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Estimating the dispersal of *Lepeophtheirus salmonis* sea lice within and among Atlantic salmon sites of the Bay of Fundy, New Brunswick

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Abstract

The objective of this study was to estimate the impact of infestation pressures on the abundance of the parasitic sea louse, *Lepeophtheirus salmonis*, in the Bay of Fundy, New Brunswick (NB), Canada, using the Fish-iTrends database for the years 2009–2018. Infestation pressures were calculated as time-lagged weighted averages of the abundance of adult female (AF) sea lice within a site (internal infestation pressure: IIP) and among sites (external infestation pressure: EIP). The EIP weights were calculated from seaway distances among sites and a Gaussian kernel density for bandwidths of 5 to 60 km. The EIP with a bandwidth of 10 km had the best fit, as determined with Akaike's information criterion, and historical AF sea lice abundance. This estimated dispersal distance of 10 km was similar to previous studies in Norway, Scotland and in New Brunswick. The infestation pressures estimated from empirical AF sea lice abundance within and among sites significantly increased the abundance of AF sea lice ($p < .001$). This study concludes that sea lice burdens within Atlantic salmon farms in the Bay of Fundy, NB, are affected by within site management and could be improved by synchronizing treatments between sites.

KEYWORDS

aquatic epidemiology, Atlantic salmon, Fish-iTrends, infestation pressure, *Lepeophtheirus salmonis*, sea lice

1 | INTRODUCTION

The Atlantic salmon, *Salmo salar* (Linnaeus: WoRMS, 2020), aquaculture industry in the Bay of Fundy, New Brunswick (NB), Canada, has been exposed to the parasitic sea louse, *Lepeophtheirus salmonis* (Krøyer: WoRMS, 2020), since its early development in the 1980s (Hogan & Trudeau, 1989) and its presence has required management since the mid-1990s (Hogans, 1995). *L. salmonis* negatively affects salmon welfare by rasping mucus, skin and underlying tissue causing the potential for increased mucus production, skin wounds (Johnson et al., 2004; Tully & Nolan, 2002) and immunocompromising its host (Fast, 2014). Moreover, sea lice have been identified as a potential transmission route for the infectious salmon anaemia virus (ISAv), which itself can cause high mortality rates in Atlantic salmon (Nylund et al., 1993, 1994), and can be further exacerbated by sea lice infection (Barker et al., 2019).

Atlantic salmon producers seek to reduce sea lice abundance on their fish to mitigate the negative effects caused by this parasite and to keep in check the potential for adult female sea lice to reproduce. The control of *L. salmonis* involves increased costs of production due to decreased growth rate and treatment (Abolofia et al., 2017; Costello, 2006).

Aside from industry-wide measures such as fallowing and single year class area management, control options for sea lice include the use of chemotherapeutic agents and non-medicinal operations (see Overton et al., 2019, for review). The effectiveness of these treatments varies with the drug or operation used, timing, method of application, sea lice life stage, season, pretreatment abundance level (Gautam et al., 2017b), frequency of application (Revie et al., 2005) and potential resistance of sea lice to the drug (e.g. emamectin benzoate [Slice®, Merck Animal Health]; Igboeli et al., 2012; Jones et al., 2012; Westcott et al., 2008).

The Fish-iTrends is a Web-based data management system that compiles data on sea lice and their treatments in Atlantic salmon marine sites for the province of NB and other Atlantic provinces (Gautam et al., 2016; additional details found in Appendix S1). This database aggregates sea lice counts for certain life stages from all aquaculture sites in their respective Bay Management Areas (BMA; additional details in Chang et al., 2011).

The sea louse undergoes multiple moults in its 8 life stages (see Johnson & Albright, 1991; updated by Hamre et al., 2013). The life stages of note are the adult male and female sea lice, the planktonic stages (nauplii I and II, and copepodid), and the pre-adult stages (I and II). The planktonic stages are passively transported by water currents (Amundrud & Murray, 2009). Water salinity and temperature affects the rate of development, mortality (Groner et al., 2016; Stien et al., 2005) and attachment of each life stage (Tucker et al., 2000). Sea lice development was more rapid at higher water temperatures (Hamre et al., 2019; Stien et al., 2005), while salinities below 22 ppt reduced survival (Groner et al., 2016). Modelling of sea lice infestation therefore often accounts for maturation and mortality in relation to water salinity and temperature (e.g. Revie et al., 2005).

Modelling the effective distance that planktonic sea lice travel can be accomplished with multiple methods: physical and biophysical models, and empirical methods (e.g. plankton tows in Nelson et al., 2017). Physical models are numerical (i.e. oceanographic) models of currents that respond to temperature, depth, wind and other physical characteristics of the water body (e.g. Murray & Gillibrand, 2006). The physical models can be adjusted with biological estimates of mortality, survival and development rates of the sea lice (e.g. Revie et al., 2005; Asplin et al., 2011, 2014).

A different approach to the estimation of dispersal distance and the impact of sea lice among aquaculture sites is with the use of the concept of infestation pressure. Simply, infestation pressure is a measure that represents the dose of exposure of parasitic stages of sea lice to potential fish hosts. The infestation pressure can originate from within a site (internal infestation pressure, or IIP) and be derived from neighbouring sites (external infestation pressure, or EIP). Both sources of infestation pressure can be calculated using several methods (e.g. Aldrin et al., 2013, 2019; Kristoffersen et al., 2013, 2014, 2018). Cantrell et al., (2018, 2019) defined infestation pressure as the density of particles representing sea lice using a biophysical model in the Broughton Archipelago, British Columbia (BC). Sandvik et al., (2016) defined infestation pressure on a scale of low (0–1 louse) to high (>10 lice) resulting from a biophysical model informed from field data. The present study, among others (e.g. Elghafghuf et al., 2020), propose data-driven methods for the estimation of infestation pressure.

Elghafghuf et al., (2020) evaluated multiple estimation approaches for infestation pressure using Fish-iTrends data from the aquaculture sites in Grand Manan, NB (see Figure 1). Five methods were evaluated using a multivariate autoregressive state-space model. The IIP and EIP were calculated using the fixed lag approach of mean reported adult female (AF) sea lice abundance with a time

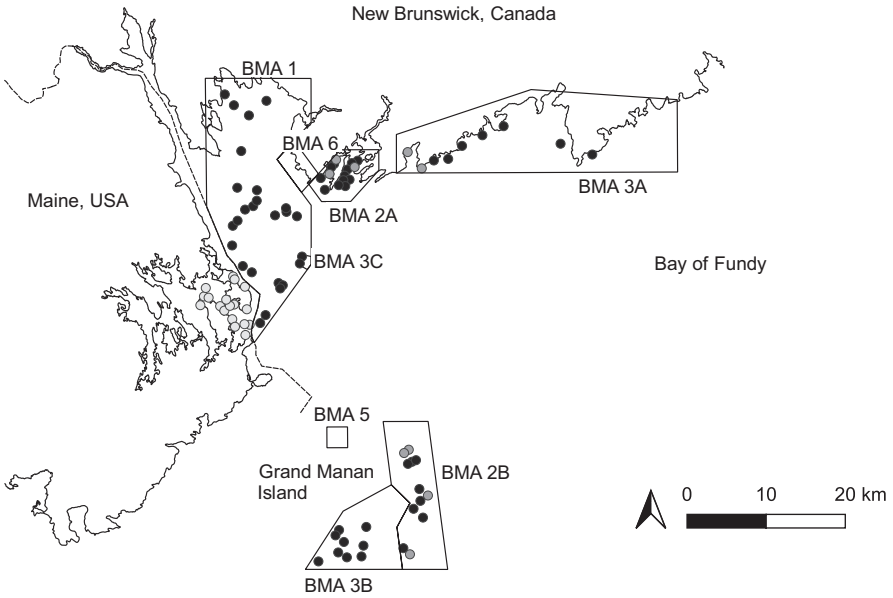

FIGURE 1 The Bay of Fundy, New Brunswick, Canada, study area demonstrating Bay Management Areas (BMA) and Atlantic salmon aquaculture sites. Sites included (black circle) and excluded (grey circle) from the final multivariable linear mixed model for the abundance of adult female *Lepeophtheirus salmonis*. Abundances of sea lice were not available from sites from Maine, USA (white circle). The locations of sites and BMA were adapted from the New Brunswick Bay of Fundy Marine Aquaculture sites map of 2017 (Department of Energy and Resource Development/Agriculture, Aquaculture, and Fisheries 2017)

lag of one to four weeks (Kristoffersen et al., 2013) and other approaches (Aldrin et al., 2019; Kristoffersen et al., 2014, 2018). The fixed lag approach had the lowest Akaike's information criterion (AIC) for the model that included both the IIP and EIP. The authors concluded that an EIP calculated with the abundance of sea lice weighted by a Gaussian KDE bandwidth of 12.5 km resulted in the lowest AIC (Elghafghuf et al., 2020).

The bandwidth of the Gaussian KDE may be taken to represent the dispersal of planktonic sea lice among neighbouring sites. Kristoffersen et al., (2013) determined the model with the lowest AIC had a kernel-weighted intensity of mean-reported abundance of gravid AF sea lice adjusted with a KDE of 30 km. Other reports suggest a range of dispersal distances from 7 to 200 km. The variation in dispersal distance is the result of highly variable environmental conditions such as wind (Salama et al., 2018), current speed and direction (Asplin et al., 2014), distance from shore (Penston et al., 2004), methodology to obtain the estimate, among others.

The dispersal of sea lice, for the whole of the Bay of Fundy, NB, has not been previously estimated. Our objective was to estimate the impact of the IIP and EIP on the abundances of sea lice for the Bay of Fundy, NB. This information has implication for the management of the NB aquaculture industry as it may suggest the need for a different BMA design for the synchronization of site production cycles (i.e. stocking and harvesting), as well as for synchronizing mitigation strategies among sites to maximize efficiency. The Fish-iTrends database offers the opportunity for empirical estimation of the maximum dispersal distance of sea lice using modelling of the IIP, EIP and treatments.

2 | MATERIALS AND METHODS

2.1 | Study area and population

All available sea lice (*L. salmonis*) information from aquaculture sites in the Bay of Fundy, New Brunswick (Figure 1), between July 2009 and November 2018, were retrieved from the Fish-iTrends data management system and included in this study. Data consisted of routine counts of pre-adult and adult male (PAAM) and AF (with and without egg strings) sea lice on Atlantic salmon from several cages at each site during their production cycle (additional details found in Appendix S1; see Gautam et al., 2016 for detailed sampling description). The Bay of Fundy adjoins the state of Maine, USA (Figure 1), and data on sea lice abundance and active sites from the Maine aquaculture industry were not available for this study.

2.2 | Selection and preparation of the outcome and abundances

Adult female sea lice were selected as the outcome for modelling. AF sea lice counts had lower variance than PAAM sea lice counts during comparison of audit technician and site staff counts, suggesting higher repeatability of AF sea lice counts within cages (Elmoslemany et al., 2013). This is perhaps not surprising since PAAM sea lice counts are based purely on morphology, which include two life stages with a disproportionate sex ratio (i.e. pre-adult males and females, and adult males). In addition, AF sea lice develop more slowly than their male counterparts (Hamre et al., 2019); therefore, the rate of population growth is limited by this slowest life stage.

Sea lice abundances were calculated for each observation (i.e. count date; Equation 1). The normalized counts of sea lice are the count of sea lice divided by the number of fish with the offset of 1.

$$\text{Abundance of AF}_{ic}(t) = \ln\left((\text{AF}_{ic} + 1)/\text{no. fish}\right) \quad (1)$$

where *AF* is adult female sea lice for *c* that is cage within site *i* and time t (day).

Caligus elongatus and *L. salmonis* chalimus sea lice were also recorded, but were not considered suitable to be included in the modelling due to their small numbers.

2.3 | Data structure

Sea lice abundances were measured at the cage level. The aquaculture industry is hierarchically structured with multiple cages within sites and multiple sites within BMAs. Regulations stipulate when sites can stock and harvest fish within BMAs (production cycles); therefore, cages and sites were uniquely identified according to their specific production cycle within BMAs.

Observations (counts) occurred as repeated measurements of sea lice throughout the production cycle. Observations were further grouped into segments, where a segment was defined as the first observation after a topical treatment followed by all additional observations until the following treatment within a production cycle. This organization of observations into segments also allowed us to account for the treatment effect on lice abundance.

A segment was limited to a single cohort of salmon, as defined by salmon with the same fish group identifier, cage, site and production cycle. The fish group identifier was used in the Fish-iTrends database to follow groups of salmon that were sometimes split or moved between multiple cages during the production cycle, including at the time of a well-boat treatment.

Descriptors for the segments included their length (the number of days from the start to the end of the segment, including the treatment date), size (the number of observations that contribute to the segment) and maximum gap (the largest number of days between observations of a segment). Short segments occurred when there were multiple treatments in short succession within a cage. Evaluation of the segments using the length, size and maximum gap information identified segments with extreme length, size and maximum gap that resulted in the creation of strict inclusion criteria for modelling.

2.4 | Defining internal and external infestation pressure

The internal and external infestation pressures were estimated using a fixed lag approach, similar to Elghafghuf et al., (2020) and Kristoffersen et al., (2013). The fixed lag is the time for AF sea lice to produce eggs and develop into a new generation of AF and PAAM sea lice. The lag time for PAAM sea lice abundance was set at 28 days and for AF sea lice abundance at 21 days. These lag times were chosen based upon a combination of a literature review, and the estimated most rapid development at the sea temperature annual maximum in the study area (15°C near Saint Andrews, NB [World Sea Temperature, 2020]). The closest analog to our settings was an estimated AF sea lice that contributed to the next generation of PAAM sea lice at a neighbouring site with a lag of approximately four weeks at water temperatures of 14°C (Aldrin et al., 2019).

The dose of exposure of infectious stages of sea lice to potential fish hosts within a site (IIP) was represented by the triangular-weighted, 15-day average of AF and PAAM sea lice abundances divided by the sum of the weights at a site 21 and 28 days prior to an observation, respectively. The EIP consisted of the triangular-weighted temporal and Gaussian KDE-weighted spatial average abundance of AF sea lice at other sites 21 days prior to an observation (additional details found in Appendix S1). Gaussian KDE weights used seaway distances among study sites, which were calculated with the 'gdistance' package, version 1.3–1 (van Etten & de Sousa, 2019) in R (R Core Team, 2020). Averages of AF and PAAM sea lice abundances were calculated across all observations (whether part of a segment or not) for a site, and no adjustments were made for observations that occurred prior to and after treatments.

2.5 | Baseline abundance of adult female sea lice

The abundance of sea lice after a bath treatment was hypothesized to be associated with the abundance of AF and PAAM sea lice prior to the application of the treatment (Gautam et al., 2017a). Gautam et al., (2017a) defined a treatment as the application of azamethiphos (Salmosan® Vet, Benchmark Animal Health) or hydrogen peroxide (Interox® Paramove® 50™, Solvay Chemicals Inc.) using a tarp enclosure or well-boat. The abundance of sea lice prior to a treatment was defined as the baseline abundance of AF sea lice and was identified for each segment. The baseline abundance of AF sea lice was the first observation within 7 days prior to and including the treatment date, provided it was indicated in the database as a pretreatment count on the treatment date; observations also had to belong to the same cohort of salmon.

2.6 | Topical and in-feed treatments

The topical treatments at the start of a segment were assigned to all the observations within that segment. Hydrogen peroxide (Interox® Paramove® 50™ and Aquaparox 50™, Alpha Chemical Limited) treatments were combined into a single category. Azamethiphos treatments were categorized according to their method of application: tarpaulin, skirt or well-boat.

A dichotomous variable was created to represent the application of an in-feed treatment (emamectin benzoate, teflubenzuron [Calicide®, Nutreco ARC Ltd], and avermectin [Ivomec®, Boehringer Ingelheim, and Noromectin®, Norbrook Laboratories Ltd.]) for a group of fish (i.e. cage level) prior to the start of a segment: present (1) and absent (0).

2.7 | Surface sea temperature

The UKMO OSTIA SST product (UK Met Office, 2005) was utilized for the sea surface temperature (hereafter, temperature) of the study area. This remote sensing product was selected instead of the in situ temperature measurements to avoid missing values and inconsistencies in measuring technique. Thakur et al., (2018) found that the UKMO OSTIA SST product had the highest concordance correlation coefficient and index of agreement compared to measurements of temperature taken on aquaculture sites in the Broughton Archipelago between 2003 and 2016.

Daily temperature values were extracted for the duration of the study for the centroid location of each aquaculture site polygon utilizing the 'raster' package, version 3.0–12 (Hijmans et al., 2019) in R. The spatial resolution was 1/20 degrees, which is approximately 6 km at the 45 degree latitude of the Bay of Fundy, NB; sites that occupied the same temperature grid shared temperature values.

2.8 | Modelling

2.8.1 | Inclusion criteria

Segment inclusion for modelling was strict. Segment length was constrained to 5 and 300 days, inclusive. Segment size was constrained to three and 20 observations, inclusive. Segments with a large gap between observations (greater than and equal to 90 days) were excluded. The BMAs 5 and 6 were not included in the modelling of the outcome as the BMA 5 is a conservation area for wild salmon and BMA 6 is for species other than Atlantic salmon. Moreover, there were no segments in the BMA 6 and only 4 segments with 13 observations in the BMA 5. A sensitivity analysis was performed to evaluate the effect of the strict inclusion criteria on the model (additional details found in Appendix S1).

2.8.2 | Multivariate linear mixed model

A multilevel mixed-effects linear regression (Pinheiro & Bates, 2000) was used to model the abundance of AF sea lice. The mixed-effects model is robust, improves the estimation of standard errors where

there is clustering of the outcome and allows the assignment of an error correlation structure. Random effects included the site cycle, cage cycle and segments. BMA was set as a fixed effect.

Models were fit with the restricted maximum likelihood estimation unless nested models were compared. The AIC was used to compare models with different residual correlation structure, different random effects levels and the EIP with different bandwidths. The final model was utilized to compare the EIP calculated with bandwidths of 5–60 km. The model was fit with an exponential correlation structure to the errors, stratified by three temperature profiles (low = 3–7°C, medium = 8–19°C and high = 12–16°C). The exponential correlation structure was selected to account for non-uniform time gaps between observations.

The model assumptions of linearity, homogeneity of variance and normality of residuals were assessed graphically for each level of the hierarchy (additional details found in Appendix S1). The linearity of temperature effects was evaluated using locally weighted scatterplot smoothing (LOWESS) plots of the outcome against the temperature for each treatment. A quadratic regression and fractional polynomial regression were used to evaluate other transformations of the interaction term that could improve the model fit.

The effect of the loss of observations with the inclusion of the $baseline_{AF}$ predictor was evaluated (additional details found in Appendix S1). The predicted temperatures for each treatment were calculated for the BMA 1 at the median values (in brackets) of IIP_{AF} (1.5), IIP_{PAAM} (2.0), EIP_{AF} at 10 km (0.3) and $baseline_{AF}$ (2.3).

All analyses, unless otherwise specified, were carried out in Stata® (2019, StataCorp), and statistical significance was set at $p < .050$.

3 | RESULTS

3.1 | Descriptive statistics of the observations modelled

There was a total of 11,658 observations and 2,398 segments included in the final multivariable linear mixed model for the abundance of AF sea lice in Atlantic salmon sites in the Bay of Fundy between 2009 and 2018. Segments had on average 8.3 observations across an average of 70.2 days. The BMA 1, 2A, 2B, 3A, 3B and 3C were included and had an average of 1,943.0 observations per group and 400.0 segments per group (Table 1). Observations were most frequent in the BMA 1 and 2A (48.1% and 28.9%, respectively). The most frequent observations were found in the highest temperature category (12–16°C), followed by the middle (8–11°C), and lowest categories (3–7°C; Table 2). A total of 62 sites produced 114 site cycles; 28 sites (45.2%) had a single production cycle, 19 sites (30.7%) had 2, 12 sites (19.4%) had 3, and 3 sites (4.8%) had 4 production cycles. There was a total of 685 cages that produced a total of 1,001 cage-cycles.

The normalized count of AF sea lice (AF count divided by the number of fish counted and offset by 1) was strongly right skewed. Therefore, these observations were log-transformed to obtain the abundance of AF sea lice (Equation 1). The abundance of AF sea lice (i.e. outcome [Equation 1]) had a mean of 1.20 (*SD* 1.52). The IIP_{AF} and EIP_{AF} had means of 1.15 (*SD* 1.34) and 0.28 (*SD* 0.36), respectively (Table 3). The $baseline_{AF}$ had mean was 1.84 (*SD* 1.44). The IIP_{PAAM} was 1.96 (*SD* 1.20). The inclusion of $baseline_{AF}$ as a predictor in the model resulted in the loss of 6,104 observations and 1,325 segments. The average EIP_{AF} with a bandwidth of 10 km was 0.28 (*SD* 0.36). The range of seaway distances among the centroid locations of sites in our study area was 0.4 to 79.2 km. The median seaway distance for the modelled sites was 26.1 km.

Azamethiphos was applied the most frequently (n_{obs} = 7,021, n_{seg} = 1,491) of all the treatments (Figure 2). The tarpaulin method of application was the most common method of application for azamethiphos (n_{obs} = 5,491, n_{seg} = 1,228). The Hydrolicer® use was started in 2018 and had the fewest applications (n_{obs} = 58, n_{seg} = 12). Treatments were applied differently within the study area. Deltamethrin (Alpha Max®) was applied in the BMA 1 and 2a and only prior to 2012 (when it was available for emergency use). The Hydrolicer® (Hydrolicer Production AS) was utilized in the BMA 3A and 3B. Azamethiphos, warm water and hydrogen peroxide treatments were applied in most of the BMAs at some point during the study period. The choice of treatments varied by temperature,

TABLE 1 Number of observations and segments per hierarchical level

		Observations per group			Segments per group		
Group var.	No. groups	Min.	Mean	Max.	Min.	Mean	Max.
BMA	6	86	1,943.0	5,609	18	400.0	1,173
Site	62	6	356.5	698	1	38.7	178
Site-cycle[a]	114	1	102.3	418	1	21.0	121
Cage	685	1	17.0	80	1	3.5	17
Cage-cycle[a]	1,001	1	11.6	53	1	2.4	11
Segment[a]	2,398	1	4.9	19	*n*/a	*n*/a	*n*/a

Note: n = 11,658, *n*/a = not applicable.

[a]Nested groups of the final multivariable linear mixed model for the abundance of adult female *Lepeophtheirus salmonis* with an external infestation pressure weighted with a kernel density estimate that had a bandwidth of 10 km.

TABLE 2 Number of observations (number of segments) categorized by the Bay Management Areas (BMA) and three temperature profiles (temp. cat.)

BMA\Temp. cat.	3–7°C	8–11°C	12–16°C	Total BMA
1	422 (89)	2,384 (461)	2,803 (623)	5,609 (1,173)
2A	235 (33)	1,064 (174)	2,072 (472)	3,371 (679)
2B	108 (25)	209 (40)	249 (50)	566 (115)
3A	126 (33)	258 (52)	594 (127)	978 (212)
3B	202 (39)	506 (102)	340 (60)	1,048 (201)
3C	0 (0)	0 (0)	86 (18)	86 (18)
Total temp. cat.	1,093 (219)	4,421 (829)	6,144 (1,350)	11,658 (2,398)

where deltamethrin and the Hydrolicer® treatments were applied at higher temperatures (range 8.8–15.1°C and 11.2–15.6°C, respectively) compared to other treatments (range 1.8–16.2°C). The mean normalized count of AF sea lice after hydrogen peroxide treatments at each temperature was lower than the mean normalized count of AF sea lice for other treatments.

The application of an in-feed treatment prior to a segment occurred for most of the modelled segments (n_{seg} = 2,053). The mean abundance of AF sea lice after topical treatment was not significantly different following the application of in-feed treatment (t = −0.66, p =.509).

3.2 | Final model

The final multilevel mixed-effects linear regression model included the variables IIP_{AF}, IIP_{PAAM}, EIP_{AF} weighted with a KDE bandwidth of 10 km, $baseline_{AF}$, BMAs, temperature and treatments, and their interaction (Table 4). It had site cycle, cage cycle, and segment random effects with an exponential correlation structure to the errors, stratified by three temperature profiles. The in-feed treatment dichotomous variable was non-significant (coefficient = −0.092, p = .179) and was not retained in the final model. No violations of model assumptions of linearity, homoscedasticity and normality were observed.

3.3 | Fixed effects

3.3.1 | Internal and external infestation pressures

The IIP_{AF} and IIP_{PAAM} were significant predictors in the final model (both p < .001). An increase of the IIP_{AF} by one unit affected the abundance of AF sea lice by a factor of 1.207 (i.e. a relative increase of 20.7%) when other predictors remained constant. Similarly, a one unit increase in the IIP_{PAAM} resulted in a relative increase of the abundance of AF sea lice by 11.0%.

The EIP_{AF} with a KDE bandwidth of 10 km was a significant predictor for the outcome (p < .001). The predictor remained significant at p < .001 for KDE bandwidths of 5–60 km. The coefficient of the EIP_{AF} had a bimodal distribution with increasing KDE bandwidths; a peak occurred at the 13 km bandwidth (Figure 3 [range for 40–60 km not displayed in graph]). The estimated coefficient was smallest at a bandwidth of 5 km and had a second nadir at 25 km. The model fit with the EIP_{AF} weighted with a KDE with a 10 km bandwidth had the lowest AIC. The AIC decreased with KDE bandwidths of 5 to 9 km with a range of ΔAIC of 0.4 to 24.8. The ΔAIC increased to 51.0 at 40 km. The abundance of AF sea lice increased by 61.2% for every increase of one unit of the EIP_{AF} 10 km predictor when other predictors remained constant.

3.3.2 | Baseline abundances of AF sea lice

The $baseline_{AF}$ was a significant predictor in the final model (p < .001). A one unit increase in the $baseline_{AF}$ resulted in an increase of 33.3% of the AF sea lice abundance when other predictors remained constant.

3.3.3 | Temperature, treatments and their interaction

Treatments and the treatment–temperature interaction were significant predictors in the final model (Wald Chi-square tests, p <.001). A quadratic regression and polynomial regression of temperature with default powers and two dimensions did not provide an improvement to the linear treatment–temperature interaction. The association between the abundance of AF sea lice and temperature was linear for most treatments; the azamethiphos applied by skirt and warm water by well-boat treatments had a slight curve, while the azamethiphos applied by tarpaulin had a stronger curving trend line.

The abundance of AF sea lice decreased with increasing temperature for the treatments deltamethrin, and azamethiphos applied by tarpaulin and well-boat as demonstrated in Figure 4 using median values for the average abundances of AF sea lice in BMA 1. With the same reference values, the estimated abundance of AF sea lice increased with increasing temperature for the treatments azamethiphos applied by skirt, warm water and hydrogen peroxide.

At the median temperature (11.7°C), deltamethrin, azamethiphos by well-boat, warm water and hydrogen peroxide treatments were estimated to decrease AF sea lice abundances by 4.0%, 34.8%, 38.0%, and 28.5%, respectively (data not shown; snapshot of data from Figure 4). The application of azamethiphos by skirt resulted in an increased of the abundance of AF sea lice by 46.2% at the median temperature.

TABLE 3 Descriptive statistics for the variables potentially predicting the outcome variable of the abundance of adult female (AF) *Lepeophtheirus salmonis* sea lice

Variable	Variable description	Mean (*SD*)	Mean (*SD*) abundance of AF sea lice after treatment	AIC
IIP_{AF}	Temporal weighted average abundance of AF sea lice with 21 day time lag	1.15 (1.34)		31,511
IIP_{PAAM}	Temporal weighted average abundance of PAAM with 28 day time lag	1.96 (1.20)		32,094
EIP_{AF}	Temporal and KDE spatial weighted average abundance of AF sea lice with 21 day time lag	0.28 (0.36)		31,852
$Baseline_{AF}$	Abundance of AF sea lice within and including 7 days prior to topical treatment	1.84 (1.44)		31,327
Temperature	Sea surface temperature from UKMO OSTIA product (°C)	11.34 (2.49)		32,374
Treatment	Topical treatment that was applied at the start of a segment			
Azamethiphos Tarpaulin			1.90 (1.29)	32,479
Azamethiphos Skirt			1.51 (1.64)	
Azamethiphos Well-boat			0.84 (1.69)	
Deltamethrin			1.80 (1.07)	
Treatment				
Warm water			1.31 (1.27)	
Hydrolicer®			2.43 (0.94)	
Hydrogen peroxide			0.78 (1.39)	
In-feed treatment	Emamectin benzoate or avermectin was applied to a cage prior to the start of a segment			
No			1.18 (1.67)	32,483
Yes			1.20 (1.43)	

Note: Results of the univariate linear mixed model are summarized by the Akaike's information criterion (AIC; null model AIC = 32,486). *SD*: standard deviation; IIP: internal infestation pressure; PAAM: pre-adult and adult male sea lice; EIP: external infestation pressure; $n = 11,658$.

3.3.4 | Bay management areas

The BMAs were non-significant in the final model (Wald Chi-square test, $p = .108$). The univariate linear mixed model with the BMAs produced an AIC of 32,478, which was slightly smaller than the null model AIC of 32,486. The BMAs were retained as a fixed effect in the final model as a potential cofounder.

3.4 | Random effects

The site-cycle random effect had a variance of 0.14 (95% confidence interval [CI] 0.10–0.21). The variances of the cage-cycle and random effects were near zero. The residual variances accounted for 80.0 to 91.6% of the total variance in the final model. The intraclass correlation coefficient (ICC) for 2 observations in the same site-cycle was between 0.09 and 0.20. The autocorrelation of the errors was between 0.92 and 0.94 per day difference.

4 | DISCUSSION

4.1 | Contributions of internal and external infestation pressure

This study had the objective to estimate the impact of the infestation pressures on the abundances of sea lice for the Atlantic salmon aquaculture sites of the Bay of Fundy, NB. The estimated infestation pressures had a significant impact on the abundance of AF for the NB aquaculture sites.

The model estimated the EIP had a dispersal distance of AF abundance of 10 km for the NB aquaculture sites using empirical evidence. This displacement distance is near the extrapolated 8 km proposed by Nelson et al., (2017) based on approximate mean flow rates of 10 cm/s around sites. This result was similar to previously reported estimates from Norway (Aldrin et al., 2013), Scotland (Amundrud & Murray, 2009; Gillibrand & Willis, 2007; Murray & Gillibrand, 2006) and Grand Manan (Elghafghuf et al., 2020). Other

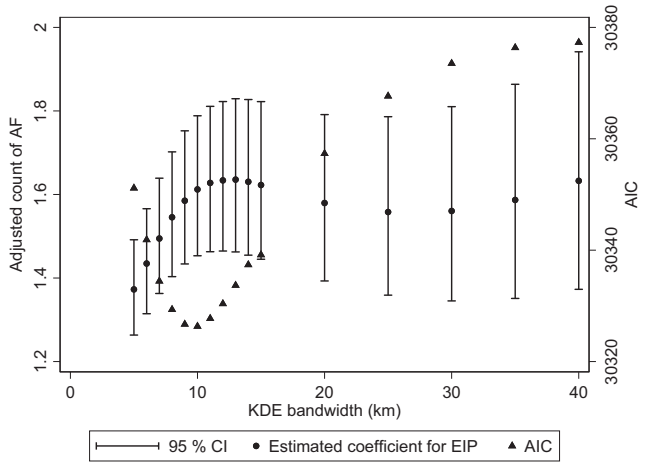

FIGURE 2 Boxplots of the mean normalized count of adult female (AF) *Lepeophtheirus salmonis* sea lice after treatment (AF count divided by the number of fish counted and offset by 1) included in the final multivariable linear mixed model with an external infestation pressure weighted with a kernel density estimate that had a bandwidth of 10 km. Counts were categorized by treatment (D: deltamethrin, AT: azamethiphos tarpaulin, AS: azamethiphos skirt, AW: azamethiphos well-boat, WW: warm water, Hy: Hydrolicer® and HP: hydrogen peroxide) and temperature profiles (L: 3–7°C, M: 8–11°C and H: 12–16°C). $n = 11{,}658$

studies estimated larger dispersal distances between 20 and 30 km (Krkošek et al., 2005; Asplin et al., 2011, 2014; Kristoffersen et al., 2013; Salama et al., 2013, 2016; Aldrin et al., 2019). The variability in the estimate of the EIP is likely a response to differing environments and modelling approaches. Water current characteristics, for example, are drastically different in Scotland (Murray et al., 2011) and NB, and likely have a large effect on the dispersal distance estimated. Modelling approaches likely also affect the estimate of the EIP; Aldrin et al. (2013), Aldrin et al. (2019) estimated 10 km and 20–30 km for two Norwegian rivers using different models with data from the Norwegian aquaculture industry.

The infestation pressure within sites (standardized estimated coefficient IIP_{AF}: 0.165, 95% CI 0.137–0.192) was an important predictor in the model. Our estimated IIP was larger than the estimate of zero for Grand Manan produced in the state-space model by Elghafghuf et al., (2020). This difference in IIP may be due to the transition matrix of the state-space model accounting for the development of PAAM to AF.

The IIP_{PAAM} standardized coefficient (0.075, 95% CI 0.054–0.096) was smaller than the other two estimated infestation pressures. This suggested the count of PAAM sea lice is not as important in estimating the abundance of AF sea lice. One reason may be that PAAM sea lice is a combination of adult males, and pre-adult that will mature into female and male in an approximate 1:1 ratio (Hamre et al., 2019).

The standardized estimated coefficient of the EIP_{AF} (0.114, 95% CI 0.089–0.138) was smaller than the standardized coefficient of the IIP_{AF}, but not the IIP_{PAAM}. The larger impact of the IIP compared to the EIP in this model may be associated with the length of time necessary to complete topical treatments at a site. Nelson et al., (2017) captured planktonic lice at higher concentrations near farms and posited sites amplify sea lice densities, and planktonic lice are rapidly displaced from sites, but concentrate in proximity to the originating sites. Aldrin et al., (2013) estimated the IIP of lice abundance was larger than the EIP. Based on hydrodynamic models, Adams et al., (2012) noted a higher rate of self-infestation compared to external infestation and concluded self-infestation may result in positive feedback, meaning that the population of sea lice on the site would increase over time because of the reproductive output of AF sea lice. Conversely, EIP was greater than IIP for Grand Manan (Elghafghuf et al., 2020) and Chile (Kristoffersen et al., 2013). These authors had multiple hypotheses for the larger effect of the EIP compared to the IIP: asynchronous treatments, better treatment effectiveness against adults compared to the juvenile life stages (Elghafghuf et al., 2018, 2020), flushing out of the planktonic life stages prior to the infestation of that site and improved management of sea lice infestation at their site compared to the infestation at their neighbours' sites. The methodology for estimation of IIP, EIP, environmental characteristics, sea lice densities and management, and aquaculture industry may all contribute to the differences in the effects of the EIP compared to the IIP.

Another source of variation in the estimates of infestation pressures are the lag times. In this study, the infestation pressures were defined by fixed lag times of 21 (AF) and 28 days (PAAM) to produce the outcome of the abundance of AF. Elghafghuf et al., (2020) found that a fixed lag of three weeks produced the best model fit for the outcome of the abundance of PAAM. In other studies (e.g. Aldrin et al., 2017, 2019), lags of approximately three to four weeks resulted in infestation at neighbouring sites. This lag suggests planktonic lice removed from a site by currents disperse at a low concentration (Nelson et al., 2017). During the approximate three to four weeks dispersal, the nauplii (I and II) lice develop into the copepodid prior to the encounter with a neighbouring site. The effect of lag time on the infestation pressures is unknown and should be evaluated in future sensitivity studies.

The standardized coefficient of the $baseline_{AF}$ (0.272, 95% CI 0.241–0.304) was larger than that of the infestation pressures. This was a surprising finding and suggests the infestation pressure within sites is more important for mitigation of sea lice compared to the infestation pressure originating from other sites. We hypothesize the effect is larger than the estimated infestation pressures because the $baseline_{AF}$ is the abundance prior to treatment and not an average of abundances over a 15-day window as for the IIP_{AF}, IIP_{PAAM} and EIP_{AF}.

These estimates of the internal and external infestation pressures for the Bay of Fundy, NB, have implications for the management of sites. The larger IIP compared to EIP suggests that improvement of mitigation strategies for within site control of sea lice has the potential to decrease the IIP, which contributes to maintaining the infestation within a site (Aldrin et al., 2013). The EIP of 10 km suggests that neighbouring sites within 10 km should apply synchronous treatments. This implies that the majority of sites in the Bay of Fundy, NB, need to have the common goal for sea lice treatment timing because

TABLE 4 Multivariable linear mixed model for the abundance of adult female (AF) *Lepeophtheirus salmonis* sea lice with an external infestation pressure weighted with a kernel density estimate that had a bandwidth of 10 km

Variable	Coefficient	95% Confidence interval	*p*-value
IIP_{AF}	0.188	0.156, 0.219	<.001
IIP_{PAAM}	0.095	0.069, 0.121	<.001
EIP_{AF}	0.478	0.374, 0.581	<.001
$Baseline_{AF}$	0.287	0.254, 0.320	<.001
Temperature (°C)	−0.111	−0.126, −0.096	<.001
Treatment			
Azamethiphos Tarpaulin	Baseline		<.001
Azamethiphos Skirt	−1.966	−2.624, −1.307	
Azamethiphos Well-boat	−1.492	−2.066, −0.919	
Deltamethrin	−0.953	−3.573, 1.668	
Warm water	−3.074	−3.630, −2.517	
Hydrolicer®	0.932	−3.564, 5.427	
Hydrogen peroxide	−2.134	−2.387, −1.881	
Treatment-Temperature interaction			
Azamethiphos Tarpaulin × Temp	Baseline		<.001
Azamethiphos Skirt × Temp	0.200	0.149, 0.252	
Azamethiphos Well-boat × Temp	0.091	0.042, 0.139	
Deltamethrin × Temp	0.078	−0.141, 0.297	
Temperature–treatment interaction			
Warm water × Temp	0.222	0.176, 0.267	
Hydrolicer® × Temp	−0.020	−0.363, 0.323	
Hydrogen peroxide × Temp	0.154	0.131, 0.176	
BMA			
1	Baseline		.108
2A	−0.015	−0.230, 0.200	
2B	−0.269	−0.571, 0.033	
3A	0.269	−0.043, 0.581	
3B	−0.005	−0.257, 0.247	
3C	−0.494	−1.196, 0.208	
Constant	1.521	1.284, 1.758	

Note: Temperature: sea surface temperature; IIP: internal infestation pressure; EIP: external infestation pressure; PAAM: pre-adult and adult male sea lice; $n = 11{,}658$.

more than 75% of sites had less than 1 km seaway distance from their nearest neighbour (Chang et al., 2011). The limited number of well-boats and tarpaulin systems presents a logistical constraint to synchronizing the treatments of entire sites in tandem; in-feed sea lice treatments are a potential method for the synchronized treatment of sea lice at multiple sites that avoids the requirement for additional equipment purchases. The EIP also has implications for the stocking of sites after fallowing and shortly after treatments because under these scenarios the sites have low to no abundances of sea lice (Aldrin et al., 2013; Kristoffersen et al., 2013, 2014).

4.2 | Treatments and temperature

Temperature had a significant effect on sea lice abundance. Temperature is an important controlling factor for sea lice as demonstrated under laboratory (Hamre et al., 2019), simulation and modelling (Revie et al., 2005; Stien et al., 2005; Stucchi et al., 2011), and field conditions (Samsing et al., 2016). The time spent in each life stage was observed to decrease with increasing temperature (Samsing et al., 2016; Stien et al., 2005). Samsing et al., (2016) observed that the proportion of copepodids that successfully attached out of the total number of copepodids in the suspension (infestation success) was highest at 10°C compared to 5°C and 20°C.

The effects of temperature on the outcome varied by treatment. There are multiple contributing factors to this association: the treatment dosage and exposure time, method of application and efficacy. Sea lice treatments are prescribed within an acceptable range of dosage and exposure time (Burridge et al., 2010). For example, hydrogen peroxide prescription guidelines are for application between 8 and 13°C (Overton et al., 2017, 2019); at low temperatures, there is poor treatment efficacy (Treasurer et al., 2000); and

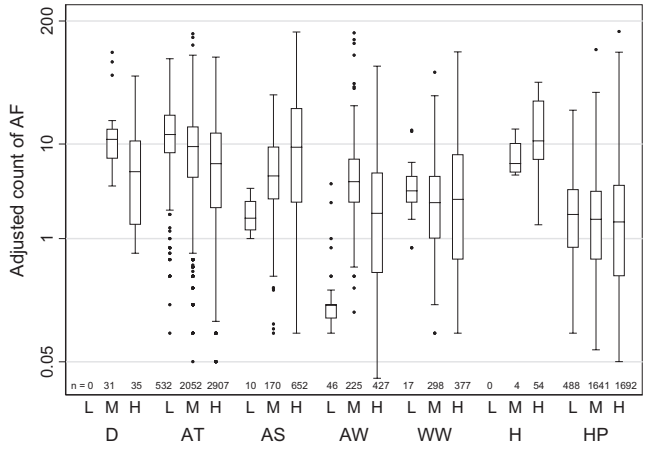

FIGURE 3 Estimated mean normalized count of adult female (AF) *Lepeophtheirus salmonis* sea lice (AF count divided by the number of fish counted and offset by 1) after treatments applied in the Bay Management Area (BMA) 1 against sea surface temperature at median values of the continuous predictors of the final multivariable linear mixed model with an external infestation pressure weighted with a kernel density estimate that had a bandwidth of 10 km. D: deltamethrin, AT: azamethiphos tarpaulin, AS: azamethiphos skirt, AW: azamethiphos well-boat, WW: warm water, and HP: hydrogen peroxide. The Hydrolicer® was not applied in BMA 1 between 2009 and 2018

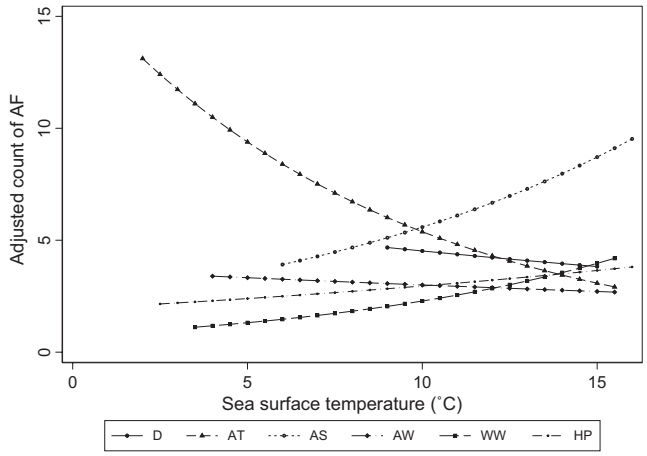

FIGURE 4 Estimated exponentiated coefficient and 95% confidence interval (CI) for the external infestation pressure (EIP) predictor weighted with a Gaussian kernel density estimate (KDE) and the Akaike's information criterion (AIC) reported from the multivariable linear mixed model for the abundance of adult female (AF) *Lepeophtheirus salmonis* sea lice where the bandwidth of the KDE was increased from 5 to 40 km. Scale is the mean normalized count of AF sea lice after treatment (AF count divided by the number of fish counted and offset by 1)

at high temperatures, there is potential for high salmon mortality (Thomassen, 1993). Between 8 and 13°C, the dosage of hydrogen peroxide needed to achieve similar efficacy decreases with increasing water temperature (Overton et al., 2017, 2019).

We found that the effect of hydrogen peroxide treatments was diminished with increasing temperature. Perhaps the exposure time was shortened for the application of hydrogen peroxide treatments at higher water temperatures, resulting in decreased activity time on the sea lice and thus reduced effectiveness of this treatment. An alternative, proposed by Overton et al., (2017), was to apply hydrogen peroxide treatment to salmon pumped from cages into the well-boat that contains cold sea water chilled on the boat or sourced from greater depths or a land-based facility.

The abundance of AF sea lice was decreased after warm water treatment, but this effect was diminished with increasing temperatures. This finding may be due to the acclimation of the sea louse to temperature change stress. Under laboratory settings, nauplii were demonstrated to adapt to a temperature rise of 20°C after acclimation at 10°C (Borchel et al., 2018). The ability to survive a drastic rise in temperature was dependent on the acclimation temperature as demonstrated with the water flea, *Daphnia pulex* (Leydig; Williams et al., 2012).

The method of application influenced the treatment response on the abundance of AF sea lice. Azamethiphos by skirt resulted in an increase of the abundance of AF sea lice as compared to the tarpaulin and well-boat methods of application for all temperatures. We suggest that the skirt provided poor control of the treatment compared to the other 2 methods of application. The skirt application method involved enclosing only the sides of a cage while keeping the bottom open and stopped being used in the region by 2013. The tarpaulin and well-boat methods provide complete enclosure of the water used for treatment, and since 2013 have been the only available methods to administer azamethiphos.

The predictor of in-feed treatment applied prior to a segment was non-significant in the final model. We anticipate the effect was minimal because in-feed treatments were frequently applied, and there may be resistance to the in-feed treatments (e.g. Jones et al., 2013; Whyte et al., 2013) reducing the impact of the variable in the model. Additionally, this predictor was particularly prone to information bias, where treatment durations may not have overlapped very well with segment lengths. Specifically, segments may have been mislabelled if the duration of the application of in-feed treatment extended only a few days into the segment and the half-life of the chemotherapeutic agent was shorter than the length of the segment. In-feed treatments do not have an immediate sea lice response and have a much longer duration of impact making them more difficult to assess independently of the other factors. Proper evaluation of in-feed treatments would require a different modelling approach than was used in this study.

4.3 | Hierarchical levels

The BMA are a unique example of zonal health management and were retained in the model despite being a non-significant predictor. This finding may imply that the BMA boundaries are not optimally effective for the management of *L. salmonis*; importantly, the BMA were designed for the management of ISAv and not specifically for sea lice (Chang et al., 2011).

Most of the variance in the abundance of AF sea lice occurred at the residual level; the variance was strongly temperature dependent. The estimated ICC for cage-cycle were much lower than the ICC estimated from another study in our study area. Elmoslemany et al., (2013) reported clustering of cages within sites with ICC values of 0.60 for AF and 0.78 for PAAM sea lice counts reported in 2011. This discrepancy may be due to the exclusion of treatments and the use of segments. Elmoslemany et al., (2013) excluded treatments as a variable in the analyses; this would increase the variability explained at the cage level. Our analysis included segments as a hierarchical level within cage-cycles. The inclusion of segments would reduce cage level clustering.

4.4 | Study design and limitations

4.4.1 | Study design

This was a retrospective cohort study that utilized complex historical data with integral hierarchical structures. The linear mixed model was selected because it is well adapted to these types of data. The model allowed for estimation of infestation pressures in the Bay of Fundy, NB, using the Fish-iTrends database.

The EIP was estimated from seaway distances between sites. Ideally, the dispersion of sea lice that contribute to the estimated EIP should be validated using sentinel cages (Salama et al., 2013; Sandvik et al., 2016). However, there may be discrepancies between abundances of sea lice measured at sites and from sentinel cages (Salama et al., 2018). Alternatively, investigating the genetic parentage of individual sea lice could improve the knowledge of lice dispersion locally (Cantrell et al., 2020).

The EIP can also be estimated from hydrodynamic models. Therefore, future research with these data will estimate the EIP using an updated hydrodynamic model for the Bay of Fundy, NB. Multiple estimates of the EIP will be generated for different scenarios such as storm events with high winds and annual freshwater input secondary to snow and ice melting (i.e. spring freshet) using methods similar to Filgueira et al., (2012). The EIP will be estimated from matrices of averaged volumetric water exchange for each link of the finite element grid of the hydrodynamic model (Filgueira et al., 2012).

4.4.2 | Limitations

The final model estimated the coefficients for the IIP and EIP that are averages in time and space. The infestation pressures were estimated for many of the sites in the Bay of Fundy, NB, for the years 2009 to 2018. The application of different methods to the dataset may reveal variability in the impact of infestation pressures estimated (e.g. Cantrell et al., 2019; Kristoffersen et al., 2014).

The estimates of infestation pressure from this study demonstrated the potential for larval infestation. The fixed lag approach to the estimates of infestation pressure means that the biological effects of temperature cannot be separated from salinity. We know from previous studies that low salinity increases sea lice mortality rates and higher temperatures increase sea lice development rates (Groner et al., 2016; Stien et al., 2005). Due to high tidal exchanges, salinity in this area of the Bay of Fundy, NB, does not vary greatly and remains near the optimal salinity (30 PSU; Chang et al., 2011; Page et al., 2015) for sea lice development and infestation (Arriagada et al., 2016; Bricknell et al., 2006). Therefore, a quantitative life cycle approach could be applied (Kristoffersen et al., 2014) to evaluate the rates of development and mortality in the light of temperature variation in our study area. However, Elghafghuf et al., (2020) found that the quantitative life cycle approach did not perform better compared the fixed lag approach.

The fixed lag approach can be utilized to evaluate the effects of temperature variation, and other environmental parameters such as weather and wind when combined with hydrodynamic modelling. Hydrodynamic models will inform the estimates of the EIP, and these effects will be evaluated in future studies. The model was limited to the available data in Fish-iTrends. There were no data from the neighbouring Maine Atlantic salmon aquaculture sites in the Bay of Fundy. There were no records of the spatial and temporal distribution of cages within sites, and the number of salmon stocked in cages. A sensitivity analysis evaluated a range of 270–840 thousand stocked fish and found little change in the estimated coefficients for the IIP and EIP (Elghafghuf et al., 2020). Kristoffersen et al., (2014) concluded that the EIP was proportional to the abundance of salmon at neighbouring sites. Therefore, the Fish-iTrends database would improve its usefulness for infestation pressure investigations if stocking densities and fish biomass were included.

This model cannot characterize the movement of sea lice in and out of sites (influx and outflux) as performed by other researchers (Adams et al., 2012; Cantrell et al., 2018). Data on the interactions between sites as performed with hydrodynamic connectivity studies may provide useful information in conjunction to the findings in this study.

Inherent to this retrospective cohort study is potential for misclassification and selection bias, and measurement error. Misclassification bias would occur when site staff counters recorded no sea lice (n_{obs} = 733) when the fish was actually infested. Measurement errors would occur due to the variability of site staff counter experience (Elmoslemany et al., 2013). Measurement error may be most likely to occur with larger numbers of sea lice on a fish (Aldrin et al., 2013). Measurement error may be present in the UKMO sea surface temperature remote sensing product as proximity to land may result in temperature contamination of the temperature at low resolutions. There is also the possibility for selection bias due to non-random sampling of salmon (Gautam et al., 2016) and the use of the $baseline_{AF}$ predictor in the model. The $baseline_{AF}$ reduced the total number of observations and was evaluated further in a small sensitivity study (additional details found in Appendix S1). We expect these biases and errors to be homogeneous across the study period and area. Furthermore, we expect the presence of any biases or errors in our model to move the effects towards the null hypothesis.

5 | CONCLUSIONS

Our objective is to estimate the impact of the infestation pressures on the abundances of *L. salmonis* sea lice for the Bay of Fundy, NB. The abundance of AF sea lice was modelled using a multivariable linear mixed model to obtain estimates of the IIP and EIP using the Fish-iTrends database. The effect of the IIP and EIP on the abundances of AF was significant in the final model. The EIP with a Gaussian KDE bandwidth of 10 km had the lowest AIC and represents the dispersal distance for infestation of a neighbouring site, which is consistent with previous findings in regional and global areas with salmon aquaculture. Future research will focus on improving the estimate of the EIP with hydrodynamic data and evaluating the infestation pressures under different scenarios. We conclude from this study that site management of sea lice has its greatest impact on the site in question and synchronizing treatments between sites remains an important component of overall success in controlling sea lice at fish farms in Bay of Fundy.

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CONFLICT OF INTEREST

The authors certify that they have no financial and non-financial interests related to the contents of this manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the Atlantic Canada Fish Farmers Association (ACFFA). Restrictions apply to the availability of these data, which were used under license for this study. Data are available from the authors with the permission of ACFFA.

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REFERENCES

Abolofia, J., Asche, F., & Wilen, J. E. (2017). The Cost of lice: Quantifying the impacts of parasitic sea lice on farmed salmon. *Marine Resource Economics*, *32*, 329–349. https://doi.org/10.1086/691981

Adams, T., Black, K., Macintyre, C., Macintyre, I., & Dean, R. (2012). Connectivity modelling and network analysis of sea lice infection in Loch Fyne, west coast of Scotland. *Aquaculture Environment Interactions*, *3*, 51–63. https://doi.org/10.3354/aei00052

Aldrin, M., Huseby, R. B., Stien, A., Grøntvedt, R. N., Viljugrein, H., & Jansen, P. A. (2017). A stage-structured Bayesian hierarchical model for sea lice populations at individual salmon farms - Estimated from multiple farm data sets. *Ecological Modelling*, *359*, 333–348.

Aldrin, M., Jansen, P. A., & Stryhn, H. (2019). A partly stage-structured model for the abundance of sea lice in salmonid farms. *Epidemics*, *26*, 9–22. https://doi.org/10.1016/j.epidem.2018.08.001

Aldrin, M., Storvik, B., Kristoffersen, A. B., & Jansen, P. A. (2013). Space-time modelling of the spread of sea lice between and within Norwegian marine salmon farms. *PLoS One*, *8*, 1–10. https://doi.org/10.1371/journal.pone.0064039

Amundrud, T. L., & Murray, A. G. (2009). Modelling sea lice dispersion under varying environmental forcing in a Scottish sea loch. *Journal of Fish Diseases*,*32*,27–44.https://doi.org/10.1111/j.1365-2761.2008.00980.x

Arriagada, G., Vanderstichel, R., Stryhn, H., Milligan, B., & Revie, C. W. (2016). Evaluation of water salinity effects on the sea lice *Lepeophtheirus salmonis* found on farmed Atlantic salmon in Muchalat Inlet, British Columbia, Canada. *Aquaculture*, *464*, 554–563. https://doi.org/10.1016/j.aquaculture.2016.08.002

Asplin, L., Boxaspen, K. K., & Sandvik, A. D. (2011). Modeling the Distribution and Abundance of Planktonic Larval Stages of *Lepeophtheirus salmonis* in Norway. In S. Jones, & R. Beamish (Eds.). *Sea lice: An Integrated Approach to Understanding Parasite Abundance and Distribution* (1st ed., p. 726). John Wiley & Sons, Inc.

Asplin, L., Johnsen, I. A., Sandvik, A. D., Albretsen, J., Sundfjord, V., Aure, J., & Boxaspen, K. K. (2014). Dispersion of sea lice in the Hardangerfjord. *Marine Biology Research*, *10*, 216–225. https://doi.org/10.1080/17451000.2013.810755

Barker, S. E., Bricknell, I. R., Covello, J., Purcell, S. L., Fast, M. D., Wolters, W., & Bouchard, D. A. (2019). Sea lice, Lepeophtheirus salmonis (Krøyer 1837), infected Atlantic salmon (Salmo salar L.) are more susceptible to infectious salmon anemia virus. *PLoS One*, *14*(1), 1–28. https://doi.org/10.1371/journal.pone.0209178

Borchel, A., Komisarczuk, A. Z., Rebl, A., Goldammer, T., & Nilsen, F. (2018). Systematic identification and characterization of stress-inducible heat shock proteins (HSPs) in the sea louse (*Lepeophtheirus salmonis*). *Cell Stress & Chaperones*, *23*, 127–139. https://doi.org/10.1007/s12192-017-0830-9

Bricknell, I. R., Dalesman, S. J., O'Shea, B., Pert, C. C., & Luntz, A. J. M. (2006). Effect of environmental salinity on sea lice *Lepeophtheirus salmonis* settlement success. *Diseases of Aquatic Organisms*, *71*, 201–212. https://doi.org/10.3354/dao071201

Burridge, L., Weis, J. S., Cabello, F., Pizarro, J., & Bostick, K. (2010). Chemical use in salmon aquaculture: A review of current practices and possible environmental effects. *Aquaculture*, *306*, 7–23. https://doi.org/10.1016/j.aquaculture.2010.05.020

Cantrell, D., Filgueira, R., Revie, C. W., Rees, E. E., Vanderstichel, R., Guo, M., Foreman, M. G. G., Wan, D. I., & Grant, J. (2019). The relevance of larval biology on spatiotemporal patterns of pathogen connectivity among open-marine salmon farms. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*, 505–519. https://doi.org/10.1139/cjfas-2019-0040

Cantrell, D. L., Groner, M. L., Ben-Horin, T., Grant, J., & Revie, C. W. (2020). Modeling pathogen dispersal in marine fish and shellfish. *Trends in Parasitology*, *36*, 239–249. https://doi.org/10.1016/j.pt.2019.12.013

Cantrell, D. L., Rees, E. E., Vanderstichel, R., Grant, J., Filgueira, R., & Revie, C. W. (2018). The use of kernel density estimation with a bio-physical model provides a method to quantify connectivity among salmon farms: Spatial planning and management with epidemiological relevance. *Frontiers in Veterinary Science*, *5*, 1–14. https://doi.org/10.3389/fvets.2018.00269

Chang, B. D., Page, F. H., Beattie, M. J., & Hill, B. W. H. (2011). Sea Louse Abundance on Farmed Salmon in the Southwestern New Brunswick Area of the Bay of Fundy. In S. Jones, & R. Beamish (Eds.). *Sea lice: An Integrated Approach to Understanding Parasite Abundance and Distribution* (1st ed., p. 726). John Wiley & Sons, Inc.

Costello, M. J. (2006). Ecology of sea lice parasitic on farmed and wild fish. *Trends in Parasitology*, *22*, 475–483. https://doi.org/10.1016/j.pt.2006.08.006

Department of Energy and Resource Development/Agriculture, Aquaculture, and Fisheries (2017). *Bay of Fundy Marine Aquaculture Sites* [map]. 1:125000. New Brunswick, Canada.

Elghafghuf, A., Vanderstichel, R., Hammell, L., & Stryhn, H. (2020). Estimating sea lice infestation pressure on salmon farms: Comparing different methods using multivariate state-space models. *Epidemics*, *31*, 100394. https://doi.org/10.1016/j.epidem.2020.100394

Elghafghuf, A., Vanderstichel, R., St-Hilaire, S., & Stryhn, H. (2018). Using state-space models to predict the abundance of juvenile and adult sea lice on Atlantic salmon. *Epidemics*, *24*, 76–87. https://doi.org/10.1016/j.epidem.2018.04.002

Elmoslemany, A., Whyte, S. K., Revie, C. W., & Hammell, K. L. (2013). Sea lice monitoring on Atlantic salmon farms in New Brunswick, Canada: Comparing audit and farm staff counts. *Journal of Fish Diseases*, *36*, 241–247. https://doi.org/10.1111/jfd.12051

Fast, M. D. (2014). Fish immune responses to parasitic copepod (namely sea lice) infection. *Developmental and Comparative Immunology*, *43*, 300–312. https://doi.org/10.1016/j.dci.2013.08.019

Filgueira, R., Grant, J., Bacher, C., & Carreau, M. (2012). A physical-biogeochemical coupling scheme for modeling marine coastal ecosystems. *Ecological Informatics*, *7*, 71–80. https://doi.org/10.1016/j.ecoinf.2011.11.007

Gautam, R., Boerlage, A. S., Vanderstichel, R., Revie, C. W., & Hammell, K. L. (2016). Variation in pre-treatment count lead time and its effect on baseline estimates of cage level sea lice abundance. *Journal of Fish Diseases*, *39*, 1297–1303. https://doi.org/10.1111/jfd.12460

Gautam, R., Vanderstichel, R., Boerlage, A. S., Revie, C. W., & Hammell, K. L. (2017a). Effect of timing of count events on estimates of sea lice abundance and interpretation of effectiveness following topical treatments. *Journal of Fish Diseases*, *40*, 367–375. https://doi.org/10.1111/jfd.12519

Gautam, R., Vanderstichel, R., Boerlage, A. S., Revie, C. W., & Hammell, K. L. (2017b). Evaluating topical treatment effectiveness in the control of sea lice burdens on Atlantic salmon in New Brunswick, Canada. *Journal of Fish Diseases*, *40*, 895–905. https://doi.org/10.1111/jfd.12569

Gillibrand, P. A., & Willis, K. J. (2007). Dispersal of sea louse larvae from salmon farms: Modelling the influence of environmental conditions and larval behaviour. *Aquatic Biology*, *1*, 63–75. https://doi.org/10.3354/ab00006

Groner, M. L., Mcewan, G. F., Rees, E. E., Gettinby, G., & Revie, C. W. (2016). Quantifying the influence of salinity and temperature on the population dynamics of a marine ectoparasite. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*, 1281–1291. https://doi.org/10.1139/cjfas-2015-0444

Hamre, L., Bui, S., Oppedal, F., Skern-Mauritzen, R., & Dalvin, S. (2019). Development of the sea louse *Lepeophtheirus salmonis* parasitic stages in temperatures ranging from 3 to 24°C. *Aquaculture Environment Interactions*, *11*, 429–443. https://doi.org/10.3354/aei00320

Hamre, L. A., Eichner, C., Caipang, C. M. A., Dalvin, S. T., Bron, J. E., Nilsen, F., & Skern-Mauritzen, R. (2013). The sea louse *Lepeophtheirus salmonis* (Copepoda: Caligidae) life cycle has only two chalimus stages. *PLoS One*, *8*(9), 1–9. https://doi.org/10.1371/journal.pone.0073539

Hogans, W. E., & Trudeau, D. J. (1989). *Preliminary studies on the biology of sea lice*, Caligus elongatus, Caligus curtus *and* Lepeophtheirus salmonis *(Copepoda: Caligoida) parasitic on cage-cultured salmonids in the lower Bay of Fundy*. Canadian Technical Report of Fisheries and Aquatic Sciences, Vol. *1715*. St. Andrews, NB: Department of Fisheries and Oceans.

Hijmans, R. J., van Etten, J., Sumner, M., Cheng, J., Baston, D., Bevan, A., … Wueest, R. (2019). *raster: Geographic Data Analysis and Modeling. R package version 3.0-12*. https://CRAN.R-project.org/package=raster

Hogans, W. E. (1995). *Infection dynamics of sea lice, Lepeophtheirus salmonis (Copepoda: Caligidae) parasitic on Atlantic salmon (Salmo salar) cultured in marine waters of the lower Bay of Fundy* (Vol. *2067*). Retrieved from http://search.proquest.com/docview/16997923?accountid=27308

Igboeli, O. O., Fast, M. D., Heumann, J., & Burka, J. F. (2012). Role of P-glycoprotein in emamectin benzoate (SLICE®) resistance in sea lice, *Lepeophtheirus salmonis*. *Aquaculture*, *344–349*, 40–47. https://doi.org/10.1016/j.aquaculture.2012.03.026

Johnson, S. C., & Albright, L. J. (1991). The developmental stages of *Lepeophtheirus salmonis* (Krøyer, 1837) (Copepoda: Caligidae). *Canadian Journal of Zoology*, *69*(4), 929–950. https://doi.org/10.1139/z91-138

Johnson, S. C., Treasurer, J. W., Bravo, S., & Nagasawa, K. (2004). A review of the impact of parasitic copepods on marine aquaculture. *Zoological Studies*, *43*, 229–243.

Jones, P. G., Hammell, K. L., Dohoo, I. R., & Revie, C. W. (2012). Effectiveness of emamectin benzoate for treatment of *Lepeophtheirus salmonis* on farmed Atlantic salmon *Salmo salar* in the Bay of Fundy, Canada. *Diseases of Aquatic Organisms*, *102*, 53–64. https://doi.org/10.3354/dao02517

Jones, P. G., Hammell, K. L., Gettinby, G., & Revie, C. W. (2013). Detection of emamectin benzoate tolerance emergence in different life stages of sea lice, *Lepeophtheirus salmonis*, on farmed Atlantic salmon, *Salmo salar* L. *Journal of Fish Diseases*, *36*(3), 209–220. https://doi.org/10.1111/jfd.12022

Kristoffersen, A. B., Jimenez, D., Viljugrein, H., Grøntvedt, R., Stien, A., & Jansen, P. A. (2014). Large scale modelling of sea lice (*Lepeophtheirus salmonis*) infection pressure based on lice monitoring data from Norwegian salmonid farms. *Epidemics*, *9*, 31–39. https://doi.org/10.1016/j.epidem.2014.09.007

Kristoffersen, A. B., Qviller, L., Helgesen, K. O., Vollset, K. W., Viljugrein, H., & Jansen, P. A. (2018). Quantitative risk assessment of sea louse-induced mortality of seaward-migrating post-smolt Atlantic salmon. *Epidemics*, *23*, 19–33. https://doi.org/10.1016/j.epidem.2017.11.001

Kristoffersen, A. B., Rees, E. E., Stryhn, H., Ibarra, R., Campisto, J. L., Revie, C. W., & St-Hilaire, S. (2013). Understanding sources of sea lice for salmon farms in Chile. *Preventive Veterinary Medicine*, *111*, 165–175. https://doi.org/10.1016/j.prevetmed.2013.03.015

Krkošek, M., Lewis, M. A., & Volpe, J. P. (2005). Transmission dynamics of parasitic sea lice from farm to wild salmon. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 689–696. https://doi.org/10.1098/rspb.2004.3027

Murray, A. G., Amundrud, T. L., Penston, M. J., Pert, C. C., & Middlemas, S. J. (2011). Abundance and Distribution of Larval Sea Lice in Scottish Coastal Waters. In S. Jones, & R. Beamish (Eds.). *Sea lice: An Integrated Approach to Understanding Parasite Abundance and Distribution* (1st ed., p. 726). John Wiley & Sons, Inc.

Murray, A. G., & Gillibrand, P. A. (2006). Modelling sea lice dispersal in Loch Torridon, Scotland. *Marine Pollution Bulletin*, *53*, 128–135. https://doi.org/10.1016/j.marpolbul.2005.09.013

Nelson, E. J., Robinson, S. M. C., Feindel, N., Sterling, A., Byrne, A., & Pee Ang, K. (2017). Horizontal and vertical distribution of sea lice larvae (*Lepeophtheirus salmonis*) in and around salmon farms in the Bay of Fundy, Canada. *Journal of Fish Diseases*, *41*, 885–899. https://doi.org/10.1111/jfd.12692

Nylund, A., Hovland, T., Hodneland, K., Nilsen, F., & Lovik, P. (1994). Mechanisms for transmission of infectious salmon anaemia (ISA). *Diseases of Aquatic Organisms*, *19*, 95–100. https://doi.org/10.3354/dao019095

Nylund, A., Wallace, C., & Hovland, T. (1993). The possible role of *Lepeophtheirus salmonis* (Krøyer) in the transmission of infectious salmon anaemia. In G. A. Boxshall, & D. Defaye (Eds.), *Pathogens of Wild and Farmed Fish: Sea Lice* (pp. 367–373). Ellis Horwood.

Overton, K., Dempster, T., Oppedal, F., Kristiansen, T. S., Gismervik, K., & Stien, L. H. (2019). Sea lice treatments and salmon mortality in Norwegian aquaculture: A review. *Reviews in Aquaculture*, *11*, 1398–1417. https://doi.org/10.1111/raq.12299

Overton, K., Samsing, F., Oppedal, F., Stien, L. H., & Dempster, T. (2017). Lowering treatment temperature reduces salmon mortality: A new way to treat with hydrogen peroxide in aquaculture. *Pest Management Science*, *74*, 535–540. https://doi.org/10.1002/ps.4751

Page, F. H., Losier, R., Haigh, S., Bakker, J., Chang, B. D., McCurdy, P., & Beattie, M. (2015). *Transport and dispersal of sea lice topical therapeutants from salmon farm net-pens and well-boats*. St. Andrews, NB.

Penston, M. J., Mckibben, M. A., Hay, D. W., & Gillibrand, P. A. (2004). Observations on open-water densities of sea lice larvae in Loch Shieldaig, Western Scotland. *Aquaculture Research*, *35*, 793–805. https://doi.org/10.1111/j.1365-2109.2004.01102.x

Pinheiro, J. C., & Bates, D. M. (2000). Mixed-Effects Models in S and S-PLUS. In J. Chambers, W. Eddy, W. Hardle, S. Sheather, & L. Tierney (Eds.), *Statistics and Computing* (1st ed.). Springer-Verlag New York, Inc.

R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/

Revie, C. W., Robbins, C., Gettinby, G., Kelly, L., & Treasurer, J. W. (2005). A mathematical model of the growth of sea lice, *Lepeophtheirus salmonis*, populations on farmed Atlantic salmon, *Salmo salar* L., in Scotland and its use in the assessment of treatment strategies. *Journal of Fish Diseases*, *28*, 603–614. https://doi.org/10.1111/j.1365-2761.2005.00665.x

Salama, N. K. G., Collins, C. M., Fraser, J. G., Dunn, J., Pert, C. C., Murray, A. G., & Rabe, B. (2013). Development and assessment of a biophysical dispersal model for sea lice. *Journal of Fish Diseases*, *36*(3), 323–337. https://doi.org/10.1111/jfd.12065

Salama, N. K. G., Dale, A. C., Ivanov, V. V., Cook, P. F., Pert, C. C., Collins, C. M., & Rabe, B. (2018). Using biological–physical modelling for informing sea lice dispersal in Loch Linnhe, Scotland. *Journal of Fish Diseases*, *41*, 901–919. https://doi.org/10.1111/jfd.12693

Salama, N. K. G., Murray, A. G., & Rabe, B. (2016). Simulated environmental transport distances of *Lepeophtheirus salmonis* in Loch Linnhe, Scotland, for informing aquaculture area management structures. *Journal of Fish Diseases*, *39*, 419–428. https://doi.org/10.1111/jfd.12375

Samsing, F., Oppedal, F., Dalvin, S., Johnsen, I., Vågseth, T., & Dempster, T. (2016). Sea lice (*Lepeophtheirus salmonis*) development times, body size, and reproductive outputs follow universal models of temperature dependence. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*, 1841–1851. https://doi.org/10.1139/cjfas-2016-0050

Sandvik, A. D., Bjørn, P. A., Ådlandsvik, B., Asplin, L., Skardhamar, J., Johnsen, I. A., & Skogen, M. D. (2016). Toward a model-based prediction system for sea lice infestation pressure. *Aquaculture Environment Interactions*, *8*, 527–542. https://doi.org/10.3354/AEI00193

StataCorp (2019). *Stata: Release 16*. Statistical Software.

Stien, A., Bjørn, P. A., Heuch, P. A., & Elston, D. A. (2005). Population Dynamics of Sea Lice *Lepeophtheirus salmonis* on Atlantic Salmon and Sea Trout. *Marine Ecology Progress Series*, *290*, 263–275.

Stucchi, D. J., Guo, M., Foreman, M. G. G., Czajko, P., Galbraith, M., Mackas, D. L., & Gillibrand, P. A. (2011). Modeling Sea Lice Production and Concentrations in the Broughton Archipelago, British Columbia. In S. Jones, & R. Beamish (Eds.), *Sea lice: An Integrated Approach to Understanding Parasite Abundance and Distribution* (1st ed., p. 726). John Wiley & Sons, Inc.

Thakur, K. K., Vanderstichel, R., Barrell, J., Stryhn, H., Patanasatienkul, T., & Revie, C. W. (2018). Comparison of remotely-sensed sea surface temperature and salinity products with in situ measurements from British Columbia, Canada. *Frontiers in Marine Science*, *5*, 1–11. https://doi.org/10.3389/fmars.2018.00121

Thomassen, J. M. (1993) Hydrogen peroxide as a delousing agent for Atlantic salmon. In G. A. Boxshall, & D. Defaye (Eds.), *Pathogens of Wild and Farmed Fish: Sea Lice*, (1st ed., p. 378). Ellis Horwood Series in Aquaculture and Fisheries Support, CRC Press.

Treasurer, J. W., Grant, A., & Davis, P. J. (2000). Physical constraints of bath treatments of Atlantic salmon (*Salmo salar*) with a sea lice burden (Copepoda: Caligidae). *Contributions to Zoology*, *69*, https://doi.org/10.1163/18759866-0690102014

Tucker, C. S., Sommerville, C., & Wootten, R. (2000). The effect of temperature and salinity on the settlement and survival of copepodids of *Lepeophtheirus salmonis* (Krøyer, 1837) on Atlantic salmon, *Salmo salar* L. *Journal of Fish Diseases*, *23*, 309–320. https://doi.org/10.1046/j.1365-2761.2000.00219.x

Tully, O., & Nolan, D. T. (2002). A review of the population biology and host-parasite interactions of the sea louse *Lepeophtheirus salmonis* (Copepoda: Caligidae). *Parasitology*, *124*, S165–S182. https://doi.org/10.1017/S0031182002001889

UK Met Office (2005). *OSTIA Level 4 Sea Surface Temperature Analysis*. Ver. 1.0. PO.DAAC, CA, USA. Retrieved from https://doi.org/10.5067/GHOST-4FK01 [2020-03-21]

van Etten, J., & de Sousa, K. (2019). *gdistance: Distances and Routes on Geographical Grids. R package version 1.1-4*. https://CRAN.R-project.org/package=gdistance

Westcott, J. D., Stryhn, H., Burka, J. F., & Hammell, K. L. (2008). Optimization and field use of a bioassay to monitor sea lice *Lepeophtheirus salmonis* sensitivity to emamectin benzoate. *Diseases of Aquatic Organisms*, *79*, 119–131. https://doi.org/10.3354/dao01887

Whyte, S. K., Westcott, J. D., Elmoslemany, A., Hammell, K. L., & Revie, C. W. (2013). A fixed-dose approach to conducting emamectin benzoate tolerance assessments on field-collected sea lice, *Lepeophtheirus salmonis*. *Journal of Fish Diseases*, *36*(3), 283–292. https://doi.org/10.1111/jfd.12055

Williams, P. J., Dick, K. B., & Yampolsky, L. Y. (2012). Heat tolerance, temperature acclimation, acute oxidative damage and canalization of haemoglobin expression in Daphnia. *Evolutionary Ecology*, *26*(3), 591–609. https://doi.org/10.1007/s10682-011-9506-6

World Sea Temperature (2020). *Saint Andrews Sea Temperature*. Retrieved from https://www.seatemperature.org/north-america/canada/saint-andrews.htm [2020-08-04]

WoRMS Editorial Board (2020). *World Register of Marine Species*. VLIZ. https://doi.org/10.14284/170

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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