Distinguishing sources of parasites on wild juvenile salmon

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1 INTRODUCTION

The dark side of modelling

Ecological problems are complex, and in an age of increasingly advanced techniques for analyzing data, the temptation is great to fit complicated mechanistic models to ecological data. For most ecologists, the more subtle problems of **parameter estimability** and **identifiability** are not immediately obvious.

Models of parasite transmission between farmed and wild salmon are one such example. The sea louse is a common copepod parasite on both farmed and wild salmon, and is easily observable (Fig. 1). As result, there are large datasets of sea lice abundance on juvenile Pacific and farmed Atlantic salmon that can be used to answer questions such as

Fig. 1. Juvenile pink salmon are particularly susceptible to morbidity and mortality due to sea lice.

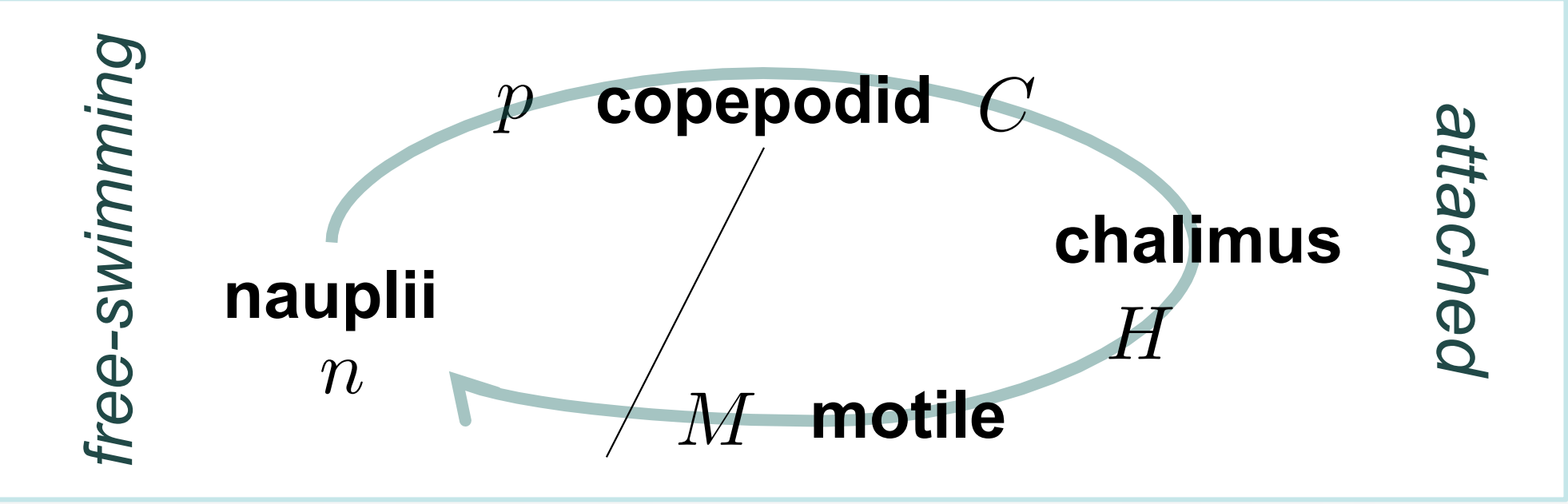


Fig. 2. **Sea lice develop through five phases**: nauplii and copepodid phases are free-swimming, copepodids attach to a host and subsequently develop through chalimus and motile stages.

- What **infection pressure** do farms put on wild juvenile salmon?
- What is the **footprint** of infectious sea lice from salmon farms?
- How do infection dynamics change with **management interventions** on farms (*i.e.*, treatment with parasiticide)?

2 THE BEGINNING

A model *for* sea lice transmission [1,2]

1. Free-living naupliar sea lice disperse from farms along a 1D migration corridor

a) Nauplii disperse with seaward advection and mortality/development according to

$$\frac{\partial n}{\partial t} - D\frac{\partial^2 n}{\partial x^2} + \gamma\frac{\partial n}{\partial x} + \mu n = 0$$

The steady-state solution for a constant point source (i.e., salmon farm) at *x* = *y is*

$$n(x) = c_n \begin{cases} e^{a_1(x)} & x \leq y \\ e^{-a_2(x)} & x > y \end{cases}$$

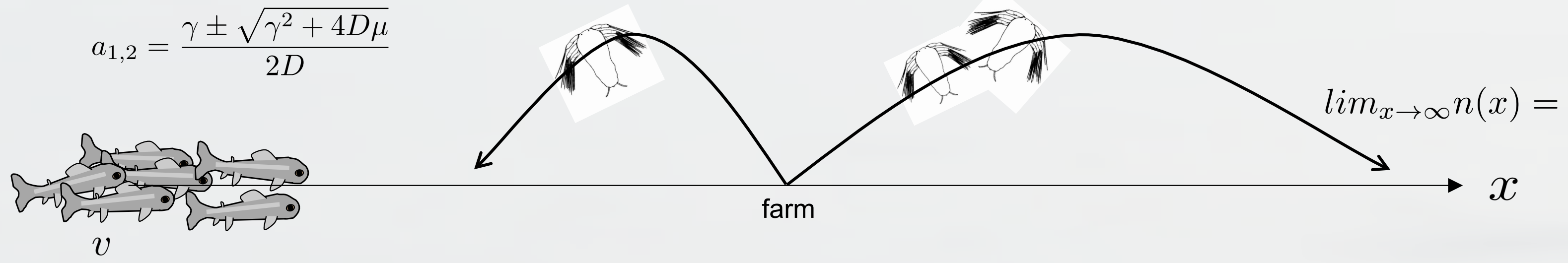
b) Nauplii develop into copepodids (Fig. 2), which also disperse

$$p(x) = c_p \begin{cases} e^{b_1(x)} & x \leq z \\ e^{-b_2(x)} & x > z \end{cases}$$

and the final distribution of infectious copepodids is given by the convolution

$$L(x) = \int_{-\infty}^{\infty} n(z)p(x-z)\,dz$$

$$a_{1,2} = \frac{\gamma \pm \sqrt{\gamma^2 + 4D\mu}}{2D}$$



$$lim_{x\to\infty} n(x) = 0$$

2. Infectious copepodid lice attach to juvenile salmon in proportion to their density, L(x), and develop through chalimus and motile stages.

$$\hat{C}(x) = \frac{\beta}{v}\left[k + \alpha\int_0^{\tau_c} L(x-vt)dt\right]$$

$$\hat{H}(x) = \frac{s_c\beta}{v}\left[k + \alpha\int_{\tau_c}^{\tau_c+\tau_h} L(x-vt)dt\right]$$

$$\hat{M}(x) = \frac{s_c s_h\beta}{v}\left[k + \alpha\int_{\tau_c+\tau_h}^{\tau_c+\tau_h+\tau_m} L(x-vt)dt\right]$$

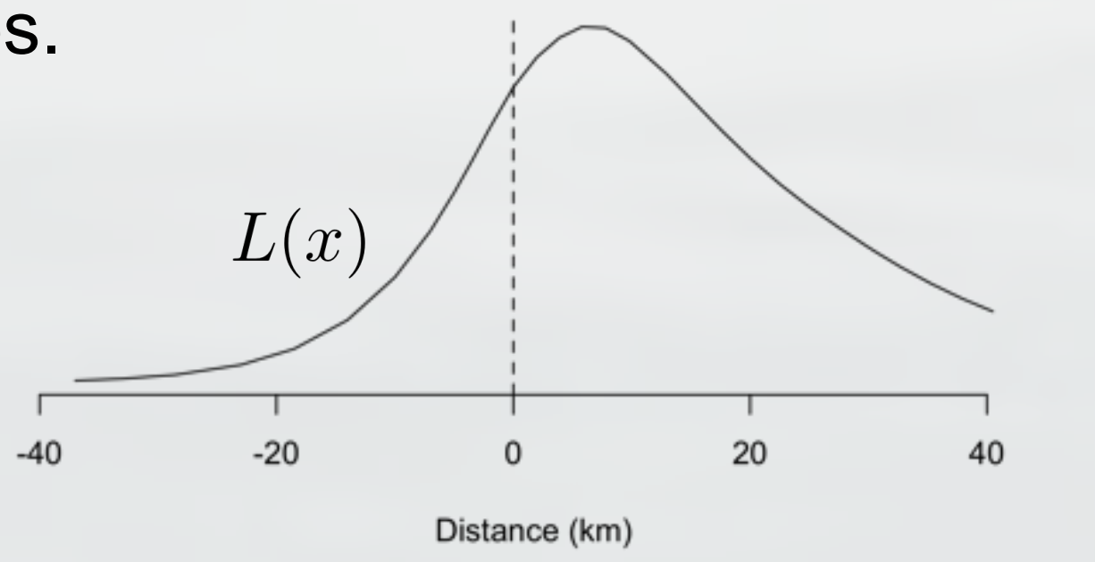


Fig. 3. The distribution of infectious larvae resulting from advection, diffusion and decay from a constant point source at the vertical dashed line.

3. Lice are assumed to be **poisson distributed** on fish, allowing us to assign probabilities to our observations of C, H, and M and calculate likelihood *etc.*[2]

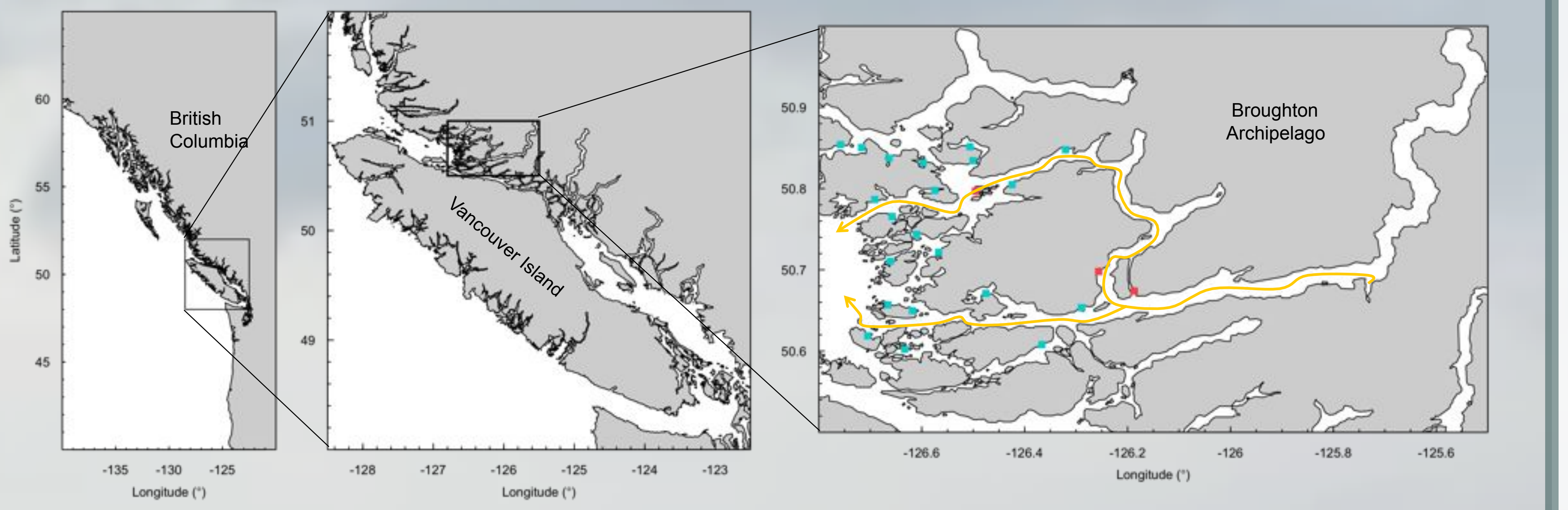


Fig. 4. The **Broughton Archipelago** is on the south central coast of British Columbia, Canada, and has been a hotspot of controversy over the impacts of salmon farming on wild salmon, including parasite transmission. The Broughton Archipelago is home to all five species of Pacific salmon and ~30 salmon farms (squares). Pink salmon are the dominant species in the region, and migrate past salmon farms as juveniles, making them particularly susceptible to the effects of sea lice (Fig.1).

3 THE PROBLEM

Estimability

Using **data cloning** techniques, we examined the estimability of 14 free parameters in the established sea lice transmission model.

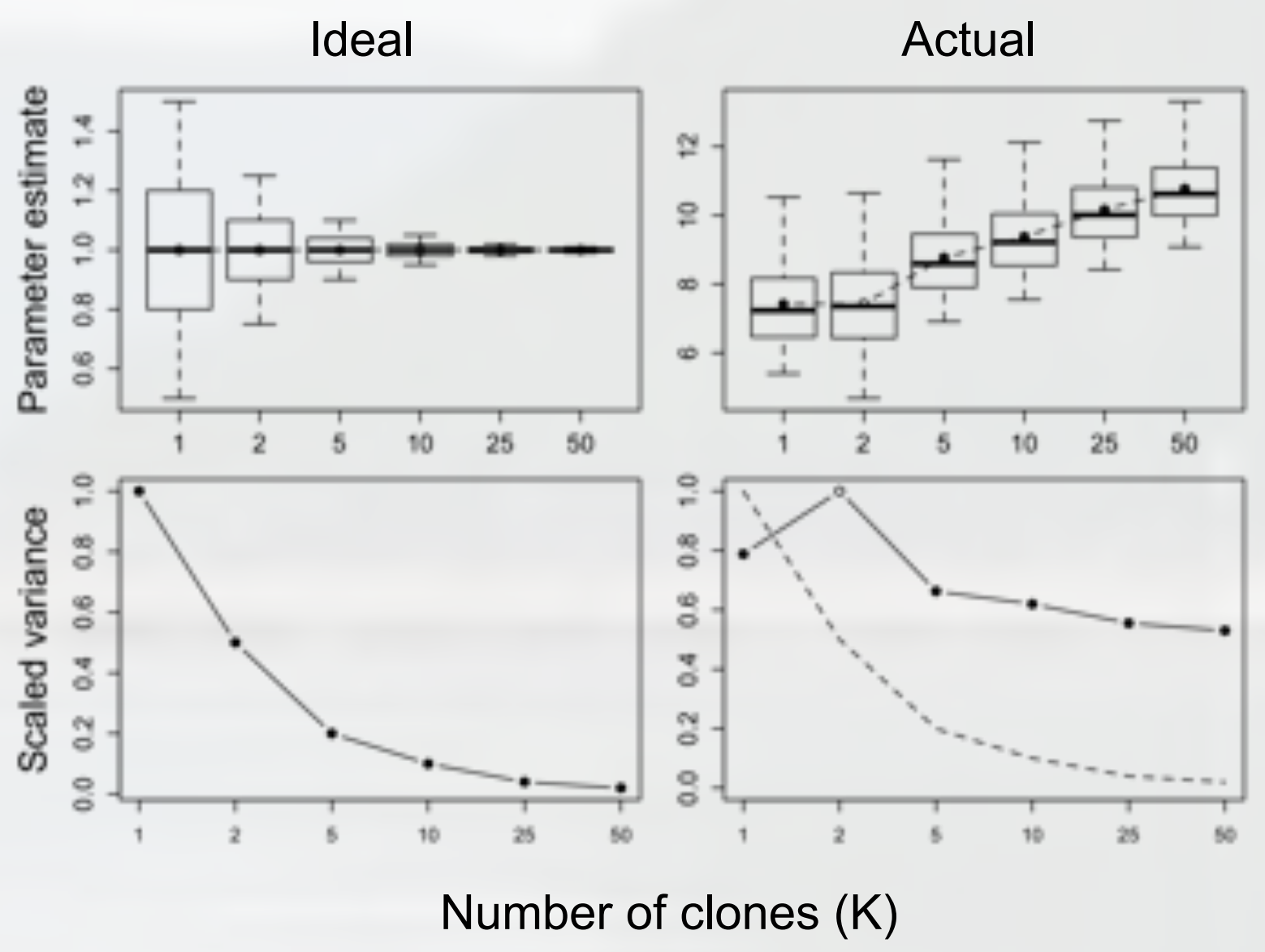


Fig 5. The parameter estimates (top) and scaled variance of parameter estimates (bottom) over 1, 2, 5, 10, 25, and 50 clones of the sea lice dataset. Ideally, variance declines at a rate of 1/K, where K is the number of clones (left). For the sea lice model, this was not the case (only 2/14 parameters shown). Open circles indicate that the MCMC algorithm did not converge (R>1.1).

4 THE SOLUTION

Add assumptions until inference is feasible[3]

We were able to distill the problem from **14** down to **6** parameters by:

- using additional data from salmon farms
- fixing the developmental time of lice from experimental data [3]
- assuming common parameters for pink and chum salmon hosts

All parameters except the background louse level (*k*) were estimable (Fig. 6). Model fits are shown in Fig. 7.

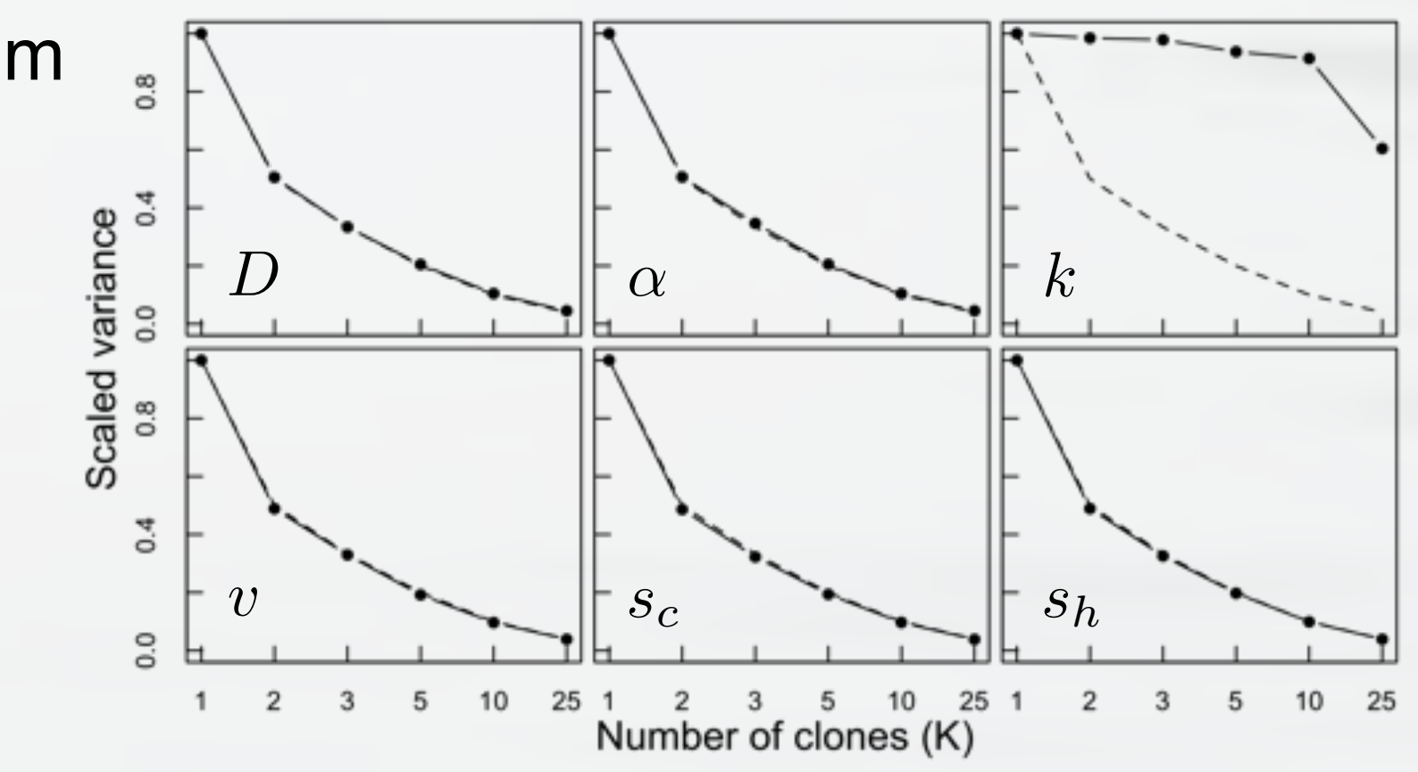


Fig. 6. Scaled variance as a function of the number of clones for 6 parameters in the reduced model (see model formulation in box 2). Dashed lines indicate the ideal scaled variance, which declines at a rate of 1/K.

BUT *k* is a parameter of interest! *What else can be done to estimate k?*

Perhaps more data need to be collected outside of the farm footprint?

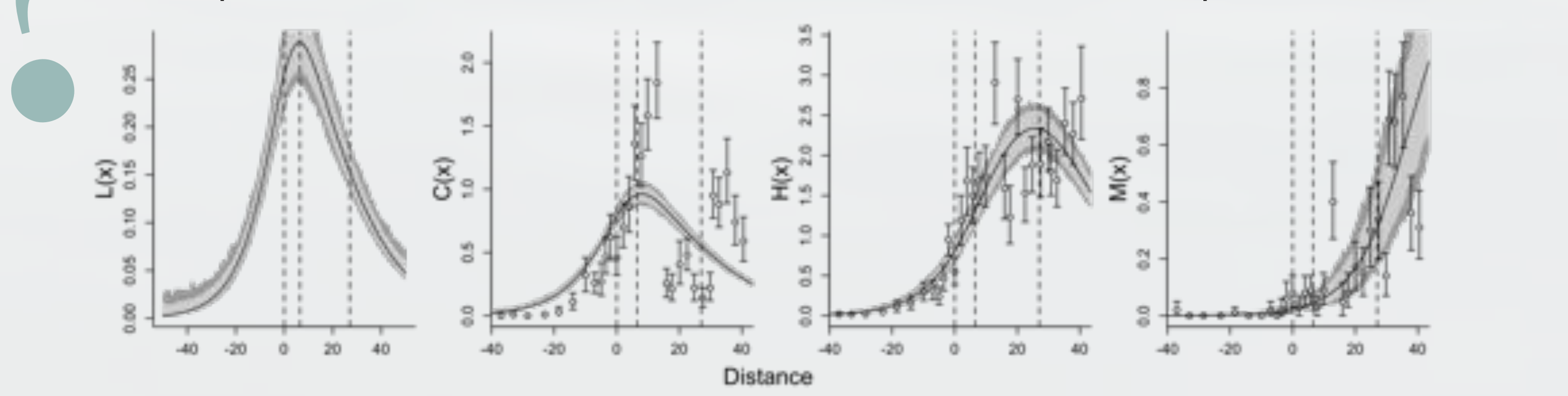


Fig 7. The expected density of planktonic copepodids (*L(x)*), and attached copepodid (*C(x)*)), chalimus (*H(x)*) and motile (*M(x)*) stage lice along a seaward migration from x=-40 to x=40 km. Vertical dashed lines indicate the locations of three salmon farms shown in red in Fig. 4. 95% and 99.9% confidence intervals on model predictions were estimated by bootstrapping parameters and taking the 95% quantiles every 1 km along the migration.

5 MOVING FORWARD

Changes to management on salmon farms

The previous model (2) assumes salmon farms are a **constant** point source of lice. However, treatments of sea lice on salmon farms with parasiticide have become more regular in recent years, resulting in lice population cycles of growth and decay [6].

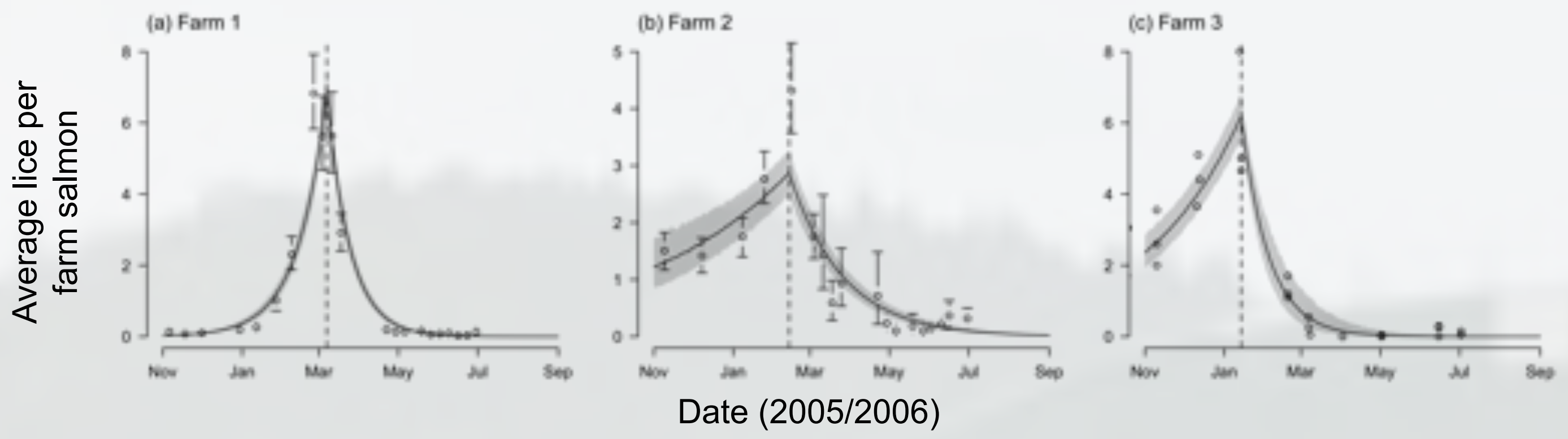


Fig. 8. Average lice per farm salmon on three different salmon farms in the Broughton Archipelago (indicated by red squares in Fig. 4), show clear cycles of exponential growth and decay around treatment dates (vertical dashed lines).

6 REINTRODUCING COMPLEXITY

Temporal dynamics of sea lice on salmon farms

To address the obvious temporal dynamics on salmon farms (Fig. 8), we have adapted the model to include the transient solution in to the advection-diffusion-decay equation (2), in the form of a Green's function

$$G(x,t) = \frac{1}{\sqrt{4\pi Dt}} exp\left[-\mu t - \frac{(x-\gamma t)^2}{4Dt}\right]$$

forced by exponential growth and decay at the point source:

$$f(t) = f_0 \begin{cases} e^{r_1(t_0-t)} & t < t_0 \\ e^{r_2(t_0-t)} & t \geq t_0 \end{cases}$$

Such that

$$n(x,t) = \int_0^t \int_{-\infty}^{\infty} G(x-\xi, t-\tau) f(\tau)\delta_y(\xi)\,d\xi\,d\tau$$

The integral equations for the expected number of lice on fish are then over space and time:

$$\hat{C}(x,t) = \beta\left[k + \alpha\int_0^{\tau_c} L(x-vt', t-t')\,dt'\right]$$

$$\hat{H}(x,t) = \beta s_c\left[k + \alpha\int_{\tau_c}^{\tau_c+\tau_h} L(x-vt', t-t')\,dt'\right]$$

$$\hat{M}(x,t) = \beta s_c s_h\left[k + \alpha\int_{\tau_c+\tau_h}^{\tau_c+\tau_h+\tau_m} L(x-vt', t-t')\,dt'\right]$$

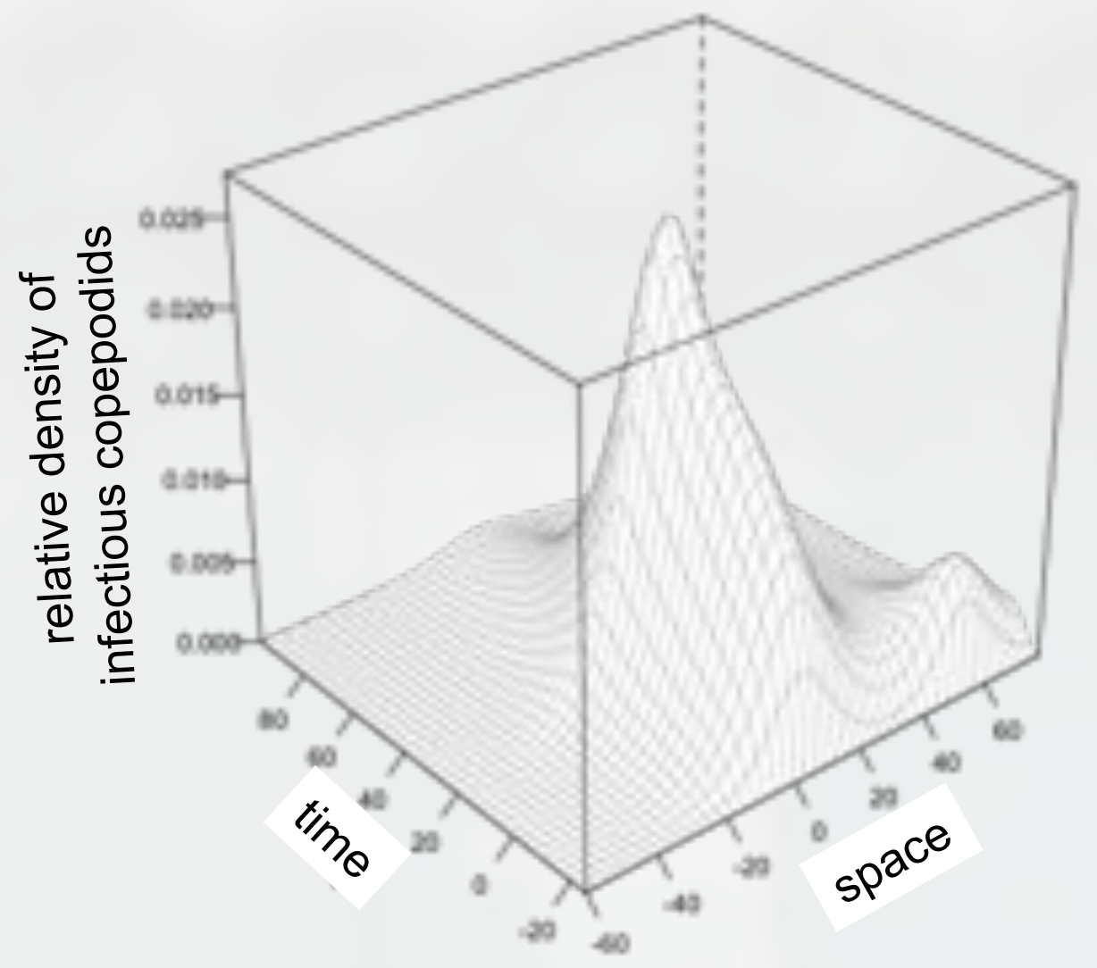


Fig. 9. The relative density infectious copepodids through space (km) and time (days) around point sources at -4, 4, and 53 km. Treatments with parasiticide, causing declines in the source strength of larvae, occurred at 18, -4 and -33 days, respectively.

This model was fit in a Bayesian framework, where experimental data or previous studies could inform priors. A simple Metropolis algorithm showed good convergence to sensible values, **but** was unable to recover known parameter values when fit to simulated data.

Is this model getting **too complex**?

Or do things have to get **worse** before they get **better**?

Want to chat about salmon, sea lice & modelling?

Please find me or email:
stephanie.peacock@ualberta.ca

Literature cited: [1] Krkosek, M., M. Lewis, and J. Volpe. 2005. Transmission dynamics of parasitic sea lice from farm to wild salmon. Proceedings of the Royal Society B, 272(1564):689–696. **[2] Krkosek**, M., M. Lewis, A. Morton, L. Frazer, and J. Volpe. 2006. Epizootics of wild fish induced by farm fish. **[3] Stien**, A., P. Bjørn, P. Heuch, and D. Elston. 2005. Population dynamics of salmon lice Lepeophtheirus salmonis on Atlantic salmon and sea trout. Marine Ecology Progress Series, 290:263–275. **[4] Lele,** S., B. Dennis, and F. Lutscher. Data cloning: easy maximum likelihood estimation for complex ecological models using Bayesian Markov chain Monte Carlo methods. Ecology Letters, 10(7):551 – 563, 2007. **[5] Lele**, S. 2010. Model complexity and information in the data: Could it be a house built on sand? Ecology, 91(12):3493–3496. **[6] Krkosek**, M., A. Bateman, S. Proboscz, and C. Orr. 2010. Dynamics of outbreak and control of salmon lice on two salmon farms in the Broughton Archipelago, British Columbia. Aquaculture Environment Interactions, 1:137–146.

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