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Sea-louse abundance on salmon farms in relation to parasite-control policy and climate change

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The ectoparasitic copepods, sea lice (*Lepeophtheirus salmonis* and *Caligus* spp.), are major pests to salmon aquaculture and can also affect the health and survival of wild salmon. Policies exist to protect wild salmon by delousing farmed fish when louse abundance exceeds a threshold, but their effectiveness under future climate change is uncertain. We fitted a Bayesian model for sea-louse population dynamics and management to timeseries data of sea lice on farmed salmon in Pacific Canada and analysed the model under scenarios of warmer climates. We found that in high-temperature years, current parasite control policy becomes ineffective as sea-louse abundance is expected to increase. We simulated two alternative management scenarios and observed that both would decrease average louse counts on farms in high-temperature years relative to the current system but relied on more delousing treatments than are currently performed. We also found evidence that non-salmonids can play a role in louse transmission to farms, as increased farm colonization of *Caligus clemensi* occurs in April, coincident with wild herring (*Clupea pallasii*) spawner abundance. Our results highlight the need for careful management of sea lice on salmon farms in warmer years and the importance of policies designed to account for future environmental change.

Keywords: aquaculture, *Caligus clemensi*, climate change, environmental policy, herring, *Lepeophtheirus salmonis*, Pacific salmon, sea lice, temperature, wild salmon

Introduction

As aquaculture production grows and wild-capture fisheries landings continue to stagnate or decline (Food and Agriculture Organization of the United Nations, 2016a), the coexistence of farmed and wild marine fishes may well depend on effective environmental policies. Many such policies are already in place to limit disease transfer between wild and farmed fish in the marine environment (Krkosek, 2010; Olaussen, 2018), but the capacity of these policies to remain effective in varying environmental conditions is unknown. The need to understand environmental policy effectiveness in the face of climate change is exemplified by wild and farmed salmon—an expanding social–ecological system

connected by infectious disease and seafood economics (Asche and Bjorndal, 2011; Lafferty *et al.*, 2015).

Wild salmon (*Oncorhynchus* spp. and *Salmo salar*) comprise an iconic group of species that has long driven cultures, economies, and ecologies (Groot and Margolis, 1991; Jacob *et al.*, 2010; Cohen, 2012), but a large portion of wild salmon populations are declining or already extirpated (Chaput, 2012; Price *et al.*, 2017). While wild salmon fisheries have deteriorated over the past several decades, salmon-farm production has expanded the public's demand for salmon (Food and Agriculture Organization of the United Nations, 2016b). Salmon farms raise domesticated Atlantic salmon (*S. salar*) at high density in net pens that allow

unrestricted flow between the farm and the external environment. This lack of barrier eliminates the need for expensive water filtration systems that limit the profitability of land-based forms of aquaculture (Bjørndal and Tusvik, 2019) and helps make Atlantic salmon the most valuable form of aquaculture globally (Food and Agriculture Organization of the United Nations, 2016b). Flow-through net pens have auxiliary benefits in that they improve water quality and fish welfare, but they also allow the transmission of pathogens and parasites to and from wild salmon that share the same coastal waters as salmon farms (Krkosek et al., 2005). Disease transfer from salmon farms can have profound population-level effects on wild salmonids (Krkosek et al., 2013; Vollset et al., 2016) and, as has been observed in other systems with disease-sensitive ectotherms (Harvell et al., 2009), it is possible that these effects could worsen due to interactions between climate warming and disease outbreaks. Understanding how environmental change will influence disease in wild and farmed salmon may be vital for protecting vulnerable wild salmon populations—and the peoples and wildlife that depend on them—in the era of climate change.

Both farmed and wild salmon are commonly parasitized by marine copepods called sea lice (Lepeophtheirus salmonis and Caligus spp.), which feed on the mucus and surface tissue of their hosts (Costello, 2006). These ectoparasites affect their hosts by causing lesions in the skin and musculature (Carvalho et al., 2020), stimulating immune and stress responses (Fast, 2014), increasing susceptibility to secondary infections (Mustafa et al., 2000), altering foraging and risk-taking behaviours (Krkosek et al., 2011), reducing growth (Costello, 2006), and ultimately decreasing survival (Krkosek, 2010). In the absence of salmon farms, sea lice often infest wild adult Pacific salmon but only infest wild juveniles at low levels. This discrepancy is primarily a result of the two life stages not overlapping in time and space (termed "migratory allopatry"; Krkosek et al., 2007; Costello, 2009), as most adult Pacific salmon undergo a coastal migration from the Gulf of Alaska to their natal freshwater systems in the fall, while most juvenile Pacific salmon migrate the opposite direction in the spring. Salmon farms break this separation by acting as semi-permanent reservoirs of sea lice that enable louse transmission between wild and farmed salmon. Consequently, sea-louse abundances on salmon farms around the world are carefully managed under environmental policies designed to reduce sea-louse transmission to wild juvenile salmon and the resulting impacts on individuals (Dawson et al., 1999; Jones et al., 2008; Krkosek et al., 2011) and populations (Connors et al., 2010; Krkosek et al., 2013; Vollset et al., 2016). While management via delousing treatments has resulted in positive conservation outcomes for some wild salmon populations (Peacock et al., 2013), an anomalously warm year in the North Pacific in 2015 (Peterson et al., 2015) raised concerns over whether these same management strategies will continue to prevent sea-louse outbreaks in high-temperature years (Bateman et al., 2016). These concerns may be warranted given that temperature governs sea-louse development rate (Johnson and Albright, 1991; Hamre et al., 2019) and thus increases the epidemic potential of the parasite (Groner et al., 2014).

Managing the spread of pests and disease can be difficult even in relatively simple systems (Chadès et al., 2011), and these challenges increase dramatically when multiple species are involved (Woodroffe, 2006; Woolhouse and Gowtage-Sequeria, 2005; Flint and Van den Bosch, 2012). For example, bovine tuberculosis is a bacterial disease with global consequences for cattle, human, and wildlife health (Caley and Hone, 2004; Gilbert et al., 2005; Renwick et al., 2007), but efforts to control its spread have been met with limited success because the bacterium has many natural hosts (Alexander et al., 2010; Gortazar et al., 2011; Nugent, 2011). The host–parasite system of salmon and sea lice is particularly complex as it involves multiple hosts and multiple parasites. In British Columbia (BC), Canada—a unique region because it is one of the world's largest producers of both farmed and wild salmon—L. salmonis infests farmed and wild salmon, as it does elsewhere, but a second species of sea louse (Caligus clemensi) infests other nearshore marine fishes in addition to salmon. Caligus clemensi is considered to be less pathogenic than L. salmonis (Johnson et al., 2004; Igboeli et al., 2014), and although C. clemensi infestations are correlated with decreased growth (Godwin et al., 2017), competitive ability (Godwin et al., 2015), and foraging success (Godwin et al., 2018) in wild juvenile salmon, no research has been published regarding its physiological effects on hosts. It has been heavily speculated that non-salmonid hosts like Pacific herring (Clupea pallasii) act as a significant source of C. clemensi to farms, but this has never been confirmed empirically.

Here, we assess whether sea-louse counts on BC salmon farms increase in higher-temperature years and we test the capacity of current parasite control policy to remain effective as coastal waters continue to warm. We simulate two alternative management scenarios to assess their effectiveness relative to the current strategy at decreasing louse counts on farms in high-temperature years. As a secondary objective, we determine whether wild herring can play a role in the transmission of C. clemensi to salmon farms. We confront these questions by performing a comprehensive hierarchical Bayesian analysis of parasite dynamics on BC salmon farms, using a 6-year time series of industry sea-louse counts from 91 farms (Figure 1).

Methods
Data
We analysed the publicly available dataset of industry sea-louse counts between 2011 and 2016 (Fisheries and Oceans Canada, 2017c), which is managed by the Canadian federal Department of Fisheries and Oceans (DFO). This industry dataset reports monthly averages of their sea-louse sampling events; raw data are not made public. For simplicity, these monthly averages are hereafter termed "counts", and the individual sea-louse enumerations are called "sampling events". Between 0 and 6 sampling events were performed on every farm each month, with over 99% of months having between 1 and 3 sampling events per farm (mean = 1.64 events month^{-1}). Salmon-farm staff conduct the sampling events by capturing 20 fish in each of three net pens by seine and dip net, anesthetizing the fish in a bath of tricaine methanesulfonate (TMS, or MS-222), and enumerating and identifying the species of the motile (i.e. pre-adult and adult) lice on each fish by eye. The industry dataset includes the month and year for each monthly count, the farm at which the count took place, the fish health surveillance zone for the farm (Figure 1), the number of sampling events that month, the age class of the fish during the count, and the previous month's count. The dataset also included comments indicating that delousing treatments were planned or had already been performed, and from these we identified the months in which treatments likely occurred; through the end of
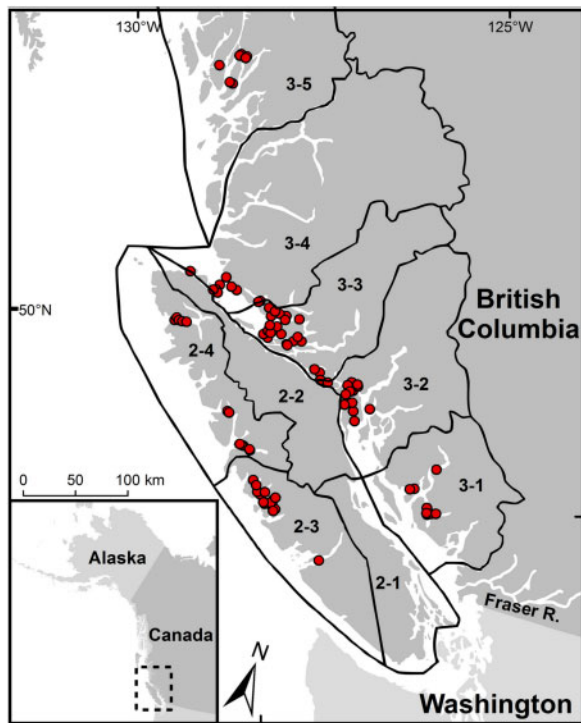
Figure 1. Locations of the 91 BC salmon farms in the industry sea lice dataset that were active (i.e. stocked with fish) for at least 1 month between 2011 and 2016. Solid black lines demarcate the boundaries of DFO fish health surveillance zones, each of which is identified by number. Figure was reproduced from Godwin *et al.* (in press).

2016, BC farms almost exclusively performed treatments using an in-feed parasiticide called emamectin benzoate (trade name SLICE®). After omitting counts lacking a full set of accompanying information ($n = 440$), we had a final dataset of 2626 monthly counts on 91 BC farms between 2011 and 2016.

DFO performs occasional, pre-arranged audits of sea-louse counts on individual farms. We previously found that industry counts are biased downwards, such that in months when DFO performs an audit, industry counts increase by ∼95% for *C. clemensi* and ∼18% for *L. salmonis* (Godwin *et al.*, in press). We therefore gathered the publicly available audit timing data (Fisheries and Oceans Canada, 2017b) and designated every monthly industry count as either "audited" or "non-audited" to later account for this bias in our model.

To estimate the relative annual abundance of wild Pacific salmon (*Oncorhynchus* spp.) in each DFO fisheries management area, we summed DFO's estimates of returning adults for every salmon population in the New Salmon Escapement Database System (NuSEDS; Fisheries and Oceans Canada, 2017d) that had data in all 6 years (2011–2016). "Populations" are defined in NuSEDS as each unique combination of spawning stream, species, and run timing. We standardized these area-specific annual abundance estimates (i.e. divided by one standard deviation) within each management area to obtain an annual index of adult salmon relative abundance for each area. The number of populations that contributed to each management area's salmon abundance index ranged from 5 to 85 (mean = 21), and the species

composition of these contributing populations varied among areas (Supplementary Table S1). We considered this acceptable for two reasons: (i) we rescaled the annual NuSEDS estimates within management areas, not among them, and (ii) our abundance indices draw from the most data-rich populations, which are likely to be indicator streams for their management areas (i.e. spawning streams that are biologically representative of productivity in a given area; Price *et al.*, 2017). Due to data limitations, we were unable to account for fish migrating through management areas in which they do not eventually spawn.

For Pacific herring (*C. pallasii*), we used the DFO's annual herring spawn index for each management area (J. S. Cleary and M. Thompson, pers. comm.) and scaled these in the same manner as for the salmon estimates. Since returning wild salmon and spawning herring are only present in certain months of the year, our model only incorporates the abundance indices in the relevant months (as detailed in the Model section below). It is possible that some regions in BC have resident herring populations that provide year-round *C. clemensi* infestation pressure, but these populations are less common than the migratory ones (Beacham *et al.*, 2008) and we lack the data to estimate their abundance.

Model

We analysed the publicly available industry sea-louse dataset to determine relationships between several potential predictors and sea-louse counts on BC salmon farms. Specifically, we assessed the potential effects on farm louse counts of several spatial and temporal covariates (as proxies for environmental conditions because the British Columbia Salmon Farmers Association declined to provide us on-farm environmental data), as well as local wild salmon and herring abundance. We fit a hierarchical model to the industry *L. salmonis* and *C. clemensi* count data using an MCMC approach. For each species, our model included a population growth rate component, which described the on-farm dynamics influenced by factors like louse density, and a colonization rate component, which was shaped by extrinsic factors like wild-host density; these terms were estimated as part of the overall model-fitting procedure. The *L. salmonis* and *C. clemensi* portions of the model were fit simultaneously.

We modelled the data using a negative binomial error distribution; in the public dataset, the reported counts (i.e. the average number of lice per fish) are arbitrarily rounded to the nearest tenth—essentially making them discrete data—so we multiplied each of these by ten to get integer counts (similar to Jansen *et al.*, 2012). We present a summary of the model notation and parameters in Table 1, while the Supplementary material provides a more detailed breakdown of the sea-louse count data by fish health zone (Supplementary Figure S1), as well as the model diagnostics (Supplementary Figures S2–S6).

The model we fit here is an expanded form of the sea-louse population dynamics model presented in Godwin *et al.* (in press). While the purpose of the previous published model was simply to test for an effect of DFO audits on industry counts, here we focus on the dynamics of sea lice on farms in relation to temperature and management and analyse the fitted model under scenarios of climate change and current vs alternative management policies. As such, the spatial and temporal predictors that were included in the previous model to reduce bias in the audit effect are in this article the focus of both fitting the model and conducting simulation analyses of climate and management scenarios. In addition,

Table 1. Summary of model notation and parameters.

Symbol	Description	Data or prior details
Response variable		
N	Motile louse count per ten fish	Discrete count
Indices for predictor variables		
t	Index for timestep (months)	72 months (January 2011–December 2016)
f	Index for farm	91 farms (all active BC farms in 2011–2016)
Model predictions and parameters		
μ	Predicted motile louse count per ten fish	
τ	Effect of delousing treatment	Fixed, $U(-100,100)$
α	Effect of DFO audit	Fixed, $U(-100,100)$
ρ	Negative binomial shape parameter	$U(-100,100)$
d	Delousing-treatment status	3 treatment statuses (treated in t, in $t-1$, or not)
	Fish health surveillance zone	7 health zones (all health zones for the 91 farms)
	Year	6 years (2011–2016)
	Month of year	12 months of year (January–December)
	Age class of farmed fish	2 age classes (<1 year in sea, >1 year in sea)
Sub-model predictions and parameters		
η	Linear function for population growth rate	
β	Linear function for colonization rate	
	Varying-intercept term for farms in η	Random, $U(-100,100)$
	Varying-intercept term for farms in β	Random, $U(-100,100)$
Subscripts		
L	Subscript for *L. salmonis*	
C	Subscript for *C. clemensi*	

our expanded model incorporates predictors for local wild salmon and herring abundance to clarify the relationships between wild fish populations and sea-louse counts on farms.

The *L. salmonis* and *C. clemensi* portions of the model were identical, except for an additional herring covariate in the *C. clemensi* portion. The *L. salmonis* portion of our model takes the form:

$$\mu_{L,t+1,f} = \overbrace{e^{\tau_{L,d,t,f}}}^{\text{Treatment decline}} \overbrace{e^{\alpha_{L,t+1,f}}}^{\text{Audit adjustment}} \left(\overbrace{e^{\beta_{L,t,f}}}^{\text{Colonization rate}} + \overbrace{e^{\eta_{L,t,f}}}^{\text{Population growth rate}} \underbrace{\overbrace{\frac{N_{L,t,f,n}}{e^{\alpha_{L,t,f}}}}^{\text{Previous count}}}_{\text{Rescaling for audit effect}} \right),$$

(1)

where a farm's mean motile *L. salmonis* count in month $t+1$ ($\mu_{L,t+1,f}$) is predicted by the proportional mortality in month t caused by recent delousing treatment on the farm ($e^{\tau_{L,d,t,f}}$), the proportional change in the count in month t due to a DFO audit on the farm in month $t+1$ ($e^{\alpha_{L,t+1,f}}$), the colonization rate on the farm in the month t ($e^{\beta_{L,t,f}}$) and the *L. salmonis* per-capita population growth rate ($e^{\eta_{L,t,f}}$), which acts on the farm's *L. salmonis* count in month t ($N_{L,t,f,n}$) after rescaling to account for the bias in counting due to a DFO audit ($e^{\alpha_{L,t,f}}$). This rescaling component divides the reported, non-audited counts by the audit effect ($e^{\alpha_{L,t,f}}$), thereby adjusting the reported counts as if they were, in fact, audited (and therefore unbiased). The spatial and temporal parameters in the colonization rate and population growth rate terms are used as proxies for temperature because of the strong seasonal, interannual, and regional patterns of temperature in BC (Pickard and McLeod, 1953; Fisheries and Oceans Canada, 2017a).

We model the per-capita population growth rate and colonization rate as exponentiated linear functions of several additive covariates; they are therefore analogous to linear predictors in generalized linear mixed-effects models (GLMMs) with logarithmic link functions. As with most modelling considerations, this was a judgement call. While the true underlying relationships are undoubtedly nonlinear [as Box (1976) famously noted, "there never was a straight line" in nature], we chose to estimate first-order approximations of the effects to avoid further complicating an already complex model. Future investigations could certainly focus on relevant nonlinearities and their implications within the system. The linear function for population growth rate incorporates covariates for month, year, health zone, farmed salmon age class, and inter- and intra-specific density dependence in month t on farm f. Similarly, the linear function for colonization rate included coefficients for year, health zone, farmed salmon age class, local wild herring abundance (for the *C. clemensi* portion of the model only), and local wild salmon abundance (for both the *L. salmonis* and *C. clemensi* portions). Both linear functions included a varying-intercept term for farm, which is analogous to a random effect on the intercept in a GLMM.

The two wild fish covariates in the linear function for colonization rate describe the effects on louse counts of wild Pacific herring and wild Pacific salmon in a given year and management area. Adult wild salmon and wild herring spawners do not aggregate in their management area's marine waters year-round, so we only consider the effects of salmon and herring in select months of the year. Since we do not know the monthly abundance of herring and salmon in each management area, we set the coefficients for these terms to be zero in all months except those in which herring and salmon are most likely to be present and influencing farm louse counts. Pacific herring in BC typically spawn in February, March, and April (Benson *et al.*, 2015), so we fit herring coefficients for each of these months plus May, to account for April colonization by larval lice that would develop and be enumerated in the May motile louse counts. July, August, and September experience the highest numbers of adult Pacific

salmon in the coastal marine environment (Groot and Margolis, 1991), so we fit salmon coefficients for these months plus October. The *L. salmonis* model does not include a herring term because *L. salmonis* is a salmonid specialist (Pike and Wadsworth, 1999).

We used our temporal and spatial predictors (i.e. month, year, and health zone) as proxies for environmental conditions, as the two main drivers of sea-louse development timing—temperature and salinity (Johnson and Albright, 1991; Hamre *et al.*, 2019) — exhibit strong seasonal, interannual, and regional patterns (Pickard and McLeod, 1953; Fisheries and Oceans Canada, 2017a). Actual on-farm temperature and salinity measurements would have allowed us to assess the influence of environmental conditions on sea-louse counts in a more direct manner, but the British Columbia Salmon Farmers Association did not provide us these data.

We fit our two varying-intercept terms (i.e. the random effects for year on population growth rate and colonization rate) with separate variance parameters, along with a third parameter for the correlation between the two. These three parameters informed an inverse-Wishart distribution that defined the covariance matrix of the multivariate normal distribution from which the random effects were ultimately drawn (as in Gelman and Hill, 2007). A detailed derivation of the original model form is presented in Godwin *et al.* (in press). We performed our analysis in R 3.2.1 (R Core Team, 2019) and JAGS 4.3.0 (Plummer, 2017) using the R package R2jags 0.5-7 (Su and Yajima, 2015).

Simulations

To test the resilience of current parasite-control policy to environmental change and to assess the performance of other potential policy options, we used our model results to simulate louse counts under three management scenarios. Currently, farms are required to treat more quickly after a threshold-breaking louse count during the wild juvenile salmon migration (i.e. March to June) than in other months (Fisheries and Oceans Canada, 2016), so some delays in treatment are permitted under current policy. These treatment delays have been associated with high sea-louse counts on some salmon farms, and a precautionary treatment prior to the wild juvenile migration has been put forth as a potential strategy for reducing farm sea-louse counts in migration months (Peacock *et al.*, 2013; Bateman *et al.*, 2016); these two factors motivated our two alternative management scenarios. Management Scenario 1 was the current parasite management strategy employed by BC farms, in which delays (i.e. the number of months) between simulated threshold-breaking counts and subsequent treatments were drawn from Poisson distributions using the observed mean delay for that month (e.g. January). Management Scenario 2 was one in which delousing treatment always occurred in the same month as the threshold-breaking count (i.e. there was no delay between threshold-breaking counts and subsequent treatment), regardless of the month. Management Scenario 3 was the same as the first, but with an additional obligatory treatment in February, prior to the wild juvenile salmon out-migration. We simulated these three management scenarios for both an average year (i.e. all years except 2015) and for 2015, when sea-surface temperatures were exceptionally high in the northeast Pacific due to the "warm blob" (Peterson *et al.*, 2015; Bateman *et al.*, 2016). According to sea-surface temperature data from BC lighthouses (Fisheries and Oceans Canada, 2017a), 2015 was 0.90°C warmer than average across the 6 years of this study (2011–2016), and 1.27°C warmer than the 50-year average; for just the salmon migration months (March–June), 2015 was 1.18°C warmer than the 6-year average and 1.63°C warmer than the 50-year average. For conciseness, we use the term "high-temperature year" to refer to the simulation results associated with the high-temperature year of 2015, and "average year" when discussing the simulation results across 2011–2014 and 2016.

We focused on *L. salmonis* for this simulation exercise because *C. clemensi* counts are not currently a consideration for parasite management on BC farms and because the audit effect was so strong for *C. clemensi* (Godwin *et al.*, in press) that simulating *C. clemensi* counts under existing conditions might not be meaningful. To reflect reality, we did not allow farms to treat in consecutive months.

We simulated counts over a calendar year, starting with the mean observed count in December of the previous year. For each iteration of the simulation, we drew the parameter estimates from one of our MCMC samples. We used the mean observed values for the simulation data. We ran the simulation 10000 times.

Results

Trends in louse counts and treatments

The observed mean monthly *L. salmonis* counts exceeded the three-louse threshold in 14.3% of all months, and in 8.5% of months during the wild juvenile salmon migration in spring. After correcting for the audit effect, the mean monthly *L. salmonis* counts exceeded the threshold in 16.6% of all months and in 10.3% of migration months. Treatment frequency in BC was highest in February, immediately prior to the wild juvenile salmon migration (Figure 2). *Lepeophtheirus salmonis* counts were accordingly their lowest during the migration period, on average. Treatment frequency declined shortly after the migration period, after which the observed mean *L. salmonis* counts, as well as those corrected for the audit effect (Godwin *et al.*, in press), stayed above the three-louse treatment threshold for September, October, and November. Treatments were, on average, effective at reducing *L. salmonis* and *C. clemensi* counts in BC from 2011 to 2016 (Supplementary Figure S7).

Wild fish populations as sea-louse reservoirs

Local wild salmon abundance had a positive effect on *L. salmonis* and *C. clemensi* colonization rates in August (Supplementary Figure S8). At maximum wild salmon abundance (i.e. the maximum observed salmon abundance index value), the mean predicted louse counts on farms in August increased substantially relative to counts at zero wild salmon abundance, but there was high uncertainty in the estimates: *L. salmonis* counts increased by 84% (95% confidence intervals: 32%, 174%) at maximum wild salmon abundance, while *C. clemensi* counts increased by 121% (10%, 420%). Local wild herring abundance also had a positive relationship with *C. clemensi* colonization in April (Supplementary Figure S8), with predicted *C. clemensi* counts increasing by 47% (6%, 140%) at maximum wild herring abundance relative to when there are no local herring. These effects of wild fish populations resulted in an increase in the relative contribution of colonization to *L. salmonis* counts in August due to salmon and to *C. clemensi* counts in August due to wild salmon and in April due to wild herring (Figure 3).
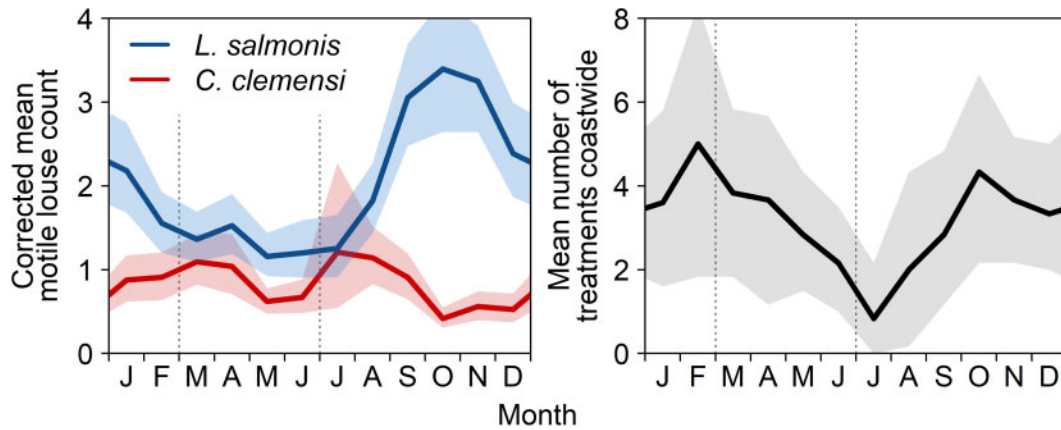
Figure 2. Mean motile louse counts on salmon farms after correction for the audit effect [as in Godwin *et al.* (in press); left panel) and the mean number of delousing treatments coastwide (right panel) between 2011 and 2016 in BC. Shaded regions represent the bootstrapped 95% confidence intervals and the dashed vertical lines bound the spring migration period for wild juvenile salmon. The louse-count and treatment data are monthly means rather than continuous data, and we connect these data with lines for visual aid.
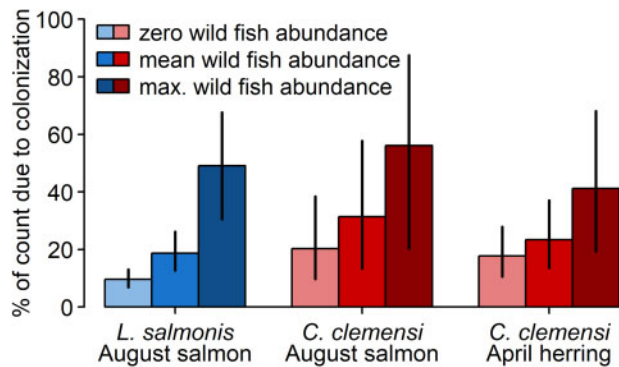
Figure 3. Influence of colonization on sea-louse counts on farmed salmon in the months that our model showed positive effects of wild fish (salmon or herring) abundance. For each positive fish effect (e.g. the effect of wild salmon on *L. salmonis* counts in August), three levels of local wild fish abundance are presented. Predictions were made using the parameter values from the MCMC samples under the conditions that treatment last occurred >2 months ago and that the farm was not audited during the month in question. All other predictors were set to the mean of observed values. The error bars give the 95% confidence intervals for the mean predictions. The remaining percentage of the sea-louse counts is from population growth.

Sea-louse outbreaks in warm years and alternative management strategies

Louse counts regularly break the three-louse threshold in months outside of the wild juvenile salmon migration, but do so less often during migration months. A notable exception to this was in 2015, when temperatures were anomalously high due to the "warm blob" (Figure 4). In this high-temperature year, 21.4% of *L. salmonis* counts broke the threshold and the mean observed count was 3.12 times higher than in average years (hereafter termed "baseline").

Under the high-temperature conditions and Management Scenario 1 (i.e. the current parasite management strategy in BC), the mean simulated *L. salmonis* count on farms during the wild
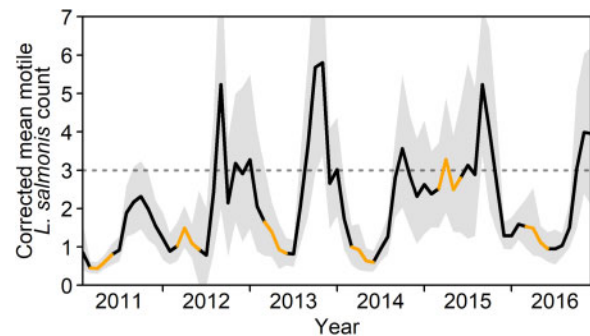

Figure 4. Audit-corrected mean motile louse counts (±95% bootstrapped confidence intervals) on BC salmon farms between 2011 and 2016. Orange lines denote counts during the wild juvenile salmon migration period (March to June) and the dashed grey line represents the current threshold for sea-louse management action.

juvenile salmon migration was 2.41 times greater than baseline, averaged across migration months (Figure 5). To reduce farm louse counts during migration in a high-temperature year to baseline levels under this status quo management strategy, our simulations showed that the treatment threshold would have had to be cut in half, from three lice to 1.5.

Management Scenario 2 (i.e. delays eliminated between outbreak diagnosis and treatment) reduced sea-louse counts during migration in high-temperature years to 1.45 times greater than baseline (Figure 5) and, again when compared to Management Scenario 1, only increased the number of annual treatments by 9.2% in average years and 17.6% in high-temperature years. Management Scenario 3 (i.e. the current strategy but with an obligatory February treatment) reduced sea-louse counts in migration months in the high-temperature year to the same level as baseline (Figure 5), but farms would have to treat 74.2% more often than they do now in average years and 10.9% more often in high-temperature years.

Discussion
Wild fish populations as sea-louse reservoirs
We found that wild adult salmon and herring function as natural reservoir host populations from which sea lice spread to salmon
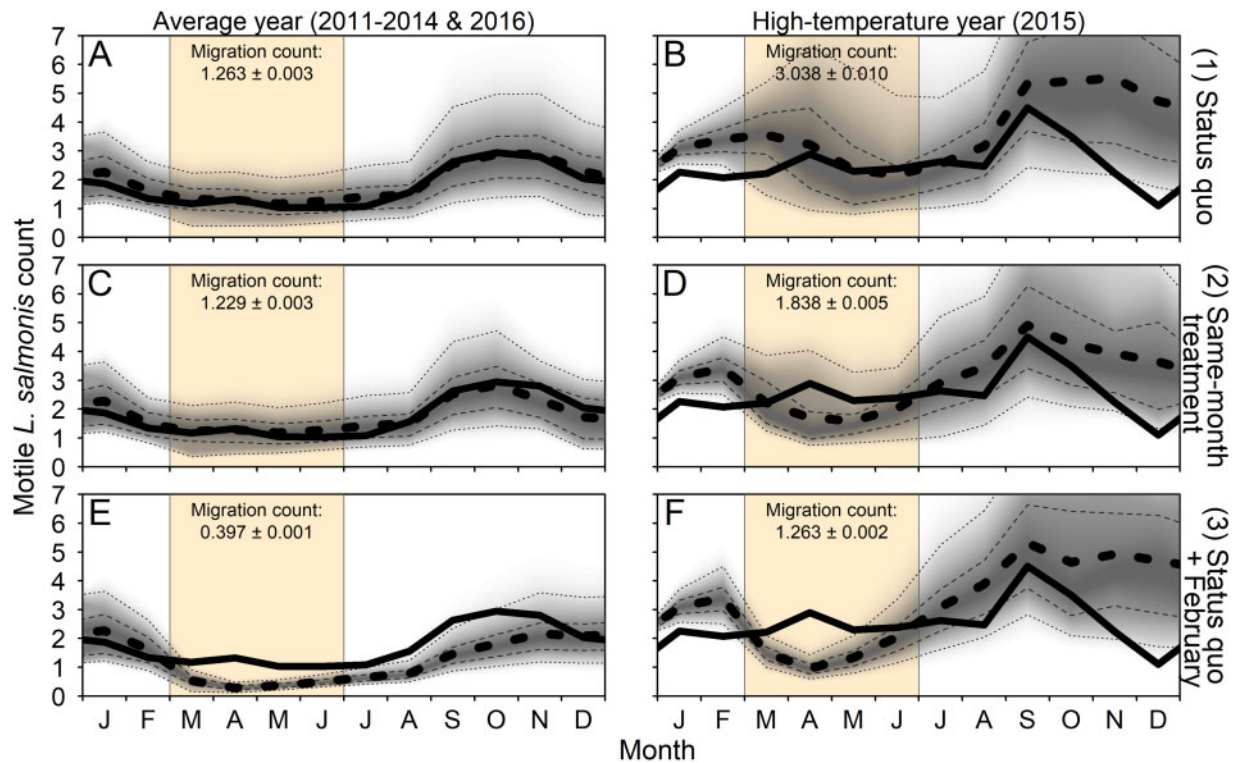
Figure 5. Simulated motile *L. salmonis* counts on farms in an average year (2011–2014 and 2016; left panels) and in a high-temperature year (2015; right panels), for three different parasite management strategies. The top panels show Management Scenario 1 (i.e. the current parasite management strategy employed by BC salmon farms), the middle panels show Management Scenario 2 (i.e. a strategy in which delousing treatments always occur in the same month as a threshold-breaking count), and the bottom panels show Management Scenario 3 (i.e. the current strategy with an additional obligatory treatment in February). The thick dashed lines indicate the monthly means of the simulated louse counts and the solid lines show the observed mean louse counts. The quantiles of the simulated counts are shaded in 0.5% increments and the thin dashed lines give the 50 and 90% quantiles. The wild juvenile salmon migration period is conveyed by the yellow-shaded regions, and the mean simulated *L. salmonis* counts ($\pm$ SE) during the migration period are given. The top-left panel reflects current louse management practices in an average year. The predicted and observed January counts differ because the simulations begin with the mean observed count in December of the previous year. Note that the monthly data are discrete and connected by lines for visualization purposes.

farms. Local wild salmon abundance had a positive effect on *L. salmonis* and *C. clemensi* colonization rates and overall counts in August (Supplementary Figure S8), suggesting that wild salmon help spread not only salmonid specialists to farms but also generalist parasites as well. This wild salmon effect may be particularly influential for *C. clemensi*, for which our model predicts population growth rates below replacement (Supplementary Figure S8), suggesting that colonization may be the primary source of these lice for farmed salmon. Previous research correlated wild salmon abundance with *L. salmonis* infestation rates on farms in one region (Marty *et al.*, 2010), and our results corroborate and expand on this work by assessing the timing and strength of the effect.

We also show evidence, for the first time, that a non-salmonid species can act as a source of parasites to salmon farms, as local wild herring abundance had a positive relationship with *C. clemensi* colonization in April. It has long been speculated that non-salmonids are involved in the dynamics of parasite populations on farms (Jones *et al.*, 2006; Beamish *et al.*, 2009), but until now there has been no empirical support for this hypothesis.

The impacts of disease in multi-host systems depend on the level of specialization of the pathogen or parasite. Parasites with

density-dependent transmission are classically considered to be unable to drive focal host species to extinction because their population densities track their hosts' (Anderson and May, 1992), but generalist parasites can avoid these host-density thresholds by persisting in the environment via other host reservoirs even when focal host population densities are low (De Castro and Bolker, 2004). Previous work has illustrated how salmon farms shift the natural relationship between *L. salmonis* and wild salmon to the generalist-parasite situation by providing year-round reservoirs of hosts for *L. salmonis* that do not exist naturally (e.g. Krkosek *et al.*, 2007; Costello, 2009). Other research found that, between 1999 and 2008, the annual pink salmon return in one BC region was correlated with the average louse abundance on the region's farms in the following spring (Marty *et al.*, 2010). Our results add another piece to this transmission puzzle by empirically suggesting that salmon farms coastwide are supplied externally through the transmission of parasites from wild to farmed salmon, resulting in immediate colonization of farms and increased *L. salmonis* counts in August. By clarifying the spatial and temporal scale of this external transmission, our results provide key information for managers to help optimize parasite management and minimize fall sea-louse outbreaks on BC salmon farms.

Our findings also provide a rare empirical example of a generalist parasite (*C. clemensi*) spreading from multiple wild-host species (wild salmon and herring) to a domesticated host reservoir. These results indicate that the broader host range of *C. clemensi* increases its transmission risk from wild to farmed fish, and theory suggests that additional host reservoirs can decrease the probability of parasite eradication (and therefore make parasite control more difficult) and increase extinction risk for a focal host species (De Castro and Bolker, 2004). Yet despite these risks and the mounting evidence that *C. clemensi* infestation negatively impacts wild salmon (Godwin *et al.*, 2015, 2017, 2018; Atkinson *et al.*, 2018), current parasite-control policy for salmon farms ignores this generalist louse species. These results beg consideration for a multi-species management approach in policies regulating pest or disease control in systems with multiple hosts and/or parasites.

Sea-louse outbreaks in warm years and alternative management strategies

We found that the current parasite-control policy is relatively effective at reducing farm lice during the wild juvenile migration in average years, but that it has limited capacity to remain effective when environmental conditions change. Temperature is a strong determinant of louse development rate (Johnson and Albright, 1991; Groner *et al.*, 2014; Hamre *et al.*, 2019), and our simulation results suggest that when louse dynamics match those seen in a high-sea-surface temperature year (2015), the risk of sea-louse outbreaks on salmon farms increases dramatically. Both alternative management scenarios we simulated decreased sea-louse counts during the wild juvenile salmon migration in high-temperature years, but both also required an increase in the number of delousing treatments annually.

We used the month and year parameter estimates from our model as proxies for temperature because we were unable to obtain farm-level temperature data from the British Columbia Salmon Farmers Association. We confirmed that these parameter estimates were indeed strongly correlated with coastwide sea-surface temperatures (Supplementary Figure S9; Fisheries and Oceans Canada, 2017a), but we did not include these coastwide temperatures in our model because: (i) the lighthouses that provided these data are not evenly distributed or in the same regions as most of the salmon farms and (ii) local variation in temperature is probably much more important for predicting sea-louse counts on salmon farms because the farms are situated in fjords and bays that vary in depth and are heavily influenced by tide, wind, and freshwater runoff (Foreman *et al.*, 2012; Foreman *et al.*, 2015). Instead, we allowed our model's random effect for farm facility to account for local variation while explicitly fitting fixed effects for month and year to account for the monthly and annual variation in environmental conditions. While our 6-year time series would normally preclude inference based on the year parameter estimates, we were fortunate in that 2015 was well documented as having uncharacteristically high temperatures coastwide due to a warming event now known as the "warm blob" (Peterson *et al.*, 2015; Bateman *et al.*, 2016), which allowed us to use 2015 as a representative "high-temperature year" in simulations. That we needed to structure our analysis in such a manner highlights the need for more transparent data sharing from salmon-farm companies.

Our simulations revealed that in warmer years such as 2015, wild juvenile salmon are likely exposed to much larger sea-louse populations on salmon farms than in a typical year. Under the high-temperature conditions of 2015 and the current parasite management strategy in BC (i.e. Management Scenario 1), the mean simulated farm louse count during migration was 2.41 times greater than in average years (baseline); the mean observed count during the 2015 migration was 3.12 times higher than baseline. The simulated data from this status quo management strategy matched the observed data very well for average years (Figure 5A) and for 2015 during the juvenile salmon migration period (Figure 5B); the simulation performed less well outside of the 2015 migration period, possibly because salmon farms did not stick to their normal management strategy in 2015 and instead reacted to their unexpectedly high louse counts by changing their treatment schedules in different ways (Bateman *et al.*, 2016). To have decreased 2015 farm louse counts during migration to baseline levels under the current management strategy, our simulations indicated that the treatment threshold would have had to have been reduced from three lice to 1.5.

We assessed the potential effectiveness of two alternative parasite management strategies (i.e. Management Scenarios 2 and 3) at controlling sea-louse outbreaks in high-temperature years. These two management scenarios were motivated based on previous observations that treatment delays may be associated with high sea-louse counts on salmon farms and that precautionary treatment prior to the wild juvenile salmon migration may reduce counts during migration months (Peacock *et al.*, 2013; Bateman *et al.*, 2016). Management Scenario 2 eliminated delays between diagnoses of sea-louse outbreaks (i.e. *L. salmonis* counts greater than three lice per fish) and subsequent delousing treatments. This strategy reduced sea-louse counts during migration in high-temperature years to 1.45 times greater than baseline (Figure 5D) by reducing the amount of time that louse populations could grow rapidly due to high temperatures (Johnson and Albright, 1991; Hamre *et al.*, 2019). Management Scenario 2 also only increased the number of annual treatments by 9.2% in average years and 17.6% in high-temperature years, suggesting that it may not be an overly expensive option for the salmon farming industry. Management Scenario 3 was identical to the current strategy, but with an additional obligatory delousing treatment in February, just before the migration period. This strategy decreased migration sea-louse counts in the high-temperature year to the same level as baseline (Figure 5F) by reducing the counts to near-zero in March and therefore minimizing the chance that counts could increase above the treatment threshold before July, even in high-temperature years. However, this option would increase the risk of sea lice evolving resistance to parasiticide treatments, with farms having to treat 74.2% more often than they do now in average years and 10.9% more often in high-temperature years. The drastic increase in the number of treatments needed for Management Scenario 3 in average years was because treatments were often not needed in these years for Management Scenario 1; adding an obligatory February treatment therefore increased the mean number of treatments per year from 0.71 to 1.23. One modification to Management Scenario 3 that might preserve its effectiveness in high-temperature years while minimizing treatments in average years would be to mandate a February treatment only when January temperatures exceeded a threshold; this strategy would have the intuitive and desirable outcomes of behaving

like the status quo in regular years while gaining the benefits of Management Scenario 3 in warmer years.

Since environmental policies often dictate the extent of human impacts in social-ecological systems, effective long-term policy options must account not only for current conditions but for future ones as well (Nelson *et al.,* 2007). The capacity to remain effective in face of environmental change is beginning to be recognized as a key consideration for new policies (Berkes, 2007; Adger *et al.,* 2011), but whether existing policies have this capacity is largely unknown. Our results indicate that minimizing sea-louse abundance on farmed salmon and the probable impacts on wild salmon will therefore require more careful management on salmon farms in warmer years. As we show with the case of parasite control on salmon farms, it may be that current policies will need revision for continued effectiveness in the face of a changing global environment.

Supplementary data
Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data availability
The datasets were derived from sources in the public domain: Fisheries and Oceans Canada, Industry sea lice counts at BC marine finfish aquaculture sites, https://open.canada.ca/data/en/dataset/3cafbe89-c98b-4b44-88f1-594e8d28838d; Fisheries and Oceans Canada, DFO audits at BC marine finfish aquaculture sites, https://open.canada.ca/data/en/dataset/5cfd93bd-b3ee-4b0b-8816-33d388f6811d; and Fisheries and Oceans Canada, NuSEDS-New Salmon Escapement Database System, https://open.canada.ca/data/en/dataset/c48669a3-045b-400d-b730-48aafe8c5ee6.

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