasites of salmonids, and are considered to be one of the main threats to Atlantic salmon farming. Sea lice infestation on a farm is usually initiated by attachment of the free-living copepodid stage derived from the surrounding water, frequently originating from adult lice on the same farm or from neighboring salmonid farms, referred to as internal and external sources, respectively. Various approaches have been proposed to quantify sea lice infestation pressure on farms to improve the management of this pest. Here, we review and compare five of these methods based on sea lice data from 20 farms located near Grand Manan island in the Bay of Fundy, New Brunswick, Canada.

Internal and external infestation pressures (IIP and EIP, respectively) were estimated using different approaches, and their effects were modeled either by a unique parameter for all production cycles or by different parameters for each production cycle, using a multivariate state-space model. Predictive variables, such as water temperature and sea lice treatments, were included in the model, and their effects across production cycles were estimated along with those of other model parameters. Results showed that models with only EIP explained the variation in the data better than models with only IIP, and that models with unique IIP and unique EIP for all cycles were generally associated with the best model fit. The simplest, fixed lag method for calculating infestation pressure had the best predictive performance in our models among the methods studied.

1. Introduction

Sea lice infestation on salmon farms is a major challenge for salmon farmers in Canada and worldwide (Costello, 2009; Chang et al., 2011; Burka et al., 2012). If unchecked, the parasites, and the methods used for their control, negatively affect salmon welfare and contribute to economic losses (Mustafa et al., 2001; Boxaspen, 2006). The prolonged period of containment in net pens during the production cycle can increase the density of the parasite host in a manner that does not likely occur in nature, providing conditions for sea lice reproductive success. Sea lice infestations on farms greatly increase the dispersal of the parasite, potentially affecting salmon populations outside of the source farm (Krkošek et al., 2007; Kristoffersen et al., 2013; Rogers et al., 2013; Nekouei et al., 2018).

Numerous approaches have been implemented to mitigate sea lice infestations, for example, reducing fish density, practicing fallow periods between production cycles, stocking cleaner fish in the pen, and using chemical treatments (Yossa and Dumas, 2016; Gonzalez and de Boer, 2017). Despite great investment in management and prevention

of sea lice infestation, sea lice control remains an ongoing issue for salmon producers (Kristoffersen et al., 2013). The management of sea lice on farmed salmon is largely reliant on the use of chemical bath or in-feed treatments, but frequent treatments increase the risk of development of resistance in sea lice (Espedal et al., 2013). The dispersal of free-living larvae connects sea lice populations on salmon farms (Adams et al., 2012; Peacock et al., 2016). Controlling the influx of such larvae from sources outside of farms is a challenge, because sea lice development is strongly dependent on environmental conditions (DFO, 2014). For instance, development is delayed by low water temperatures (Butler, 2002). Neighboring farms are important sources of sea lice infestation, particularly since nauplii are well adapted to live in the surrounding waters for several days freely moving up and the down the water column following coastal water movements (Hayward et al., 2011). Connectivity among neighboring farms has become a major concern to producers in recent years as better tools are developed to explore oceanographic influences of sharing the same ecological resource. One study in Norway reported as much as 28 % of sea lice infestations originate from neighboring farms (Aldrin et al., 2013).

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Many methods have been used to quantify within-farm (internal) and between-farm (external) sea lice infestation pressures. In Chile, Kristoffersen et al. (2013) used the mean abundance of reported gravid female lice with two-week lag as a predictor of internal infestation pressure. For external infestation pressure, they summed the sea lice output (estimated as the abundance of gravid females two weeks prior to infestation multiplied by the number of fish on the farm) from neighboring farms weighted by seaway distance between farms using a Gaussian kernel. In Norway, Kristoffersen et al. (2014, 2018) estimated the production of infective copepodids on farms based on the reported adult female lice abundance, number of fish on a given farm, and water temperature, using the simple model suggested by Stien et al. (2005). They also quantified the external pressure on a farm by adding the potential output of sea lice from neighboring farms weighted by seaway distance using the kernel function proposed by Aldrin et al. (2013). Recently, Aldrin et al., 2019 introduced a more sophisticated approach to quantify the sea lice infestation pressure on Norwegian coastal farms. They estimated the time-lag structures that represent pre-adult and adult lice recruitment from the previous generations of adult females for different water temperatures. For the external pressure, Aldrin et al., 2019 used a nonlinear function to account for different shapes of the seaway distance to weight the output of sea lice from neighboring farms.

In practice, data from sea lice monitoring systems in aquaculture often contain missing values. These complicate the estimation of infestation pressure from the reported abundance of adult female lice in the past. Sea lice data are also inherently noisy, and the major components of such noise are observation and process errors (Elghafghuf et al., 2018). Observation errors can be considered sampling and measurement errors, while process errors may occur due to unobserved conditions, such as fluctuations in the true sea lice population. Modeling techniques that can handle different life stages of the parasite, deal with missing values, and take process and observation errors into account are of great interest when it comes to modeling sea lice data. State-space models (Harvey, 1989; Shumway and Stoffer, 2017, Chapter 6) are flexible approaches that can accommodate many such features of sea lice data.

This study is part of an ongoing research project which aims to build a predictive tool for sea lice abundance within aquaculture farms in New Brunswick, Canada. The objective is not to study causation; rather our goal is to evaluate existing methods for estimating sea lice infestation pressure on aquaculture farms. The primary aim of the current research is to compare different sea lice infestation pressure estimation approaches on salmon farms in Grand Manan, New Brunswick, Canada, using a multivariate autoregressive state-space model. Factors such as water temperature, and bath and in-feed treatments were accounted for in the model. This comparison will help in choosing an appropriate approach to estimate sea lice infestation pressure on farms. The secondary aim is to explore the predictive form for the infestation pressures (i.e., the relationships among their predicted values) obtained by the different estimation methods.

2. Material and methods

2.1. Sea lice data

Data were extracted from the sea lice monitoring system, *Fish-iTrends* (fishitrends.com). A more complete description of the monitoring system can be found elsewhere (e.g., Gautam et al., 2016). Briefly, salmon producers in the region are obliged to regularly report their sea lice levels and treatment data in *Fish-iTrends*. Regional regulations require weekly samples of at least five fish per net pen from a minimum of six net pens when the water temperature is above 5 °C (Gautam et al., 2017). In the case of bath treatments, pre- and post-treatment sea lice counts are performed on ten fish (minimum), as required by industry regulations. In all occasions, fish-level sea lice counts

are reported for different parasite life stages; chalimus, pre-adult males and females together with adult males (PAAM), and adult females (AF; both gravid and non-gravid). To reduce observation error, it has become common practice in the industry to report combined counts for pre-adults and adult males, because the two categories are visually difficult to distinguish in the field (Elmoslemany et al., 2013).

In this study, we restricted our analyses to data from active salmon farms located near Grand Manan Island in the Bay of Fundy, collected between week 20 (middle May) in 2010 and week 42 (middle October) in 2016. The dataset comprised 41 production cycles from 21 marine farms (2.4 cycles per farm) including four truncated cycles. Within the same farm, consecutive cycles were interrupted by fallow periods (ranging from 29 to 75 weeks) during which no fish were stocked on the farm.

The mean sea lice abundance was computed as the number of lice on fish divided by the number of sampled fish at the farm level. If bath treatment took place in a certain week, only post-treatment counts were used to compute sea lice abundance for that week. Because of weather conditions that may limit sea louse counts, the dataset contained many missing values, and such missing values occurred across all parasite life stages. We initially used all data (i.e., data from all cycles including those truncated) to estimate infestation pressure, whereas the final analysis was carried out on data excluding the truncated production cycles and further five cycles due to either invalid records or long sequences of missing counts. The remaining production cycles (32 cycles from 20 farms) varied in length and comprised 3,045 farm-weeks, including 940 weeks of missing sea lice abundances.

The mean reported PAAM and AF abundances for each week were considered as a bivariate response variable for each production cycle. In-feed treatments (ivermectin, emamectin benzoate, or/and telubenzuron) were applied to fish in all production cycles (1–26 applications per cycle), and bath treatments (hydrogen Peroxide or/and azamethiphos) were applied in 23 cycles (1–10 applications per cycle) for at least one pen in each farm. Furthermore, three different water temperature datasets were available for all farms and production cycles. These included *in situ* water temperature, sea surface temperature (SST), and UK Meteorological Office sea surface temperature (MOSST). The MOSST data were smoothed and had no missing values, whereas the *in situ* temperature and SST contained missing values. We model *in situ* water temperature and use other datasets (SST and MOSST) for comparative purposes when missing *in situ* temperature values are interpolated (Section 2.5).

2.2. Multivariate autoregressive state-space model

We used a multivariate autoregressive state-space (MARSS) model (Holmes et al., 2012) to estimate the effects of sea lice infestation pressure on PAAM lice abundance along with other key parameters for sea lice populations on aquaculture farms in Grand Manan. The model consists of two type of processes, state and observation. For a single farm with bivariate time series (PAAM and AF), the state process with the predictive covariates: bath treatment ($x_{bath,t}$), in-feed treatment ($x_{feed,t}$), internal infestation pressure ($x_{IIP,t}$), external infestation pressure ($x_{EIP,t}$), and water temperature ($x_{temp,t}$) can be written as

$$\begin{bmatrix} \theta_{p,t} \\ \theta_{a,t} \end{bmatrix} = \begin{bmatrix} b_p & 0 \\ b_{ap} & b_a \end{bmatrix} \begin{bmatrix} \theta_{p,t-1} \\ \theta_{a,t-1} \end{bmatrix} + \begin{bmatrix} u_p \\ u_a \end{bmatrix} + \begin{bmatrix} \beta_{bath,p} & \beta_{feed,p} & \beta_{IIP,p} & \beta_{EIP,p} & \beta_{temp,p} \\ \beta_{bath,a} & \beta_{feed,a} & 0 & 0 & \beta_{temp,a} \end{bmatrix} \begin{bmatrix} x_{bath,t} \\ x_{feed,t} \\ x_{IIP,t} \\ x_{EIP,t} \\ x_{temp,t} \end{bmatrix} + \begin{bmatrix} w_{p,t} \\ w_{a,t} \end{bmatrix}, \quad (1)$$

where $\tilde{\theta}_t = \begin{bmatrix} \theta_{p,t} \\ \theta_{a,t} \end{bmatrix}$ is the state vector for PAAM and AF abundances (on ln-scale) at time t , where p and a stand for PAAM and AF, respectively.

These state processes describe the development of PAAM and AF lice abundances (at the population level) as autoregressive processes of lag one (AR-1). The diagonal elements of $\tilde{\mathbf{B}} = \begin{bmatrix} b_p & 0 \\ b_{ap} & b_a \end{bmatrix}$ are AR-1 parameters to quantify the intra-specific effects, i.e. contributions of sea lice abundance at t to $t + 1$, while the off-diagonal element, b_{ap} , is to allow for a one-week transition from PAAM to AF, i.e., PAAM at time $t - 1$ contributions to AF at time t . The vector $\tilde{\mathbf{u}} = \begin{bmatrix} u_p \\ u_a \end{bmatrix}$ is a scaling parameter; and $\tilde{\mathbf{X}}_t^T = [x_{bath,t} \ x_{feed,t} \ x_{IIP,t} \ x_{EIP,t} \ x_{temp,t}]^T$ contains predictive covariates and $\tilde{\boldsymbol{\beta}} = \begin{bmatrix} \beta_{bath,p} & \beta_{feed,p} & \beta_{IIP,p} & \beta_{EIP,p} & \beta_{temp,p} \\ \beta_{bath,a} & \beta_{feed,a} & 0 & 0 & \beta_{temp,a} \end{bmatrix}$ is their coefficients. Furthermore, $\tilde{\mathbf{W}}_t = \begin{bmatrix} w_{p,t} \\ w_{a,t} \end{bmatrix}$ is a vector of the state-process errors at time t . These errors are assumed to follow a bivariate normal distribution with zero means and variance-covariance matrix $\tilde{\mathbf{Q}} = \begin{bmatrix} q_p & q_{ap} \\ q_{ap} & q_a \end{bmatrix}$. Moreover, the observation process of the model can be written as

$$\begin{bmatrix} y_{p,t} \\ y_{a,t} \end{bmatrix} = \begin{bmatrix} \theta_{p,t} \\ \theta_{a,t} \end{bmatrix} + \begin{bmatrix} v_{p,t} \\ v_{a,t} \end{bmatrix}, \quad (2)$$

where $\tilde{\mathbf{Y}}_t = \begin{bmatrix} y_{p,t} \\ y_{a,t} \end{bmatrix}$ is based on the processes $\tilde{\theta}_t$ and represents the observed PAAM and AF lice abundances (on ln scale) at time t on the farm. $\tilde{\mathbf{V}}_t = \begin{bmatrix} v_{p,t} \\ v_{a,t} \end{bmatrix}$ is a vector of observation error components at time t , and these errors are assumed to follow a bivariate normal distribution with zero means and variance-covariance matrix $\tilde{\mathbf{R}} = \begin{bmatrix} r_p & r_{ap} \\ r_{ap} & r_a \end{bmatrix}$.

Assuming independence (for error terms) among farms/cycles, the model described in (1) and (2) can be extended to allow for multiple farms/production cycles. For n (farms/cycles) bivariate time series, the multivariate version of the MARSS model can be written as

$$\theta_t = \mathbf{B}\theta_{t-1} + \mathbf{u} + \boldsymbol{\beta}\mathbf{X}_t + \mathbf{W}_t \quad (3)$$

$$\mathbf{Y}_t = \theta_t + \mathbf{V}_t, \quad (4)$$

where \mathbf{B} , $\boldsymbol{\beta}$, \mathbf{Q} , and \mathbf{R} are block diagonal matrices with n submatrices $\tilde{\mathbf{B}}$, $\tilde{\boldsymbol{\beta}}$, $\tilde{\mathbf{Q}}$, and $\tilde{\mathbf{R}}$.

It is worth noting that the MARSS model defined above is a multivariate log-linear version of the state-space Gompertz model (Elghafghuf et al., 2018), widely used in ecology (e.g., Dennies and Ponciano, 2014).

For model estimation, we used the EM algorithm described in Holmes (2010) and implemented in the R-package ‘MARSS’ (Holmes et al., 2012). The MARSS package employs the Kalman filter and smoother for state estimation. Standard errors and confidence intervals for parameter estimates were computed from the estimated Hessian matrix based on the asymptotic normality assumptions. Furthermore, we used the first observations of the multivariate time series as starting values for the latent processes.

2.3. Estimation approaches for infestation pressure

In this section five approaches for estimating infestation pressures of sea lice on salmon farms are reviewed. Table 1 summarizes these five methods and their features.

From parasite management perspective, sea lice infestation pressure on salmon farms is often divided into internal (within-farm) and external (between-farm) pressures. Throughout the paper, IIP_{it} and EIP_{it} denote the internal and external sea lice infestation pressures on farm i at week t , respectively. We also use $IIP_{i,d}$ to denote the internal infestation pressure on farm i when it is computed at the day level. Furthermore, we denote the mean adult female lice abundance on farm i at time t as $AF_{i,t}$. Finally, Grand Manan salmon farms were assumed to be in similar size (the actual number of fish on the farm was initially

Table 1
Summary of estimation approaches for infestation pressure of sea lice and their features.

Method	FL	DD	CAF	QLC	WALS
Summary	AF at week $t - 3$	AF at lag time depending on temperature	AF at multiple temperature-dependent lags	AF at multiple temperature-dependent lags adjusted by reproduction	AF at 16 weeks adjusted by weights depending on temperature
Feature	Single fixed lag	Single temperature-dependent lags	Multiple temperature-dependent lags	Multiple temperature-dependent lags	Multiple temperature-dependent lags
Lag time	Data driven Week level Backwards/forwards	Lab experiment Week level Backwards	Lab experiment Day level Forwards	Lab experiment Day level Forwards	Data driven Week level Backwards
Nature of method					
Computation					
Direction of computation					
Weighting infestation pressure from neighbours	Gaussian kernel density	Gaussian kernel density	The relative risk of infection between farms as a function of distance	The relative risk of infection between farms as a function of distance	Nonlinear distance weighting

unavailable) so the number of fish on a farm was not part of the IIP and EIP computations.

2.3.1. Fixed lag (FL) approach

The IIP was calculated from the mean reported adult female lice abundance on the farm at time $t - l$, where l is the lag time (i.e., the approximate time required for eggs to develop into PAAM stages). The IIP of farm i at week t can be written as

$$IIP_{it} = AF_{i,t-l} \quad (5)$$

External infestation pressure was determined based on the computed internal infestation pressure on farms and seaway distance between farms (i.e., EIP was computed by summing the IIP from neighboring farms weighted by seaway distance). The EIP on farm i at week t from neighboring farms was computed using

$$EIP_{it} = \sum_j IIP_{jt} w_1(D_{ij}), \quad (6)$$

where IIP_{jt} is the internal infestation pressure on the neighbouring farm j at time t , $w_1(D_{ij})$ are Gaussian kernel weights computed based on seaway distance (D_{ij}) between farms. The Gaussian kernel density takes the form

$$w_1(D_{ij}) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{1}{2\sigma^2} D_{ij}^2},$$

where we denote the standard deviation σ as the kernel's bandwidth.

To determine a reasonable bandwidth for a Gaussian kernel function, sea lice outputs from neighbouring farms were evaluated at different values for σ (i.e., $\sigma = 2.5, 5, 7.5, 10, 12.5$, and 15 km) using sensitivity analyses. In these analyses, corrected sample-size AIC (AICc) values from MARSS models with IIP and EIP (and all other predictors) were used to evaluate different bandwidths for Gaussian kernels. Furthermore, AF with different lags ($l = 1, 2, 3$, and 4) as internal infestation pressure variables were assessed in the sensitivity analyses. The FL approach has been used previously (e.g., Kristoffersen et al., 2013).

2.3.2. Degree days (DD) approach

Instead of using a fixed lag time for AF to affect PAAM abundance, we used a lag time dependent on water temperature using a degree days approach. A degree day is time multiplied by water temperature (e.g., 7 days at 10°C are the same as 10 days at 7°C ; 70 degree days). The IIP variable was therefore constructed as the past AF abundance with time lags varying by water temperature. We set time from egg hatching to PAAM stages to 190 degree days; this is 35 degree days from egg hatching to infective copepodids plus 155 degree days for chalimus to PAAM stages (Kristoffersen et al., 2014). Because data were reported weekly, AF abundance and water temperature were approximated to be equal throughout the week. The IIP of a certain week was represented by the AF abundance in a previous week, from which the cumulative water temperature first reached at least 190 degree days. This can be written as

$$IIP_{it} = AF_{i,t-l_k}, \quad (7)$$

where $l_k = l_k(i, t)$ that satisfies the inequality $7 \times \sum_{q=0}^r T_{i,t-q} \geq 190$, and T is water temperature.

Similar to the FL approach, the EIP for farm i at week t was computed by weighting and summing the IIP of the neighboring farms using (6).

2.3.3. Contributing adult female (CAF) approach

This is another temperature-dependent lag time approach introduced by Kristoffersen et al. (2014). First, the weekly data were converted into daily data by assigning observations to the middle of the weeks and linearly interpolating between these middle points. The daily IIP for farm i on day d was computed as

$$IIP_{i,d} = \sum_{\tau < d} AF_{i,\tau} I_{(\tau+h_\tau=d)}, \quad (8)$$

where $AF_{i,\tau}$ is the AF abundance on farm i at day $\tau = d - h_\tau$; h_τ is the smallest r so that $\sum_{q=0}^r T_{i,\tau+q} \geq c$, where c is the time from the minimum AF development time until eggs are produced and for the eggs to then further develop into PAAM stages (Kristoffersen et al., 2018), and I is an indicator function. The threshold c was set at 126 degree days (Kristoffersen et al., 2018). The daily IIP for farm i in week t was aggregated weekly using

$$IIP_{it} = \sum_{d \in t} IIP_{i,d}. \quad (9)$$

To obtain the EIP of farm i at week t , the weekly IIP estimates from farms were adjusted by $w_2(\cdot)$ and summed for all the neighboring farms j of farm i . This can be given by

$$EIP_{it} = \sum_{j \neq i} IIP_{jt} w_2(D_{ij}), \quad (10)$$

where $w_2(D_{ij})$ is the relative risk of infection between farms i and j as a function of between-farm distance, and is computed as

$$w_2(D_{ij}) = \exp[\phi_1(D_{ij}^{\phi_2} - 1)/\phi_2] / \exp[\phi_1(D_{jj}^{\phi_2} - 1)/\phi_2]. \quad (11)$$

The parameters ϕ_1 and ϕ_2 in (11) were set at -0.351 and 0.568 , respectively, as estimated in Aldrin et al. (2013) and used by Kristoffersen et al. (2018). Note that the distance $D_{jj} = 0$ (Aldrin et al., 2013).

2.3.4. Quantitative life cycle (QLC) approach

The QLC approach was proposed by Kristoffersen et al. (2014), and was based on estimated lengths of sea lice life stages from an experimental study conducted by Stien et al. (2005). Similar to the CAF approach, the weekly data were converted into daily values through linear interpolation between the mid-week values. Daily AF abundance and water temperature were used to estimate the daily production of louse eggs in salmon farms. Assuming 150 eggs per egg string, the daily hatched sea lice larvae per adult female louse on farm i was computed using

$$E_{i,d} = n_{\text{egg}} (T_{i,d} - 10 + \beta_1 \beta_2)^2 \beta_1^{-2}, \quad (12)$$

where n_{egg} is the number of eggs in the two egg strings per AF louse, and β_1 and β_2 are parameters describing the relationship between water temperature (T) and the average minimum development time of the egg stage. As estimated in Stien et al. (2005), the parameters β_1 and β_2 were set to 41.98 and 0.338 respectively.

The daily IIP for farm i on day d was defined as,

$$IIP_{i,d} = \sum_{\tau < d} AF_{i,\tau} E_{i,\tau} S_{h_\tau} I_{(\tau+h_\tau=d)}, \quad (13)$$

where $S_{h_\tau} = (1 - 0.17)^{h_\tau}$ is a reduction factor assuming a daily mortality of 17 % (i.e., the lice abundance was reduced by S_{h_τ}).

As in the CAF approach, the daily IIP was then summed over all days of the week using (9) to obtain the weekly IIP_{it} , and EIP_{it} was therefore computed using (10).

2.3.5. Weighted average lag structure (WALS) approach

The WALS approach was proposed by Aldrin et al., 2019, who estimated the time-lag structure that represents the PAAM recruitments from previous AF generations for different water temperatures. Aldrin et al., 2019 quantified IIP based on AF in previous weeks, water temperature, and the number of fish on the farm. As described in Aldrin et al., 2019, and assuming the same number of fish on the farms, IIP for farm i at week t can be modeled using

$$IIP_{it} = \sum_{l=1}^{16} AF_{i(t-l)}^* \varphi_{lit}, \quad (14)$$

where $AF_{i(t-l)}^* = [AF_{i(t-l)}]^\alpha$ and α is a positive parameter for a nonlinear

dependence of the previous weeks of AF. The coefficients φ_{lit} vary smoothly by increasing the number of lags and are defined as

$$\varphi_{lit} = \gamma_{it}^a [1 - \gamma_{it}^s (l - \gamma_{it}^c)^2]_+ / c_{it}, \quad l = 1, 2, \dots, 16. \quad (15)$$

The right-hand side of (15) is defined as follows: c_{it} is a normalization constant to ensure $\sum_{l=1}^{16} \varphi_{lit} = \gamma_{it}^a$, and $[\cdot]_+$ represents the non-negative part of the quantity. Other parameters are defined as

$$\gamma_{it}^a = \gamma^{a*} \exp[\beta^a (T_{it} - 9)]$$

$$\gamma_{it}^s = \gamma^{s*} \exp[\beta^s (T_{it} - 9)]$$

$$\gamma_{it}^c = 1 - \frac{1}{\sqrt{\gamma_{it}^s}} + \gamma^{c*} \exp[\beta^c (T_{it} - 9)],$$

where $T_{it} - 9$ is the water temperature centred at 9 °C. The parameters γ^{a*} , β^a , γ^{s*} , β^s , γ^{c*} , and β^c respectively were set at 0.262, 0.165, 0.165, 0.217, 7.445, and -0.118, as estimated in Aldrin et al., 2019.

The EIP for farm i at week t was then quantified as

$$\text{EIP}_{it} = \left[\sum_{j \neq i} \text{IIP}_{ijt}^{\text{Ne}} \right]^\delta, \quad (16)$$

where δ is a positive parameter accounting for nonlinearity of the sum of lice output from the neighbouring farms. $\text{IIP}_{ijt}^{\text{Ne}}$ is the contribution from farm j and is defined as

$$\text{IIP}_{ijt}^{\text{Ne}} = \text{IIP}_{jt} w_3(D_{ij}), \quad (17)$$

where $w_3(D_{ij}) = \pi_0 \exp[\pi_1 (D_{ij}^{\pi_2} - 1) / \pi_2]$. The parameters δ , π_0 , π_1 , and π_2 were set at 0.709, 0.503, -0.374, and 0.692 respectively, as in Aldrin et al., 2019, to which the reader is referred for detailed explanations of the WALs approach.

Finally, it is worth noting that the degree-day-dependent approaches have different directions of calculation (forward and backward calculations). Depending on the water temperature at the time of AF that is expected to affect PAAM and the timing of PAAM in a question, PAAM development is either delayed (no effect of AF on PAAM for some time points) or occurs quickly (PAAM at time t is affected by AF at multiple time points in the past) in forward calculations. This is not the case for PAAM when backward calculations are performed; however, AF at one time point may affect PAAM at multiple time points.

2.4. Modeling paired PAAM and AF abundances

We modeled the PAAM and AF lice abundances as a bivariate response, using the MARSS model defined in (1) and (2). The two response variables were log-transformed after adding offsets to avoid zero entries. We used Box-Cox analyses (Venables and Ripley, 2002) for estimating PAAM and AF offsets. The two offsets were estimated as fairly similar, and therefore they were both approximated to be equal to 0.03. Each single time series (i.e., each life stage within a production cycle in a farm) was assumed to have its own latent process. In addition to IIP and EIP, predictive and intervention variables included in the models were, water temperature, and bath and in-feed treatments. The continuous variables (i.e., water temperature, IIP, and EIP) were ln-transformed and centred at the mean. The dichotomous variables (i.e., bath and in-feed treatments) were modeled assuming effects that last one and four weeks for bath and in-feed treatments, respectively (Elghafghuf et al., 2018). All predictors were modeled in the state equation of the model and had effects on both PAAM and AF abundances, except for the IIP and EIP variables, where the effect was only on the PAAM abundance. The AF abundance at time t was allowed to be affected by the abundance of PAAM at $t - 1$; such an effect was represented by the off-diagonal parameter in the block diagonal matrix, **B**. Finally, the covariances of observation and process errors between PAAM and AF were estimated.

From all possible combinations of IIP and EIP (no effect, unique effect, and different effects), we fitted nine MARSS models for each estimation approach of infestation pressure. No effect means the variable was not included in the model; unique effect means the variable effect was estimated across production cycles and represented by one parameter; and different effects were represented by one parameter per production cycle. In all scenarios, PAAM and AF were parametrized separately. All other parameters in the model were assumed to be unique across farms and production cycles.

Models fits were compared based on AICc (Hurvich et al., 1990) within the same method, and between methods. A model with the smallest AICc value was considered to be the model best fitting the data. Finally, the model residuals and autocorrelations were inspected to ensure no serial autocorrelations or trends.

2.5. Dealing with missing values in predictive variables

in situ water temperature and sea lice abundance datasets had missing values, most of these between January and March. For *in situ* water temperature, missing data were locally interpolated using the cubic curve approach implemented in the *cipolate* command of Stata 15 (StataCorp, 2017). The approach used two data points before and two data points after for each missing observation. If the cubic curve interpolation behaved unreasonably compared with the SST and MOSST datasets (visually assessed), the two data points before the missing values were moved backwards or/and the two data points after the missing values moved forwards, and the cubic curve was re-fit based on the new observations. In the (few) cases where the cubic-curve interpolation did not work, or if the missing values were at the beginning or the end of the series, a linear interpolation or extrapolation was used, respectively, (*ipolate* command, Stata 15) for short sequences of missing values. Finally, a sine-cosine curve was used to interpolate missing *in situ* temperature in five production cycles from four farms where the local approaches did not work because of long sequences of missing values and/or the occurrence of these sequences at both ends of the time series. This was performed by linearly modeling the *in situ* water temperature and including the variables $\sin(2\pi w/52)$ and $\cos(2\pi w/52)$, where w is the week number, in the model.

AF abundance was also interpolated, but only for the purpose of computing the infestation pressure variables. Missing observations in the AF abundance as a response variable were allowed, as the MARSS model seamlessly accommodates missing outcomes. To this aim, a bivariate autoregressive state-space model was applied to PAAM and AF data (on ln scale) from each farm separately. If the farm had multiple production cycles, model parameters were assumed to be the same across these cycles. The model was adjusted by bath and in-feed treatments and *in situ* water temperature, and assumed full variance-covariance matrices for the process and observation errors. Further, the AF and PAAM time series were linked, i.e., the PAAM abundance at time $t - 1$ was allowed to affect AF abundance at time t . Finally, missing AF abundance was imputed by the estimated state values in the bivariate sea lice state-space model, after back transforming these estimates.

2.6. Sensitivity analysis

We evaluated the assumption of equal fish numbers on farms by recomputing the infestation pressure variables for all methods based on approximate numbers of stocked hosts extracted from the local authorities' database. These numbers represented total fish stocked, unadjusted for mortalities or partial harvests, and ranged between 270,000 and 840,000 fish. Sea lice outputs from farms were weighted by the number of stocked fish on the farm. For each of the five approaches, new infestation pressure variables (computed with farm size weights) were modeled using state-space models with unique parameters, and outputs from these models were compared with results

Table 2

Descriptive statistics for variables (including infestation pressure variables quantified by FL, DD, CAF, QLC, and WALS) in the sea lice dataset from 32 production cycles across 20 farms in Grand Manan, New Brunswick, Canada.

Variable	Mean	SD	Minimum	Quantiles			Maximum
				2.5 %	50 %	97.5 %	
Response							
PAAM	4.737	9.816	0	0	1.067	32.58	141.8
AF	3.440	6.184	0	0	0.767	20.76	75.15
Predictors							
Water temperature	9.290	2.797	1.000	3.000	10.00	13.00	15.10
FL							
ln(IIP + .03)	-0.512	2.046	-3.511	-3.507	-0.410	2.988	3.921
ln(EIP + .03)	-0.728	1.184	-3.507	-2.824	-0.775	1.386	1.769
DD							
ln(IIP + .03)	-0.439	2.057	-3.507	-3.507	-0.332	3.001	3.921
ln(EIP + .03)	-0.813	1.148	-3.507	-2.868	-0.831	1.232	1.480
CAF							
ln(IIP + .03)	1.263	2.487	-3.507	-3.507	1.638	4.998	5.800
ln(EIP + .03)	3.076	1.433	-3.507	0.103	3.059	5.349	5.892
QLC							
ln(IIP + .03)	1.539	2.874	-3.507	-3.507	1.895	5.966	7.636
ln(EIP + .03)	3.460	2.101	-3.507	-1.948	3.630	6.633	7.374
WALS							
ln(IIP + .03)	-1.575	1.434	-3.507	-3.507	-1.616	1.042	2.443
ln(EIP + .03)	-0.488	0.860	-3.507	-2.168	-0.475	0.957	1.345
Chemical treatments					Farm-weeks		
Bath treatment	No treatment				2954		
	At least 1 treated cage in the farm				91		
In-feed treatment	No treatment				2266		
	Treatment				779		

from the corresponding models with equal farm sizes.

3. Results

3.1. Descriptive statistics

Bivariate time series of PAAM and AF abundances from 32 production cycles on 20 farms were used in the present study. The cycle lengths ranged from 73 to 126 production weeks, with a total of 3,045 farm-weeks, including approximately 30 % of weeks with missing PAAM and AF abundances. Production cycles within the same farm were consecutive and temporally unrelated with cycles of other farms. The reported abundances of the parasite varied across farms and cycles between 0–141.8 (4% zero counts) and 0–75.2 (9% zero counts) lice per fish at the farm level for PAAM and AF, respectively. The distributions of response, predictive, and intervention variables across the dataset are shown in Table 2. Fig. 1 shows the PAAM and AF abundances (on ln scale) and timing of bath and in-feed treatments for two consecutive production cycles separated by a fallow period for two selected farms.

We set the lag time for FL IIP at $l = 3$, which resulted in best model fit compared to models with other considered lag times. This 3-week lag time showed a good approximation of required time for *Lepeophtheirus salmonis* eggs to develop into PAAM at the mean water temperature of Grand Manan. The FL EIP variable based on a bandwidth of 12.5 was associated with the lowest AICc value; such a bandwidth was used for weighting distances among farms in FL, as well as in DD. The results showed that sea lice patterns were nicely tracked by the interpolated data (based on visual assessments), and scattered observations within the long missing-values sequences guided the approach to perfectly trace these patterns. Fig. 2 shows the pattern of actual and interpolated AF abundance (on ln scale) for the same farms as in Fig. 1.

3.2. The predictive form of IIP and EIP variables

The infestation-pressure variables (on ln scale) from the different approaches were plotted against each other. The IIP variables are displayed in the lower triangle of the scatterplot matrix in Fig. 3; the upper

triangle of the matrix presents the EIP variables. For both IIP and EIP, FL and DD were strongly and linearly related, indicating similarity between FL and DD. Such similarities appeared to be stronger for EIP than for IIP. This may be because FL and DD used the same kernel function for weighting seaway distance in quantifying EIP. The second strongest linear relationships were between CAF and DD, and CAF and FL. These relationships were less scattered for IIP compared with EIP and more shifted from the origin for EIP than for IIP. On the other hand, the IIP and EIP variables based on QLC were weakly related to the same variables from the other approaches. There was also a weaker correlation between WALs and the other approaches for IIP, and between WALs and QLC for EIP.

3.3. Comparison of approaches

The performances of the estimation approaches were compared based on the AICc values from the MARSS models that included the IIP and EIP variables of these approaches (Table 3).

3.3.1. Either IIP or EIP in the model

All approaches showed that estimating only EIP effects on PAAM abundance resulted in substantial improvements in the model fit compared with the baseline model that included neither EIP nor IIP. The changes in AICc ranged between 25.2–46.4 and 4.1–26.2 for unique and different EIP effects, respectively, with the smallest AICc values for WALs and FL. For only IIP in the model, with exception of CAF all methods showed improvements in the model fit relative to the baseline model (Δ AICc varied from 10.1 to 18.2). When IIP effects were estimated as different parameters, only FL had slightly lower AICc than the baseline model (Δ AICc= 1.7). In summary, all approaches to quantifying infestation pressure showed that models with EIP fit the data better compared to models with IIP.

3.3.2. Both IIP and EIP in the model

With both IIP and EIP in the model, FL had the lowest AICc values across all estimation approaches no matter whether effects were unique or different among production cycles. Within the same method, the

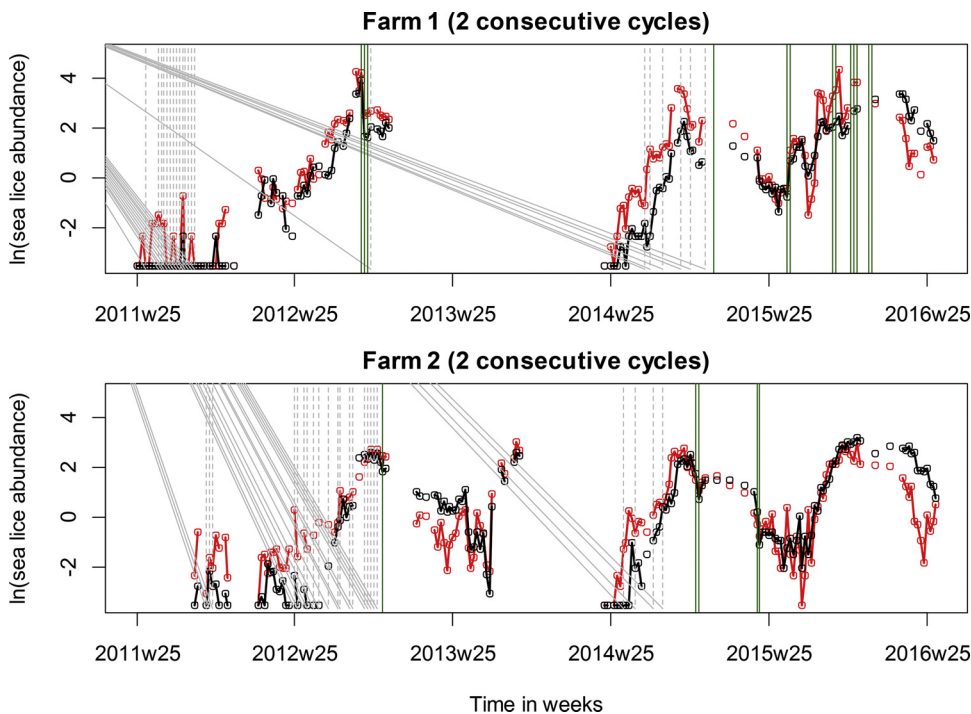


Fig. 1. Mean abundances (on ln scale) of pre-adult and adult male (PAAM) pooled together (red) and adult female (AF; black) lice for two consecutive production cycles in two selected farms (for illustrative purposes) in Grand Manan, New Brunswick, Canada. The vertical dashed (gray) and solid (green) lines represent the timings of in-feed and bath treatments respectively. Years and weeks of the production cycles are indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

model with unique IIP and unique EIP had the lowest AICc value for almost all estimation approaches. Furthermore, all methods agreed that models with unique EIP for all cycles, but different IIP, had lower AICc values than models with unique IIP for all cycles and different EIP ($\Delta AICc$ from 1.0 to 10.6), except for WALS where the AICc value based on the model with unique IIP and different EIP was about four units smaller than the value from the model with unique EIP and different IIP across production cycles. Finally, the CAF, and QLC approaches had the highest AICc values among their models and across methods, when both IIP and EIP effects were allowed to be varied by cycle.

3.3.3. Effects of IIP and EIP on PAAM abundance

Parameter estimates from MARSS models with unique IIP and EIP

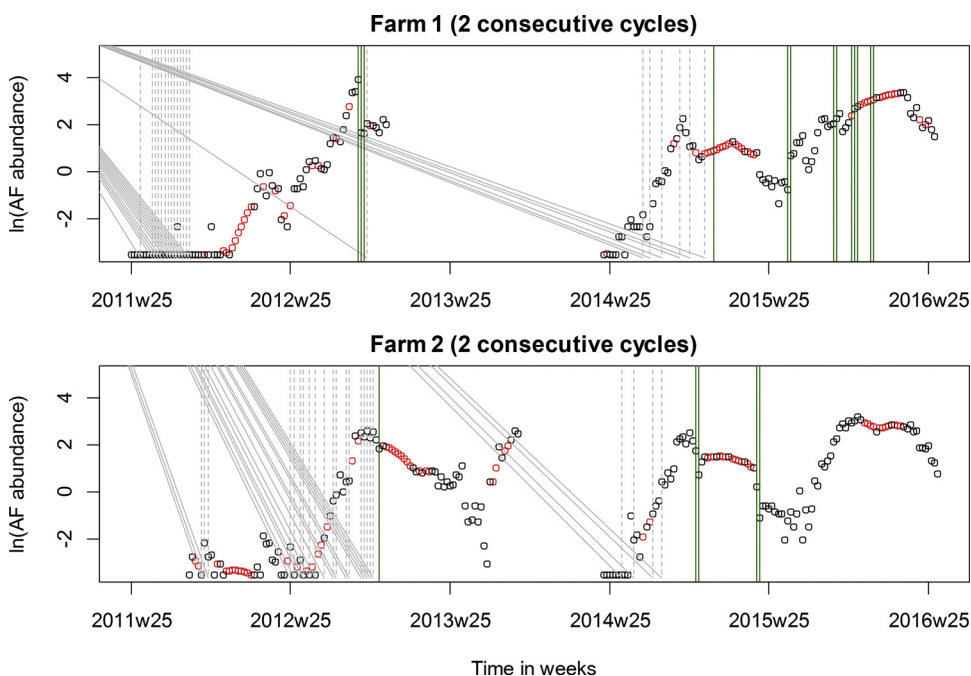


Fig. 2. The natural log of actual (black circles) and interpolated (red circles) adult female lice abundance for two consecutive production cycles in two selected farms in Grand Manan, New Brunswick, Canada. The vertical dashed (gray) and solid (green) lines represent the timings of in-feed and bath treatments respectively. Years and weeks of the production cycles are indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

effects for all cycles are presented in Table 4. In general, the effect of EIP from all approaches increased PAAM lice abundance, while only FL, DD, and WALS variables of IIP had non-negligible effects on PAAM lice. The standardized coefficients of IIP from FL, DD, and WALS were, respectively, estimated to be 0.055 ($C_{IIP} * SD$; SD is the standard deviation), 0.049, and 0.026 on the natural logarithmic scale. This means, an increase of SD in the IIP variable (i.e. 1 SD change) results, on average, in increases of approximately 5.5 %, 4.9 %, and 2.6 % in PAAM lice abundance (ln scale) per week across farms for FL, DD, and WALS, respectively. The standardized EIP coefficients were also variable by approach and estimated at 0.091, 0.076, 0.077, 0.092, and 0.082 for FL, DD, CAF, QLC, and WALS, respectively. These results indicate that each 1 SD increase in EIP elevates the ln PAAM lice abundance (on average)

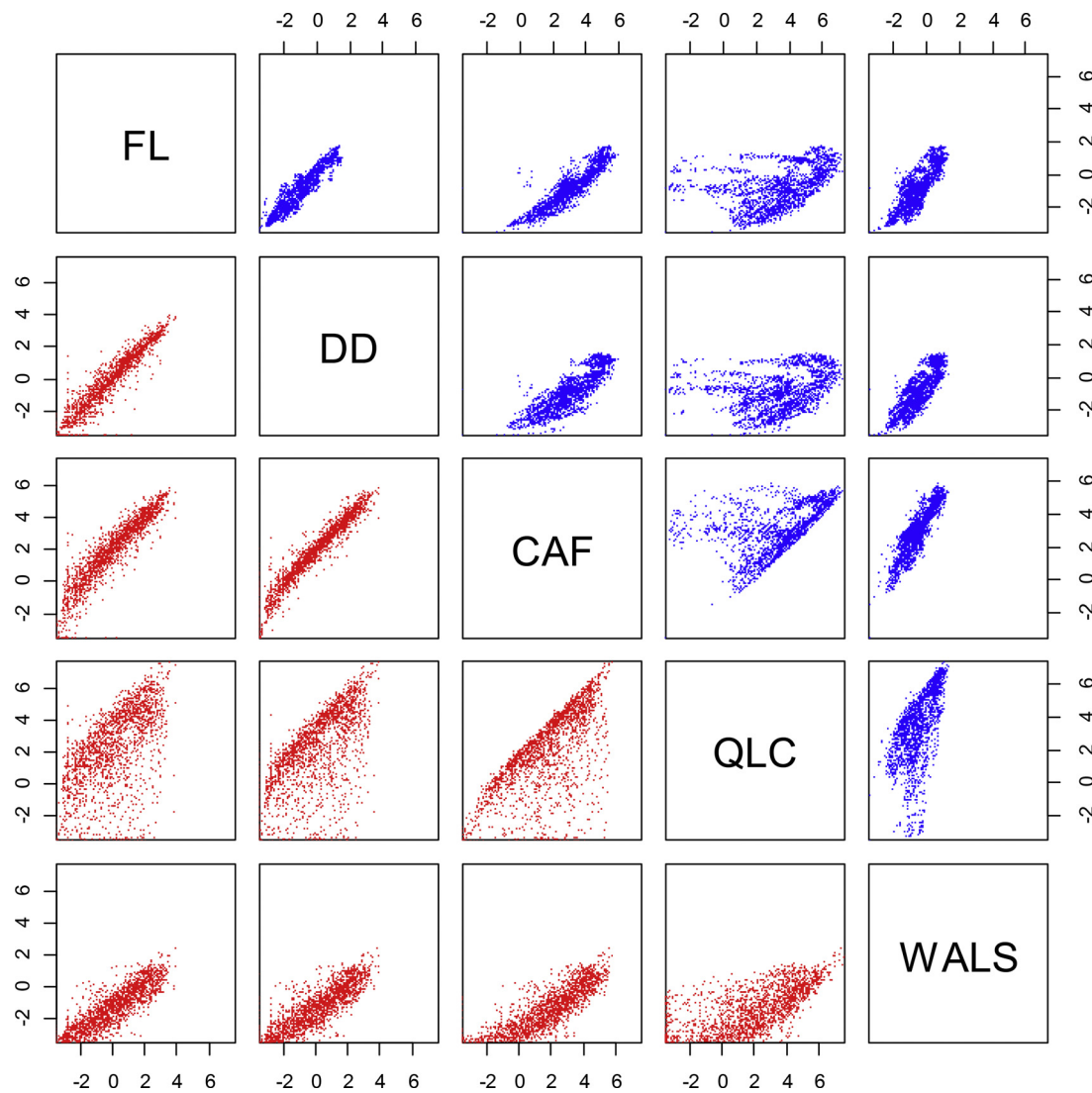


Fig. 3. A scatterplot matrix for internal (red, lower triangle) and external (blue, upper triangle) infestation pressure variables (on ln scale) quantified by fixed lag (FL), degree-day (DD), contributing adult female (CAF), quantitative life cycle (QLC), and weighted average lag structure (WALS) approaches based on sea lice data from 32 production cycles across 20 farms in Grand Manan, New Brunswick, Canada. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

by 9.1 %, 7.6 %, 7.7 %, 9.2 %, and 8.2 % per week for FL, DD, CAF, QLC, and WALS, respectively.

3.4. Summary by estimation approach

The FL IIP and EIP variables explained the variation in the PAAM-abundance data best for almost all models across methods, whereas WALS and QLC came second and third, respectively. However, the WALS and QLC performances were fairly similar when models did not include different effects. On the other hand, models based on DD and CAF variables had larger AICc values compared with other methods, and the AICc values from DD models were much smaller than the ones based on CAF.

3.5. Other model parameters

The effect of water temperature on PAAM abundance was somewhat variable among methods (Table 4). The largest and smallest coefficient estimates were for FL and WALS respectively, whereas water temperature showed negligible effects on PAAM in QLC. The effect of water temperature on AF abundance was fairly similar among the five

approaches. Bath and in-feed treatments reduced PAAM and AF abundances, although their effects were different. Bath treatments had a larger reduction rate of lice, and similar between PAAM and AF, than in-feed treatments that showed effects only on AF lice. Other model parameters were fairly similar among the five approaches and slightly different between PAAM and AF abundances. The estimated increase in sea lice abundances from the \mathbf{u} and \mathbf{B} parameters, was slightly greater for AF than for PAAM across a plausible range of state-process values. Furthermore, the results showed that the process errors of PAAM and AF were highly correlated (in \mathbf{Q} matrix), whereas the correlation between observation errors (in \mathbf{R} matrix) for PAAM and AF were estimated to be close to zero. Notably, the process error variance for both PAAM and AF abundances was larger than the observation error variances. This may be because different production cycles are subject to different environmental conditions and circumstances.

Finally, the sensitivity analysis that was carried out to study the impact of the equal farm size assumption showed minor changes in the IIP and EIP coefficients for the models with unique parameter configurations. For instance, the EIP estimates from the sensitivity analysis for FL, QLC, and WALS were 0.072, 0.039, and 0.095, respectively. The IIP coefficients for FL, QLC, and WALS were, respectively, 0.000, -0.002,

Table 3

Performance of quantifying approaches for infestation pressure of sea lice on farms (FL, DD, CAF, QLC, and WALs), given by corrected sample-size Akaike's Information Criterion (AICc; log-likelihood in parentheses) based on multivariate state-space models fitted to sea lice data from 32 production cycles on 20 farms located in Grand Manan, New Brunswick, Canada.

Method		No IIP	Unique IIP among cycles	Different IIP across cycles
FL	No EIP	8582.3 (-4274.1)	8567.9 (-4265.9)	8580.6 (-4240.7)
	Unique EIP among cycles	8536.0 (-4249.9)	8531.5 (-4246.7)	8538.7 (-4218.7)
	Different EIP across cycles	8557.7 (-4229.3)	8547.5 (-4223.1)	8549.8 (-4192.3)
DD	No EIP	8582.3 (-4274.1)	8572.2 (-4268.0)	8585.4 (-4243.1)
	Unique EIP among cycles	8547.9 (-4255.9)	8545.2 (-4253.5)	8554.4 (-4226.6)
	Different EIP across cycles	8572.5 (-4236.7)	8564.0 (-4231.4)	8578.3 (-4206.6)
CAF	No EIP	8582.3 (-4274.1)	8583.5 (-4273.7)	8603.9 (-4252.4)
	Unique EIP among cycles	8557.1 (-4260.5)	8558.5 (-4260.1)	8578.8 (-4238.8)
	Different EIP across cycles	8578.2 (-4239.5)	8579.8 (-4239.3)	8600.4 (-4217.6)
QLC	No EIP	8582.3 (-4274.1)	8564.1 (-4264.0)	8599.0 (-4249.9)
	Unique EIP among cycles	8535.9 (-4249.9)	8536.9 (-4249.3)	8566.9 (-4232.8)
	Different EIP across cycles	8576.3 (-4238.6)	8577.5 (-4238.1)	8601.8 (-4218.3)
WALS	No EIP	8582.3 (-4274.1)	8565.5 (-4264.7)	8588.2 (-4244.5)
	Unique EIP among cycles	8537.2 (-4250.5)	8537.1 (-4249.5)	8560.2 (-4229.5)
	Different EIP across cycles	8556.2 (-4228.5)	8556.0 (-4227.4)	8571.0 (-4202.9)

and 0.019. Also, FL still had the smallest AICc value among all methods (Table S1, Supplementary Information).

4. Discussion

In the present study we compared five different approaches to quantifying sea lice infestation pressure on salmon farms, using weekly data from aquaculture sites in Grand Manan, New Brunswick, Canada from May 2010 to October 2016. The main reasons for our choice of estimation approaches were the differences in the nature of the methods, ways of weighting inter-farm infestations, and computation feasibility. The performances of these approaches were evaluated based on modeling the quantified IIP and EIP from each approach in a set of nine MARSS models, including all the combinations of modeling effects where the effect was absent, estimated as a unique parameter, and estimated as different parameters.

4.1. Computation of infestation pressure

The main problem encountered in computing the infestation pressure was the missing information for key variables (e.g., AF abundance and/or water temperature). In the data used here, most of the missing values occurred at the beginning of each calendar year, which may be due to the weather conditions that inherently limit sampling. One of the advantages of the analytical approach used in this study, the state-space model, is that it seamlessly accommodates missing data and provides estimates of their values (Holmes et al., 2018). Here, the predicted latent states, which are conditionally estimated on all data, were used for interpolating missing observations in AF time series.

The CAF and QLC IIP variables were forward-computed based on daily data and then aggregated to weeks, while in other approaches they were immediately backward-computed from the weekly data. In degree-day-dependent approaches, we searched the offspring (in the PAAM series) of AF at time t by forward summing water temperature, which may result in PAAM that came from AF at multiple time points. If the calculation is performed backwards, PAAM at time t is only affected by one AF time point because the move in the series is one step ahead each time. Mathematically, the forward and backward computations produced different results, and these results depended on the temperatures at the two time ends (i.e., the times of AF and their observed PAAM). Practically, PAAM at time t is likely to come from AF at

multiple time points, because PAAM contained mobile lice of different ages; this is supported by the forward computation.

The IIP and EIP distributions were different among approaches, and these differences were more pronounced between CAF, QLC, and WALs. This may be because the number of hatched eggs and the survival proportion were not considered in CAF, but were in QLC. Furthermore, the difference in the distributions of IIP and EIP between QLC and WALs may be attributable to the nature of the two methods; whereas QLC is based on lab-experiment quantities (Stien et al., 2005; Kristoffersen et al., 2014), WALs uses Norwegian data-driven estimates. For FL and DD, the distributions of IIP and EIP were fairly similar, which may be due to the fact that FL and DD did not allow for PAAM to be affected by multiple time points of AF, and because they both used a Gaussian kernel for EIP computation.

4.2. Comparison of method performance

The difference between FL and DD was in the lag time used to approximate the time required for louse eggs to develop into PAAM stages; the FL approach used a lag time that did not depend on water temperature, whereas DD had a temperature-dependent lag time. Based on the model fit, we found IIP and EIP variables from FL contributed more to the development of PAAM infestation than the DD variables and other approaches, although FL and DD employed the same weighting function for EIP. The performance of QLC was much better than the performance of CAF, in agreement with Kristoffersen et al. (2014), although Kristoffersen et al. (2014) used a threshold of 194 degree days. This highlights the importance of taking the reproduction and survival of sea lice into account when a degree-day approach is implemented. Also, CAF always performed poorly compared to DD, suggesting that computing daily infestation pressure without taking sea lice reproduction into account does not improve the method performance, as compared with the backward computation at weekly levels (i.e., the DD approach). Furthermore, WALs and QLC had a comparable performance when the infestation pressure was modeled as a unique effect for all production cycles. However, WALs outperformed QLC when effects varied by cycle and had the advantage of being easier to implement.

Finally, including water temperature in the PAAM model played an important role for method performances, with exception of QLC that has water temperature dependence in sea lice fecundity (Eq. (10)). It

Table 4
Parameter estimates based on multivariate state-space models with shared parameters fitted to sea lice data from 32 production cycles on 20 farms located in Grand Manan, New Brunswick, Canada. The internal (IIP) and external (EIP) infestation pressure variables are computed using five different methods: fixed lag (FL), degree days (DD), contributing adult female (CAF), quantitative life cycle (QLC), and weighted average lag structure (WALS).

Parameters	β_{IIP}	β_{EIP}	β_{bath}	β_{feed}	β_{temp}	μ		B matrix		Q matrix		R matrix	
						PAAM	AF	PAAM	AF	PAAM	AF	PAAM	AF
FL													
PAAM	.027 (.013)	.077 (.014)	-.617 (.070)	-.018 (.034)	.192 (.021)	.085 (.014)	.903 (.013)	.117 (.015)	.283 (.019)	.128 (.014)	.106 (.021)	.006 (.016)	.006 (.016)
AF	—	—	-.599 (.058)	-.097 (.026)	.074 (.016)	.052 (.011)	—	.881 (.014)	.128 (.014)	.227 (.015)	.006 (.016)	.120 (.015)	.120 (.015)
DD													
PAAM	.024 (.011)	.065 (.013)	-.604 (.069)	-.016 (.022)	.186 (.020)	.082 (.011)	.915 (.013)	.116 (.013)	.281 (.018)	.130 (.009)	.108 (.018)	.005 (.007)	.005 (.007)
AF	—	—	-.600 (.057)	-.097 (.024)	.073 (.016)	.053 (.010)	—	.882 (.013)	.130 (.009)	.227 (.015)	.005 (.007)	.121 (.015)	.121 (.015)
CAF													
PAAM	-.007 (.006)	.054 (.011)	-.575 (.069)	-.036 (.028)	.150 (.018)	.082 (.012)	.942 (.011)	.132 (.012)	.255 (.017)	.122 (.012)	.123 (.017)	.008 (.012)	.008 (.012)
AF	—	—	-.599 (.059)	-.111 (.025)	.070 (.016)	.051 (.011)	—	.866 (.012)	.122 (.012)	.234 (.015)	.008 (.012)	.117 (.016)	.117 (.016)
QLC													
PAAM	.008 (.008)	.044 (.008)	-.585 (.067)	-.041 (.036)	-.039 (.035)	.086 (.014)	.926 (.010)	.134 (.013)	.258 (.017)	.117 (.012)	.121 (.018)	.011 (.014)	.011 (.014)
AF	—	—	-.601 (.059)	-.114 (.028)	.080 (.017)	.049 (.011)	—	.865 (.013)	.117 (.012)	.234 (.015)	.011 (.014)	.116 (.016)	.116 (.016)
WALS													
PAAM	.018 (.008)	.095 (.017)	-.596 (.068)	-.003 (— ^a)	.110 (.016)	.075 (.010)	.922 (.009)	.122 (.013)	.268 (.017)	.124 (.012)	.115 (.018)	.007 (.013)	.007 (.013)
AF	—	—	-.601 (.058)	-.102 (.022)	.074 (.016)	.052 (.010)	—	.877 (.012)	.124 (.012)	.228 (.015)	.007 (.013)	.120 (.015)	.120 (.015)

compensated the IIP and EIP effects on PAAM.

4.3. IIP versus EIP

The EIP variable was positively associated with PAAM abundance; the larger the EIP, the higher the PAAM abundance. The EIP effect was estimated by all approaches to be larger than the IIP effect. These findings indicate that EIP explained the variation in the PAAM data better than IIP, which means that the infestation pressure from the neighbouring farms played a more important role in sea lice transmission than the pressure originating from within the same farm in the Grand Manan area. These findings are in line with results reported by Kristoffersen et al. (2013) for Chilean data. The unsynchronized treatments and fallow periods with neighbouring farms may elevate the effects of EIP.

Only the IIP variable from FL, DD, and WALS was associated with a (small) elevation in the PAAM infestation. Kristoffersen et al. (2013) showed a smaller size effect for IIP than for EIP in Chilean salmon farms, and, in Norway, Kristoffersen et al. (2014) did not detect an effect of IIP on PAAM counts; however, the IIP variable was modeled as a dichotomous predictor (zero/non-zero) in the initial phases of marine production. In fact, when infestation first occurs on a farm, lice are still juveniles while adult lice infestations often do not appear until many weeks later (Murray and Salama, 2016). This process may repeat itself after each application of bath treatment, within a shorter time frame, because bath treatments may reduce adult lice levels to almost zero, but it has smaller, if any, impacts on juvenile stages (Elghafghuf et al., 2018). These factors and other environmental drivers, such as water currents, may mitigate the effects of IIP. At the other extreme, Aldrin et al. (2013) reported that most of sea lice infestations in Norwegian salmonid farms originated within the farm. The model used in Aldrin et al. (2013) is different compared with the modeling approach used in the present study and the size of the data set in this study is much smaller relative to the Norwegian data modeled in Aldrin et al. (2013), the results from the two studies cannot directly be compared. Also, the discrepancies in the effect of external infestation pressures between these studies may be attributable to the regional geographical characteristics, farm densities, and lice abundances, among other potential factors.

4.4. Unique versus different parameters for infestation pressure

One of the MARSS model features is that the effect of infestation pressure (or other effects) on sea lice abundance can be estimated for each production cycle separately (i.e., each production cycle can have its own parameter), or as a one parameter for all production cycles (i.e., the effect can be estimated across cycles). The advantage of the former is being able to distinguish between IIP and EIP effects that are different among cycles from those that are similar, and the disadvantage is the large number of resulting parameters. The latter has few parameters in the model, but ignores between-cycle variation (Elghafghuf et al., 2018). Almost all the infestation pressure estimation approaches showed that models with unique IIP and EIP for all production cycles were associated with lower AICc, indicating that estimating the effects of infestation pressure as a single parameter across cycles was better than estimating it for each cycle separately, which may be helpful in generalizing results. Practically, these findings indicate that farms in Grand Manan are exposed to similar infestation pressures. This may be true because Grand Manan is a small area and farms there are relatively close to each other, so they may exchange sea lice through release of nauplii stages that drift with water currents before attaching to a new host as a copepodid.

4.5. Study implications and limitations

This research contributes to the building of predictive tools for sea

lice abundance within salmon farms in New Brunswick, Canada. The comparison of existing estimation methods for sea lice infestation pressure will fill a knowledge gap in this area and assist the choice of most appropriate approaches to estimating sea lice infestation pressure on farms, and therefore, enable producers to make informed decisions to optimize control of sea lice infestations. In the present study, we found that EIP had a substantial contribution to PAAM lice abundance on fish. Our interpretation of this is that most of the sea lice infestations in the present data were from infective copepodids that drifted with the sea currents to the farm from outside sources (outside sources in our study are neighboring farms). This may be true because Grand Manan is a relatively small area and salmon farms there are interconnected through proximity, while wild Atlantic salmon populations are very sparse in this area. These results highlight, for the producer, the importance of sharing sea lice abundance information among neighboring farms, to reasonably predict future infestations that may improve the management and reduce sea lice burdens in the region.

The actual numbers of stocked fish on Grand Manan farms were not available for farm production during the study period, which is a limitation of the present study, because sea lice production has been shown to be associated with the total sea lice output per farm (Frazer et al., 2012). We assumed the same size for all Grand Manan farms, and such an assumption was evaluated based on rough numbers of stocked fish using a sensitivity analysis. The results of the sensitivity analysis showed minor changes in the IIP and EIP coefficients, but the relative ordering of approaches remained the same. In particular, the FL method was still associated with the smallest AICc value. Because the main goal of this study was to evaluate the performance of estimation methods for sea lice infestation pressure, the impact of the same farm-size assumption on the main conclusions of the study could be expected to be minor, because the assumption was applied to all methods.

5. Conclusions

Our findings showed that the simplest method for quantifying infestation pressures, namely the fixed lag method (FL), had the best predictive performance for PAAM sea lice among all considered methods. When effects were estimated as a one parameter across production cycles, QLC and WALs performed similarly. However, WALs had better performance than QLC when infestation pressures were estimated separately to each cycle. The research indicated that models with only EIP explained the variation in the data better than models with only IIP, and that models with unique IIP and unique EIP for all cycles were generally associated with the best model fit. The study showed that Grand Manan farms had similar levels of within-farm infestations and these farms were exposed to similar external pressures of infectious lice copepodids. Optimal parasite management may require more efforts to reduce the abundance of sea lice regionally, not just within-farm, through synchronized treatments and focusing on regional management approaches. Furthermore, the adult female lice abundance on farms three weeks previous greatly contributed to future PAAM infestations in the region.

Declaration of Competing Interest

The authors have no conflicts of interest to declare.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.epidem.2020.100394>.

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