

# The dynamics of coupled populations subject to control

Stephanie J. Peacock<sup>1,\*</sup> · Andrew W. Bateman<sup>1,2,3</sup> · Martin Krkošek<sup>2,3</sup> · Mark A. Lewis<sup>1,4</sup>

Received: August 25, 2015 / Accepted: January 19, 2016

**Abstract** The dynamics of coupled populations have mostly been studied in the context of metapopulation viability with application to, for example, species at risk. However, when considering pests and pathogens, eradication, not persistence, is often the end goal. Humans may intervene to control nuisance populations, resulting in reciprocal interactions between the human and natural systems that can lead to unexpected dynamics. The incidence of these human-natural couplings has been increasing, hastening the need to better understand the emergent properties of such systems in order to predict and manage outbreaks of pests and pathogens. For example, the success of the growing aquaculture industry depends on our ability to manage pathogens and maintain a healthy environment for farmed and wild fish. We developed a model for the dynamics of connected populations subject to control, motivated by sea louse parasites that can disperse among salmon farms. The model includes exponential population growth with a forced decline when populations reach a threshold, representing control interventions. Coupling two populations with equal growth rates resulted in phase locking or synchrony in their dynamics. Populations with different growth rates had different periods of oscillation, leading to quasiperiodic dynamics when coupled. Adding small amounts of stochasticity destabilized quasiperiodic cycles to chaos, while stochasticity was damped for periodic or stable dynamics. Our analysis suggests that strict treatment thresholds, although well intended, can complicate parasite dynamics and hinder control efforts. Synchronizing populations via coordinated management among farms leads to more effective control that is required less frequently. Our model is simple and generally applicable to other systems where dispersal affects the management of pests and pathogens.

**Keywords** aquaculture, dispersal, ecosystem service, phase locking, population dynamics, synchrony

## 1 Introduction

As the global human population grows, there is an increasing need to understand how interactions between human and natural systems alter ecosystems and the services they provide (Millennium Ecosystem

<sup>1</sup> Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

<sup>2</sup> Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada M5S 3B2

<sup>3</sup> Salmon Coast Field Station, Simoom Sound, British Columbia, Canada V0P 1S0

<sup>4</sup> Mathematical and Statistical Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2G1

\*Corresponding author: [stephanie.j.peacock@gmail.com](mailto:stephanie.j.peacock@gmail.com)

Assessment 2005). Social and ecological systems have traditionally been studied separately, but their integration as coupled human and natural systems (CHANS) can reveal unexpected dynamics due to nonlinearities and thresholds in the way that humans and ecosystems interact (Liu *et al* 2007). CHANS can exhibit emergent properties, not present in isolated human or natural systems but resulting from the interactions between them. There is a need to integrate studies of human actions with the natural dynamics of populations and communities to understand relevant feedbacks and develop effective policy that reduces human degradation of essential ecosystems services.

The natural dynamics of pests and pathogens have been of interest to scientists for some time, due to the economic importance of agricultural pests (Oerke 2006) and human cost of transmissible diseases (Keeling and Gilligan 2000, *e.g.*). The role of dispersal among populations in hindering control efforts has long been recognized (Levins 1969, *e.g.*). Theoretical models of coupled populations have shown that if neighbouring populations fluctuate out of phase, such that high abundances at one location correspond to low abundances at another, dispersal can increase the probability of persistence via the rescue effect (Brown and Kodric-Brown 1977; Kendall and Fox 1998). The rescue effect is often thought of as beneficial in the context of population viability of endangered species, but in the context of disease, dispersal among local populations with asynchronous dynamics may hinder efforts to eradicate disease (*e.g.*, Bolker and Grenfell 1996). Mathematical models (*e.g.*, Liebhold *et al* 2004; Holt and McPeck 1996; Hastings 1993) and observational data (*e.g.*, Ranta *et al* 1995; Steen *et al* 1996) have suggested that dispersal will tend to synchronize local populations. Synchronized populations are more susceptible to extinction because stochastic events or human intervention can cause catastrophic losses when all populations are at low abundance, with little opportunity for recolonization. Paradoxically, dispersal could therefore help or hinder efforts to control disease in metapopulations depending on whether dispersal results in synchronized pathogen dynamics, or the rescue effect (Abbott 2011).

Treatments with chemotherapeutants and wildlife culls (*e.g.*, to reduce disease transmission) are examples of control efforts that result in an immediate decline in the unwanted populations, but resurgence may be swift if nearby populations persist. The optimal allocation of control effort among subpopulations may depend on the level of connectivity and relative growth rates of the populations. For example, in control of the yellow legged herring gull, a nuisance species in the western Mediterranean, the magnitude of the cull and life stage to be targeted depends on the dispersal rate (and relative growth rates) among gull populations (Brooks and Lebreton 2001). Tuberculosis in New Zealand possums can be controlled by culling infected individuals with poison baits, but the effectiveness of this control depends on the timing of application and spatial configuration of habitat patches (Fulford *et al* 2002). In general, asynchrony in the dynamics of disease among host local populations likely decreases the probability of successful eradication (Earn *et al* 1998). Indeed, it has been proposed that efforts to eradicate measles on a global scale were hampered after vaccination programs of the late-1960s inadvertently resulted in the decorrelation of measles epidemics in UK cities (Bolker and Grenfell 1996).

The motivation for this study came from parasite dynamics in open-net aquaculture; a coupled human and natural system where the eradication of pathogens has proved difficult. The rapid expansion of aquaculture (FAO 2014) has resulted in changes to coastal ecosystems including the emergence of disease (Walker and Winton 2010) and transmission of pathogens between farmed and wild fish (Heggberget *et al* 1993). In regions where farmed and wild fish coexist, the health of the system depends on effective management of disease in farmed fish (Peacock *et al* 2013; Tompkins *et al* 2015). Connectivity among populations in the marine environment is typically higher than in terrestrial systems (McCallum *et al* 2003), and dispersal of pathogens among host populations can complicate disease control.

In particular, parasitic copepods known as sea lice or salmon lice, predominantly *Lepeophtheirus salmonis* and *Caligus* spp., have been a persistent problem in salmon aquaculture, costing millions of dollars in treatment and reduced feed conversion ratios, negatively impacting fish health, and damaging public perception of farmed salmon (Costello 2009). Many approaches have been taken to minimize sea louse outbreaks, including biomass restrictions to limit host density, strategic siting of farms, the

use of cleaner fish that prey on sea lice, and the application of chemotherapeutants (Rae 2002; Brooks 2009). Sea louse populations on salmon farms within a region are connected via the dispersal of free-living larvae (Adams et al 2012), and studies have shown that critical host density thresholds for sea lice exist at regional scales (Frazer et al 2012; Jansen et al 2012; Kristoffersen et al 2013). It has been estimated that 28% of infections are due to the influx of larvae from neighbouring farms (Aldrin et al 2013). This connectivity among farms affects the growth of sea louse populations on any given farm and the efficacy of treatments. Furthermore, frequent and less effective use of chemotherapeutants may facilitate the evolution of resistance in sea lice (Aaen et al 2015), which is a major challenge facing the aquaculture industry (Igboeli et al 2014). Coordination of management among farms may be key in effectively managing sea lice (Kristoffersen et al 2013), as well as the spread of other pathogens. Many studies have focused on statistical analyses of monitoring data to uncover the relationships among farms (e.g., Jansen et al 2012; Aldrin et al 2013; Rogers et al 2013; Revie et al 2002) but much can be learned from applying more general theoretical models of population and disease dynamics (e.g., Frazer et al 2012).

In this paper, we develop a simple model for the dynamics of two populations connected by dispersal, where each population is subject to external control when it reaches a threshold density. The model complements previous work examining sea louse populations on individual salmon farms (Krkošek et al 2010; Rogers et al 2013) and within a region (Jansen et al 2012; Aldrin et al 2013) to explicitly examine how connectivity between parasite populations on adjacent farms can alter the timing and frequency of treatments. This work also builds on our general theoretical understanding of how dispersal (Hastings 1993; Goldwyn and Hastings 2011; Dey et al 2015; Kendall and Fox 1998) and intervention (Chau 2000; Sah et al 2013) affect the dynamics of coupled populations. The model was motivated by sea lice on farmed salmon, but has general applicability to other systems where dispersal affects control, such as in agricultural pests of crops within a region (Ives and Settle 1997), and transmissible diseases in wildlife (Tompkins et al 2015) and humans (e.g., Bolker and Grenfell 1996).

## 2 Methods

### 2.1 A simple model for growth and control

Analyses of sea louse population dynamics on isolated salmon farms suggest that parasite populations grow exponentially in the absence of treatment (Krkošek et al 2010; Rogers et al 2013). Exponential growth is not unique to sea lice, and has been observed in birds (Van Bael and Pruett-Jones 1996), mammals (Silva 2003), and insects (Birch 1948), and has been used to describe dynamics of other agricultural pests (e.g., Samways 1979). Although negative density dependence will regulate populations at some point, management intervention in the case of pests and parasites may prevent populations from reaching such high densities. Thus, although the following model was motivated by sea louse parasites on salmon farms, it likely has broad applicability and may inform management of other pests and parasites. In developing the model, we refer to populations in adjacent patches rather than parasites on adjacent salmon farms to maintain this generality.

The dynamics of two populations that are continuously coupled by dispersal are described by,

$$\begin{bmatrix} u \\ v \end{bmatrix}' = \begin{bmatrix} r_{uu} & r_{uv} \\ r_{vu} & r_{vv} \end{bmatrix} \begin{bmatrix} u \\ v \end{bmatrix}, \quad (1)$$

where  $u$  is the population density in patch one,  $v$  is the population density in patch two,  $r_{ii}$  is the internal growth rate of population  $i$  where  $i = u$  or  $v$  and  $r_{ij}$  is the connectivity probability from population  $j$  to population  $i$ . We refer to the total growth rate of population  $i = u$  or  $v$  as the row sum of internal growth

and connectivity:  $r_{ii} + r_{ij}$ . The solutions for  $u(t) = f_u(t, u_0, v_0)$  and  $v(t) = f_v(t, u_0, v_0)$  are given in Appendix A.

We included control treatments by forcing a reduction in a population when it reached the threshold abundance of  $N_{\max}$ . Many countries, including Norway, Ireland, the United States, and Canada, require salmon farms to treat their fish with chemotherapeutants when a threshold sea louse abundance is reached, but this threshold may vary among regions (Brooks 2009). For our simulations, we chose  $N_{\max} = 3$  motile lice per fish, based on guidelines in Pacific Canada that recommend treatment when farmed salmon have an average of three lice per fish (British Columbia Ministry of Agriculture and Lands 2005), but the value of the threshold is arbitrary for the qualitative analysis we perform here. Observations suggest that chemotherapeutants may kill up to 95% of motile sea lice on treated farmed salmon (Lees et al 2008), although treatment efficacy may be lower in many regions and is undoubtedly changing (Aaen et al 2015). We assumed that treatments were effective, and when either  $u(t)$  or  $v(t)$  exceeded  $N_{\max}$ , we modelled a treatment of that population by forcing the dynamics to reset with the initial condition for the treated population being a 95% reduction from the threshold (i.e.,  $N_{\min} = (1 - 0.95)N_{\max}$ ), and the initial condition for the untreated population being equal to the density prior to treatment of the other population. For example, starting with initial population densities  $u_k$  and  $v_k$  at  $t = 0$ , if  $u(t)$  reaches the threshold  $N_{\max}$  at time  $t = T_u$ , the system would be reset with  $t = 0$  and initial conditions  $u_{k+1} = N_{\min}$  and  $v_{k+1} = f_v(T_u, u_k, v_k)$ . The subscript  $k$  here represents the treatment number counted across both populations. In the following section, we develop a discrete-time model that describes the population density at treatment  $k + 1$  based on the population density at treatment  $k$ .

## 2.2 Discrete-time treatment dynamics

We aimed to understand the conditions under which the populations will become synchronized, settle into a regular pattern of alternating treatments, or have unpredictable treatment timing. To this end, we reduced the dimensionality of the system while retaining key properties (Schaffer 1985) by deriving a discrete-time map for the population density in a focal population when the other population is treated. This approach is related to ‘‘peak to peak’’ dynamics of time series data in which past maxima are used to predict future peaks in time-series oscillations (e.g., Rinaldi et al 2001). A similar approach is also often used to reduce the dimensionality of a system of three or more differential equations by plotting successive points where the three-dimensional phase dynamics pass through a two-dimensional plane, called a Poincaré section (e.g., Hastings and Powell 1991; Schaffer 1985).

Given the initial population densities in the two patches, we solved Eq. (1) for the time,  $T_u$ , until population  $u$  reaches the treatment threshold (Appendix A) and the time,  $T_v$ , until population  $v$  reaches the treatment threshold. We calculated  $\tilde{T} = T_u - T_v$ , where  $\tilde{T} < 0$  indicates that the treatment of  $u$  will happen next, and  $\tilde{T} > 0$  indicates that the treatment of  $v$  will happen next. The population densities after the next treatment  $k + 1$  are therefore

$$\begin{bmatrix} u \\ v \end{bmatrix}_{k+1} = \underbrace{(1 - H(\tilde{T})) \begin{bmatrix} N_{\min} \\ f_v(T_u, u_k, v_k) \end{bmatrix}}_{u \text{ is treated}} + \underbrace{H(\tilde{T}) \begin{bmatrix} f_u(T_v, u_k, v_k) \\ N_{\min} \end{bmatrix}}_{v \text{ is treated}}, \quad (2)$$

where  $H(\tilde{T})$  is the Heaviside step function that equals zero when  $\tilde{T} < 0$  and one otherwise. We used the dynamical system described by (2) to construct a return map that takes the  $u$  when  $v$  is initially treated,  $u^*$ , and returns  $u$  the next time  $v$  is treated,  $\phi(u^*)$ . We refer to  $\phi(u^*)$  as the population density (in patch one) at re-treatment (of patch two). We show in Appendix B that the general equation for this return map is

**Table 1** Summary of scenarios for how increasing connectivity affects dynamics.

| Scenario | Growth rates |              |                          |                          |
|----------|--------------|--------------|--------------------------|--------------------------|
|          | $u$ internal | $v$ internal | from $u$ to $v$          | from $v$ to $u$          |
|          | $r_{uu}$     | $r_{vv}$     | $r_{vu}$                 | $r_{uv}$                 |
| A        | 1.00         | 1.00         | 0.01 $\rightarrow$ 1.00* | 0.01 $\rightarrow$ 1.00* |
| B        | 1.00         | 1.00         | 0.01 $\rightarrow$ 1.00  | 0.01                     |
| C        | 1.00         | 0.50         | 0.01 $\rightarrow$ 1.00  | 0.01 $\rightarrow$ 1.00  |
| D        | 1.00         | 0.50         | 0.01 $\rightarrow$ 1.00  | 0.01                     |

\*Under scenario A, we considered connectivity increasing to 2.00 when assessing the frequency of treatments.

$$\phi(u^*) = \underbrace{H(\tilde{T}_0) f_u(T_{v0}, u^*, N_{\min})}_{m=0} + \underbrace{\left[ \sum_{m=1}^{\infty} H(\tilde{T}_m) \prod_{n=0}^{m-1} [1 - H(\tilde{T}_n)] \right] f_u(T_{vm}, N_{\min}, v_{m-1})}_{m \geq 1}, \quad (3)$$

where treatment of  $u$  occurs  $m$  times before  $v$  is treated again. The time between treatment  $m - 1$  and the next treatment of  $v$  is denoted  $T_{vm}$ , and  $\tilde{T}_m = T_{um} - T_{vm}$ . The value of  $m$  depends on the relative growth rates of the two populations and the magnitude of connectivity. The values of  $T_{um}$  and  $T_{vm}$  cannot be solved for explicitly (Appendix A), therefore we simulated the dynamics using a recursive algorithm to obtain the shape of  $\phi(u^*)$  (Appendix C).

### 2.3 Parameter sensitivity

We investigated the dynamics of the return map for a limited number of parameter combinations with each growth rate constrained between zero and two. A comprehensive description of the dynamics of the return map under all parameter combinations was impossible because the return map had to be simulated, so we focused on results from four scenarios that describe parameter changes that might occur in networks of salmon farms (Table 1). First, we considered a scenario where the internal growth rates were constant and equal at  $r_{uu} = r_{vv} = 1.00$  and connectivity increased from 0.01 to 1.00 in increments of 0.01 ( $r_{uv} = r_{vu} = r_{ij}$ , scenario A). This scenario could represent two salmon farms being brought closer together, increasing exchange of parasites between them. Second, we considered increasing  $r_{vu}$  from 0.01 to 1.00, but connectivity in the other direction constant at  $r_{uv} = 0.01$  (scenario B). This scenario could represent an increase in the advection of larvae from one farm to another. The third scenario had connectivity equal and increasing as in scenario A, but  $u$  had twice the internal growth rate as  $v$  ( $r_{uu} = 1.00, r_{vv} = 0.50$ , scenario C). Similarly, in scenario D,  $u$  had twice the internal growth rate as  $v$ , but  $r_{vu}$  increasing from 0.01 to 1.00. Different internal growth rates could represent different host population sizes or environmental conditions affecting growth on the two farms.

In each scenario, for each value of the appropriate control parameters (i.e.,  $r_{vu}$ , and  $r_{uv}$  in scenarios A & C; Table 1), we simulated the return map over 2000 iterations starting at  $u_0^* = 2.7$ . We constructed a bifurcation diagram by plotting the values of  $\phi(u^*)$  for the last 500 iterations, over the value of the control parameter. We present the results for  $u_0^* = 2.7$ , but we examined the bifurcation diagrams starting from several values of  $u_0^*$  to check that the long-term dynamics were not dependent on the initial conditions (Online Resource, Fig. S1).

We also considered the long-term frequency of treatments over increasing connectivity between populations. To calculate the frequency of treatments, we first iterated the return map 500 times starting at  $u^* = 2.7$  to remove transient dynamics and then simulated the dynamical system given by Eq. 2 for 100 treatments, where treatments were counted across both populations. If the two populations were treated at

the same time, we considered it two treatments. The frequency of treatments was then calculated as 100 divided by the time taken to reach 100 treatments. To examine how connectivity affects the frequency of treatments independent of overall increases in the growth rates, we also considered a variation on scenario A in which the internal growth rate declined as connectivity increased such that  $r_{ii} = 1 - r_{ij}$  and the total growth rates to populations remained constant (Online Resource).

## 2.4 Testing for chaos

Under certain parameter values, the numerically-calculated return map given by Eq. (3) had a discontinuity at the point where  $u$  was treated  $m$  times or  $m + 1$  times, depending on the population density  $u^*$  at the first treatment of  $v$  (see Results). This discontinuity resulted in cyclic behaviour that was difficult to classify by numerical simulations as periodic or chaotic (Galvanetto 2000). Chaos is extreme sensitivity to initial conditions, and can be classified by calculating the rate of divergence between two trajectories that are initially close (Hastings et al 1993). This rate is known as the Lyapunov exponent  $\lambda$  where  $\epsilon_n = \epsilon_0 e^{\lambda n}$ ,  $\epsilon_0 \ll 1$ , and  $\epsilon_n$  is the difference between a perturbed and fiducial trajectory after  $n$  iterations of the return map. Positive exponents indicate that two trajectories will diverge and therefore the dynamics are sensitive to the initial condition, characteristic of chaos (Sprott 2003; Hastings et al 1993).

To determine if the return map lead to chaotic dynamics under the scenarios we considered, we numerically calculated the Lyapunov exponent for all parameter combinations (Table 1) as,

$$\lambda = \sum_{n=1}^{10^4} \log \left( \frac{|\epsilon_n|}{\epsilon_0} \right). \quad (4)$$

For discontinuous return maps such as ours, Eq. (4) is not valid if the fiducial and perturbed trajectories project onto different pieces of the return map (Galvanetto 2000). To avoid this problem, we chose a small initial difference between the trajectories of  $\epsilon_0 = 10^{-8}$ . At each iteration of the return map, we readjusted the two trajectories bringing them back together along the line of separation such that the difference between them was  $\epsilon_0$ , with the sign of the difference equal to the sign of  $\epsilon_{n-1}$  (Sprott 2003, p. 116-117):

$$\epsilon_n = \phi \left( \phi^{n-1}(u^*) + \frac{\epsilon_{n-1}}{|\epsilon_{n-1}|} \epsilon_0 \right) - \phi^n(u^*) \quad (5)$$

where  $\phi^n(u^*)$  represents the  $n^{\text{th}}$  iteration of the fiducial trajectory (i.e.,  $\phi^2(u^*) = \phi(\phi(u^*))$ ). This correction made it very unlikely that the two trajectories would project onto different pieces of the return map, as the difference between them remained relatively small. In all our simulations, we verified that  $\epsilon_n \ll 1$ , suggesting that the two trajectories had projected on to the pieces of the return map.

In the numerical calculation, the value of the Lyapunov exponent may depend on the choice of  $u_0^*$  (Earnshaw 1993), so we repeated the calculation of Eq. (4) for three randomly-chosen values between  $N_{\min}$  and  $N_{\max}$ . For each starting value, we iterated the map 200 times to remove transient dynamics and then used the subsequent 10 000 iterations in the calculation of  $\lambda$  (Sprott 2003). We report the mean value of  $\lambda$  over the three values of  $u_0^*$  for each value of connectivity described in section 2.3.

## 2.5 Stochasticity

Environmental stochasticity may influence the growth of populations, as is the case for sea louse populations on salmon farms (Aldrin et al 2013; Rogers et al 2013). We added stochasticity to the return map and evaluated its influence on the long-term dynamics. At each iteration, we multiplied  $\phi(u^*)$  by a

log-normal distribution with mean one and standard deviation on the log scale of  $s = 10^{-2}$  (Hilborn and Mangel 1997). We compared the stochastic dynamics for parameters that corresponded to a quasiperiodic cycle with a Lyapunov exponent close to zero in the deterministic model versus those that produced periodic dynamics or had a single equilibrium with a Lyapunov exponent that was relatively large and negative in the deterministic model. We examined 200 iterations of the return map for two trajectories: one fiducial trajectory starting at  $u_0^* = 2.7$  and a second perturbed trajectory initially separated by a small distance  $\epsilon_0 = 10^{-8}$  from the fiducial trajectory. We compared the difference between these trajectories over increasing iterations and also calculated the Lyapunov exponent, with and without stochasticity in the model. In calculating the Lyapunov exponent for the stochastic return map, we used an independent sequence of log-normal values for the fiducial and perturbed trajectories. To ensure the value of  $\lambda$  in the stochastic model was not sensitive to the particular log-normal random values in the simulation, we repeated the calculation 50 times and report the mean and range.

### 3 Results

#### 3.1 Simulations of simple model

Simulations of the model predicted that for two isolated populations (i.e.,  $r_{ij} = 0 \forall i \neq j$ ), each population will oscillate with treatments occurring at regular intervals. The frequency of treatments was dictated by the internal population growth rate  $r_{ii}$ , with higher growth rates resulting in more rapid resurgence of the population after treatment and therefore a higher frequency of treatments.

When we coupled the two populations, the dynamics were more complex. Simulations displayed a range of behaviour including alternating treatments (i.e., phase locking; Fig. 1a), synchrony between the populations (Fig. 1b), or seemingly chaotic dynamics (Fig. 1c; Table 2). To better understand this complex behaviour, we considered a one-dimensional discrete-time return map describing the change in  $u$  in between treatments of  $v$ .

#### 3.2 Discrete-time treatment dynamics

For two populations that have identical growth rates but low connectivity, the return map had a stable equilibrium in the open interval  $(N_{\min}, N_{\max})$  (the exact value depended on the level of connectivity) and unstable equilibria at  $N_{\min}$  and at  $N_{\max}$ . This dynamical behaviour is termed phase locking because the two populations had the same period but their dynamics were shifted out of phase by a fixed amount (Becks and Arndt 2013). The consequence was alternating treatments of  $u$  and  $v$ , with a stable equilibrium for the population density  $u$  whenever  $v$  was treated (Fig. 1a & 2a). If both populations were treated at the same time,  $u$  was exactly at the unstable equilibrium. In this case, the two populations remained synchronized because the period of their oscillations was identical.

If the stable equilibrium was at the treatment threshold  $N_{\min}$  or  $N_{\max}$ , then the dynamics of the two populations tended towards synchrony. From our limited investigation of parameter space, this was observed when connectivity between the populations was equal and greater than the internal growth rates of the populations (i.e.,  $r_{ij} = r_{ji} > r_{ii} = r_{jj}$ ; Table 2). Synchrony also occurred if the internal growth rates were unequal, but the total growth rates of the two populations were equal (i.e.,  $r_{uu} + r_{uv} = r_{vv} + r_{vu}$ ) and one population had a lower growth rate and higher connectivity to the other population. In this case, the population with higher connectivity became entrained by the dynamics of the “source” population.

A third type of behaviour occurred when the total growth rates of the populations were not equal. In this case, the two populations oscillated with different periods. There was a discontinuity in the return map where  $u$  went from being treated once to twice (or two to three times, depending on the relative growth rates) before  $v$  was treated (Fig. 2c). This discontinuity resulted in periodic or seemingly chaotic

behaviour. Unlike in phase locking or synchrony, the population density  $u$  was not the same each time  $v$  was treated (Fig. 1c).

**Table 2** Summary of parameter values under which different dynamics were observed.

| Internal growth rate | Connectivity                                    | Behaviour                  | Figure       |
|----------------------|---|----------------------------|--------------|
| $r_{uu} = r_{vv}$    | $(r_{uv} = r_{vu}) \leq (r_{uu} = r_{vv})$      | Phase locking              | Fig. 2a      |
|                      | $(r_{uv} = r_{vu}) > (r_{uu} = r_{vv})$         | Synchrony                  | Fig. 2b & 4a |
|                      | $r_{uv} \neq r_{vu}$                            | Cycles                     |              |
| $r_{uu} \neq r_{vv}$ | $r_{uv} = r_{vu}$ ; incl. $r_{uv} = r_{vu} = 0$ | Cycles                     | Fig. 2c      |
|                      | $(r_{uu} + r_{uv}) = (r_{vu} + r_{vv})$         | Synchrony or phase locking | Fig. 4b & S8 |
|                      | Else  | Phase locking or cycles    | Fig. 2c      |

### 3.3 Parameter sensitivity

Increasing the connectivity between two patches resulted in changes to the long-term values of  $\phi(u^*)$ , the population density at re-treatment (Fig. 3 and Fig. S1). Some of these changes happened abruptly when the connectivity crossed a threshold (Fig. 3c,d) while others happened gradually (Fig. 3a). When the two populations had equal internal growth rates and equal connectivity, increasing the connectivity lead to increasing population density at re-treatment, until connectivity equalled the internal growth rates (scenario A in Table 1; Fig. 3a). At that point, the dynamics were phase-locked such that the population density at re-treatment was always the initial population density (i.e.,  $(\phi(u^*) = u^*) \forall u^*$ ; see Online Resource Figs S2-S5 for illustrative animations).

When connectivity was increased from  $u$  to  $v$  only (e.g., scenario B in Table 1), the return map had a discontinuity because the total growth rate of  $v$  was higher than that of  $u$ . In that case, we observed periodic dynamics, the simplest being a two-point cycle that occurred near  $r_{vu} = 0.8$  (Fig. 3b). In these two point cycles, after the initial treatment of  $v$ ,  $u$  will be treated once, then after the next treatment of  $v$ ,  $u$  will be treated twice. This cycle repeats itself resulting in a pattern of treatments  $v, u, v, u, v, u, v, u, u, u$ , etc., with  $u$  having a lower population density at the treatment of  $v$  if  $u$  has been treated twice since the previous treatment of  $v$ .

When the internal growth rates of the populations were not equal (i.e., scenarios C and D in Table 1), the dynamics tended to be cyclic (Fig. 3c,d). However, abrupt changes from cyclic dynamics to stable points occurred as connectivity was increased to the point where the return map touched or crossed the 1:1 line. For example, in scenario D, when  $r_{vu}$  neared 0.51, the dynamics tended towards phase locking (Fig. S5). As connectivity increased from  $r_{vu} = 0.35$  to  $r_{vu} = 0.51$ , the stable point approached  $N_{\min}$  and the magnitude of the rescue effect decreased because  $u$  had a lower population density on treatment of  $v$ . When the total growth rates were exactly equal (i.e.,  $r_{vu} = 0.51$  such that  $(r_{uu} + r_{uv}) = (r_{vu} + r_{vv})$ ), the two populations became synchronized (Fig. 3d; Table 2).

Increasing the connectivity between the patches did not necessarily result in a monotonic increase in the frequency of treatments (Fig. S6). For illustration, we focus on the frequency of treatments under scenario A, but with connectivity increasing to  $r_{uv} = r_{vu} = 2.00$ , and on scenario D with connectivity between  $r_{vu} = 0.35$  and 0.52. In these scenarios, the internal growth rates were held constant (Table 1). Thus, we expected that the frequency of treatments would increase with increasing connectivity because the the total growth rate to the populations was increasing. However, we observed a sharp decline in the frequency of treatments in scenario A when connectivity exceeded the internal growth rate (Fig. 4a).



In scenario D, the frequency of treatments declined over the region of phase locking (see Fig. 3d) as the stable point approached  $N_{\min}$ , reducing the impact of the rescue-effect. The minimum frequency of treatments occurred where populations became synchronized at  $r_{vu} + r_{vv} = r_{uv} + r_{uu}$  (i.e.,  $r_{vu} = 0.51$ , Fig. 4b). In the Online Resrouce, we also considered a decline in the internal growth rate as connectivity increased such that  $r_{ii} = 1 - r_{ij}$  and the total growth rates to populations remained constant in order to examine how connectivity affects the frequency of treatments independent of overall increases in the growth rates. These simulations also showed a decrease in the frequency of treatments when populations became synchronized, and frequency of treatments remained low as connectivity increased further (Fig. S7).

### 3.4 Testing for chaos

The time series of population density appeared chaotic when the period of the population cycles in the two patches was different (Fig. 1c). The bifurcation diagrams showed large regions of parameter space that had potentially chaotic dynamics (Fig. 1c and Fig. 3c-d). However, the Lyapunov exponent was not greater than zero in any of the scenarios (Fig. 3c-d), indicating the dynamics were not chaotic. Instead, the dynamics of two populations with different internal periods of oscillations appeared quasiperiodic. For periodic cycles, after iterating the return map a finite number of times, we returned to the exact value at which we started (e.g., Fig. 5b). Quasiperiodic cycles are differentiated from periodic cycles by cobwebbing the return map; over several treatments of  $v$ ,  $\phi(u^*)$  returned to the original branch of the return map very near to the starting point but not exactly at the starting point, such that the dynamics were shifted slightly (e.g., Fig. 5d). We note that a precise distinction between quasiperiodic and periodic dynamics is limited by the the number of times we could numerically iterate the return map.

### 3.5 Stochasticity

Small amounts of stochasticity added to the return map tended to shift quasiperiodic dynamics towards chaos such that two population initially close had very different population densities after 200 iterations. However, when the dynamics were periodic, the stochasticity was damped such that the fiducial trajectory and the perturbed trajectory remained relatively close over 200 iterations of the return map (Fig. 5a). A small change in  $r_{vu}$  from 0.72 to 0.71 in scenario C caused a transition from periodic to quasiperiodic dynamics (Fig. 5b,d). In the quasiperiodic case, the two trajectories drifted apart as the stochasticity accumulated (Fig. 5c). For scenario D, when  $r_{vu}$  was increased from 0.31 to 0.32, the deterministic dynamics went from quasiperiodic to phase locking (Fig. 3d). In this case, as in scenario C, stochasticity caused the trajectories to diverge for  $r_{vu} = 0.31$  corresponding to the quasiperiodic dynamics, but stochasticity was damped when the deterministic dynamics exhibited phase locking (Fig. S9). This shows that small amounts of stochasticity can accumulate, when dynamics are not stable or periodic, and result in sensitivity to initial conditions that is characteristic of chaotic dynamics. Indeed, the Lyapunov exponents for the stochastic version of the model shown in Fig. 5 were  $\lambda = 14.19$  (range 14.16 to 14.21) for  $r_{vu} = 0.71$ , compared to  $\lambda = -0.001$  for the deterministic model. The Lyapunov exponent was also positive but smaller for the periodic dynamics corresponding to  $r_{vu} = 0.72$ , which showed damped oscillations (Fig. 5a).

## 4 Discussion

The current magnitude and extent of coupled human and natural systems is unprecedented and there is an urgent need to better understand the consequences of accelerating human impacts on natural ecosystems

and the services that they provide (Millennium Ecosystem Assessment 2005). In this study, we considered the reciprocal interactions between the natural dynamics of parasite populations and human intervention in the form of parasite control. The resulting dynamics were surprisingly complex, and demonstrate the potential for unexpected behaviour to result in policies that are well-meaning but have unintended and potentially perverse consequences for the health of ecosystems.

#### 4.1 Implications for sea louse management

In Pacific Canada, salmon farms must treat with chemotherapeutants when sea louse populations exceed three motile sea lice per fish, a guideline that is meant to protect juvenile wild salmon from sea louse infestations during a vulnerable period of their migration (British Columbia Ministry of Agriculture and Lands 2005; Brooks 2009). However, our model showed that strict threshold control of parasites according to this policy may lead to asynchronous or even chaotic dynamics on adjacent farms connected by dispersal. In practice, whether dynamics are truly chaotic may not matter; given the timeframe of observations and management decisions, periodic dynamics may be just as challenging to predict and control. Increasing connectivity between populations tended to increase the frequency of treatments, unless populations were synchronized. Frequent, uncoordinated treatments are a problem because they may hasten the evolution of sea louse resistance to current chemotherapeutants by allowing sea lice that are resistant to treatment to disperse and find mates on nearby, untreated farms (Aaen *et al* 2015). Further, asynchronous parasite dynamics among farms make it difficult to ensure low parasite abundance during the wild juvenile salmon migration. Paradoxically, because threshold treatments tend to decouple parasite populations when not coordinated, this well-intended policy could mean high sea louse abundances on salmon farms along the migration route, transmission to juvenile salmon (Krkošek *et al* 2006; Marty *et al* 2010) and adverse impacts on wild salmon populations (Krkošek *et al* 2011; Peacock *et al* 2013).

The current treatment threshold policy does reduce louse abundance on farms, but more coordinated efforts to synchronize the parasite dynamics among farms may reduce reliance on chemotherapeutants. We found that at low levels of dispersal, the frequency of treatments increased with increasing connectivity, suggesting that dispersal among farms hinders control efforts. However, the frequency of treatments declined substantially when connectivity was high enough that parasite dynamics were synchronized between farms (Fig. 4a). In reality, dispersal of sea lice among farms is likely too low to synchronize parasite dynamics on adjacent farms by itself (Adams *et al* 2012; Foreman *et al* 2015, although shared environmental effects may help, see below). But for populations that were weakly coupled but had similar internal growth rates (e.g., have a similar number/age of hosts and are exposed to similar environmental conditions), synchrony could be induced by either treating populations at the same time (even if one population had not reached the threshold) or coordinating stocking and harvest among adjacent farms so that they start with the same initial conditions. Such strategies may reduce the potential for the rescue effect in louse populations on adjacent farms and therefore lower the frequency of treatments, but require coordinated effort among multiple stakeholders (e.g., different levels of government and industry). Pest management plans that require this kind of cooperation have been recommended (e.g., Brooks 2009; Peacock *et al* 2013), but are still not implemented in many areas, including Pacific Canada.

#### 4.2 Model limitations

Our simple model did not consider exogenous forces on the population dynamics such as variability in growth rates due to shared environmental conditions. Such forces are likely, due to the effect of temperature and salinity on settlement success (Bricknell *et al* 2006), developmental rates (Groner *et al* 2014; Stien *et al* 2005) and survival (Johnson and Albright 1991a) of sea lice. Environmental conditions have been proposed to result in synchrony of local population dynamics over wide geographic scales (i.e.,

Moran effects; Moran 1953). Indeed, such an effect has been shown in a variety of systems (e.g., Cheal et al 2007; Grenfell et al 1998). Sea louse populations on farmed salmon show annual cycles (Marty et al 2010) that may be driven, in part, by changes in salinity and/or temperature (Johnson and Albright 1991b). The relative contributions of dispersal versus environment in driving synchrony of local populations is an ongoing question in ecology (Lande et al 1999), and sea lice in networks of salmon farms may provide an ideal model system due to the extensive monitoring of louse populations and environmental conditions on salmon farms. These data have been used in statistical analyses aimed at management applications (e.g., Rogers et al 2013; Revie et al 2003), but could also be useful in answering questions of general interest in ecology.

### 4.3 Dynamics of coupled populations

There has been considerable theoretical interest in how dispersal affects the dynamics of coupled populations (e.g., Dey et al 2014, 2015; Hastings et al 1993; Kendall and Fox 1998; Goldwyn and Hastings 2011; Franco and Ruis-Herrera 2015). Our analysis expands on previous theoretical work in several ways. First, we considered control of populations when a threshold abundance was reached. Previous work has considered density dependence as part of the intrinsic dynamics of local populations (e.g., the Ricker model, Dey et al 2015; Hastings et al 1993) or periodic interventions such as feeding and harvest (e.g., Chau 2000). We consider a nonlinear reciprocal interaction between parasite populations and control intervention that had not yet been explored, although our approach shares similarities with work on Adaptive Limiter Control, discussed below (e.g., Sah et al 2013). Second, we analyzed a continuous-time population model that may be more representative for some species, but were able to simplify our analysis by considering a discrete time return map for the population density in one patch at the time of treatment in the other. This dynamical-systems approach has gained attention recently in the context of peak to peak dynamics (Rinaldi et al 2001) and statistical methods for analyzing time series data (Sugihara et al 2012), but also has broader applications for simplifying analyses of continuous-time models for interacting populations (Schaffer 1985). Finally, we varied both the internal growth rates and connectivities in our populations to explore scenarios where growth rates of the two populations differed and connectivity was not necessarily reciprocal. Many studies of coupled populations only consider equal connectivity (although see Dey et al 2014; Franco and Ruis-Herrera 2015).

Increasing connectivity between two populations subject to control was expected to increase the frequency of treatments, but the simple model we developed displayed much more complex dynamics. Our results were consistent with other population models that show high connectivity leads to synchrony of populations while lower levels of connectivity lead to out-of-phase dynamics (Dey et al 2015, 2014). If the two populations had different periods due to unequal growth rates, the dynamics underwent periodic or quasiperiodic cycles. When dynamics were periodic, added stochasticity was damped such that the difference between nearby trajectories remained small. Hastings (Hastings 1993) analyzed a coupled discrete logistic model and also found that the addition of stochasticity resulted in chaos for parameter values corresponding to a four-point cycle in the deterministic model, but stable population densities for parameter values corresponding to a two-point cycle in the deterministic model. This result highlights the fine line between predictable deterministic dynamics and chaos (Hastings 1993).

Previous work on threshold interventions in population dynamics have incorporated Adaptive Limiter Control (ALC; e.g., Sah et al 2013). ALC involves a threshold intervention as in our model, but works to the opposite effect: where we consider control of a population when it goes above a threshold, ALC avoids population crashes by forcing immigration when the population drops below a threshold. Despite this difference, high thresholds for ALC tend to decouple subpopulations in a similar manner to our strict treatment threshold (Sah et al 2013). This decoupling has opposite effects on fluctuations of the metapopulation depending on the migration rate between subpopulations. At high migration rates, subpopulations

tend to be positively correlated, such that decoupling due to ALC is effective at increasing stability of the overall metapopulation. However, at low migration rates, subpopulations are more likely to be fluctuating out of phase and therefore ALC exacerbates this negative synchrony and decreases metapopulation stability. Sah *et al* (2013) found both theoretical and empirical evidence that these effects of ALC generally act to increase persistence of populations and metapopulations. Considering populations of pests and pathogens, persistence is not the desired outcome, providing an intriguing possibility that by decoupling populations, threshold effects may actually hinder eradication unless coordinated.

#### 4.4 Conclusion

The complexity of coupled human and natural systems has gained attention as we recognize and attempt to understand our impact on natural ecosystems. For aquaculture, the interaction between farm management and natural pathogen dynamics, including dispersal among farms, may lead to unpredictable dynamics that undermine our ability to maintain a healthy environment for both farmed and wild salmon. The successful management of disease in coastal ecosystems likely requires cooperation among different companies to synchronize and stabilize pathogen dynamics. This example emphasizes that human-natural couplings cross the boundaries of policy and governance, and cooperation among stakeholders at different levels is required to achieve the common goal of healthy and sustainable ecosystems that can support adaptive human populations.

**Acknowledgements** We thank three reviewers and the Handling Editor for constructive feedback on earlier versions. Funding for this work came from the Natural Sciences and Engineering Research Council of Canada (Vanier CGS to SJP, PDF to AWB, Discovery and Accelerator grants to MAL and MK), a Bill Shostak Wildlife Award and Fisher Scientific Scholarship to SJP, a Canada Research Chair and Killam Fellowship to MAL, a Sloan Fellowship in Ocean Science to MK, and a Killam Postdoctoral Fellowship to AWB. No funders had input into the design of the study.

#### References

- Aaen SM, Helgesen KO, Bakke MJ, Kaur K, Horsberg TE (2015) Drug resistance in sea lice: a threat to salmonid aquaculture. *Trends in Parasitology* 31(2):72–81, doi: 10.1016/j.pt.2014.12.006, URL <http://linkinghub.elsevier.com/retrieve/pii/S1471492214002098>
- Abbott KC (2011) A dispersal-induced paradox: Synchrony and stability in stochastic metapopulations. *Ecology Letters* 14(11):1158–1169, doi: 10.1111/j.1461-0248.2011.01670.x
- 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, doi: 10.3354/aei00052, URL <http://www.int-res.com/abstracts/aei/v3/n1/p51-63/>
- Aldrin M, Storvik B, Kristoffersen AB, Jansen PA (2013) Space-Time Modelling of the Spread of Salmon Lice between and within Norwegian Marine Salmon Farms. *PLoS ONE* 8(5):e64,039, doi: 10.1371/journal.pone.0064039, URL <http://dx.doi.org/10.1371/journal.pone.0064039>
- Becks L, Arndt H (2013) Different types of synchrony in chaotic and cyclic communities. *Nature communications* 4:1359, doi: 10.1038/ncomms2355, URL <http://www.ncbi.nlm.nih.gov/pubmed/23322047>
- Birch L (1948) The intrinsic rate of natural increase of an insect population. *The Journal of Animal Ecology* pp 15–26, URL [www.jstor.org/stable/1605](http://www.jstor.org/stable/1605)
- Bolker BM, Grenfell BT (1996) Impact of vaccination on the spatial correlation and persistence of measles dynamics. *Proceedings of the National Academy of Sciences* 93(22):12,648–12,653, URL <http://www.pnas.org/content/93/22/12648.abstract>

- Bricknell IR, Dalesman SJ, O'Shea B, Pert CC, Luntz AJM (2006) Effect of environmental salinity on sea lice *Lepeophtheirus salmonis* settlement success. *Diseases of Aquatic Organisms* 71(3):201–212, doi: 10.3354/dao071201, URL <http://www.int-res.com/abstracts/dao/v71/n3/p201-212/>
- British Columbia Ministry of Agriculture and Lands (2005) Fish Health Program 2003-2005. Tech. rep., Ministry of Agriculture and Lands, URL [http://www.agf.gov.bc.ca/ahc/fish\\_{\\_}health/Fish\\_{\\_}Health\\_{\\_}Report\\_{\\_}2003-2005.pdf](http://www.agf.gov.bc.ca/ahc/fish_{_}health/Fish_{_}Health_{_}Report_{_}2003-2005.pdf)
- Brooks EN, Lebreton JD (2001) Optimizing removals to control a metapopulation: Application to the yellow legged herring gull (*Larus cachinnans*). *Ecological Modelling* 136(2-3):269–284, doi: 10.1016/S0304-3800(00)00430-0
- Brooks KM (2009) Considerations in developing an integrated pest management programme for control of sea lice on farmed salmon in Pacific Canada. *Journal of Fish Diseases* 32(1):59–73, URL <http://login.ezproxy.library.ualberta.ca/login?url=http://search.ebscohost.com/login.aspx?direct=true{&}db=eih{&}AN=36551408{&}site=ehost-live{&}scope=site>
- Brown JHJ, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58(2):445–449, doi: 10.2307/1935620, URL <http://www.esajournals.org/doi/abs/10.2307/1935620>
- Chau NP (2000) Destabilising effect of periodic harvest on population dynamics. *Ecological Modelling* 127(1):1–9, doi: 10.1016/S0304-3800(99)00190-8, URL <http://www.sciencedirect.com/science/article/pii/S0304380099001908>
- Cheal AJ, Delean S, Sweatman H, Thompson AA (2007) Spatial synchrony in coral reef fish populations and the influence of climate. *Ecology* 88(1):158–69, doi: 10.1890/0012-9658(2007)88[158:SSICRF]2.0.CO;2, URL <http://www.ncbi.nlm.nih.gov/pubmed/17489464>
- Costello MJ (2009) How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. *Proceedings of the Royal Society B: Biological Sciences* 276(1672):3385–3394, doi: 10.1098/rspb.2009.0771, URL <http://rspb.royalsocietypublishing.org/content/276/1672/3385>
- Dey S, Goswami B, Joshi A (2014) Effects of symmetric and asymmetric dispersal on the dynamics of heterogeneous metapopulations: Two-patch systems revisited. *Journal of Theoretical Biology* 345:52–60, doi: 10.1016/j.jtbi.2013.12.005, URL <http://dx.doi.org/10.1016/j.jtbi.2013.12.005>
- Dey S, Goswami B, Joshi A (2015) A possible mechanism for the attainment of out-of-phase periodic dynamics in two chaotic subpopulations coupled at low dispersal rate. *Journal of Theoretical Biology* 367:100–110, doi: 10.1016/j.jtbi.2014.11.028, URL <http://dx.doi.org/10.1016/j.jtbi.2014.11.028>
- Earn DJD, Rohani P, Grenfell BT (1998) Persistence, chaos and synchrony in ecology and epidemiology. *Proceedings of the Royal Society of London Series B: Biological Sciences* 265(1390):7–10, URL <http://rspb.royalsocietypublishing.org/content/265/1390/7.abstract>
- Earnshaw JC (1993) Lyapunov exponents for pedestrians. *American Journal of Physics* 61(5):401, doi: 10.1119/1.17231, URL <http://scitation.aip.org/content/aapt/journal/ajp/61/5/10.1119/1.17231>
- FAO (2014) The State of World Fisheries and Aquaculture 2014. Tech. rep., Food and Agriculture Organization of the United Nations, Rome, URL [www.fao.org/publications](http://www.fao.org/publications)
- Foreman MGG, Chandler PC, Stucchi DJ, Garver KA, Guo M, Morrison J, Tuele D (2015) The ability of hydrodynamic models to inform decisions on the siting and management of aquaculture facilities in British Columbia. Canadian Science Advisory Secretariat Research Document 2015/005:vii + 49 p., URL <http://www.dfo-mpo.gc.ca/csas-sccs/>

- Franco D, Ruis-Herrera A (2015) To connect or not to connect isolated patches. *Journal of Theoretical Biology* 370:72–80, doi: 10.1016/j.jtbi.2015.01.029, URL <http://dx.doi.org/10.1016/j.jtbi.2015.01.029>
- Frazer LN, Morton A, Krkošek M (2012) Critical thresholds in sea lice epidemics: evidence, sensitivity and subcritical estimation. *Proceedings of the Royal Society B: Biological Sciences* 279(1735):1950–1958, doi: 10.1098/rspb.2011.2210, URL <http://rspb.royalsocietypublishing.org/content/279/1735/1950>
- Fulford G, Roberts M, Heesterbeek J (2002) The Metapopulation Dynamics of an Infectious Disease: Tuberculosis in Possums. *Theoretical Population Biology* 61(1):15–29, doi: 10.1006/tpbi.2001.1553, URL <http://linkinghub.elsevier.com/retrieve/pii/S0040580901915539>
- Galvanetto U (2000) Numerical computation of Lyapunov exponents in discontinuous maps implicitly defined. *Computer Physics Communications* 131(1):1–9, doi: 10.1016/S0010-4655(00)00055-2, URL <http://www.sciencedirect.com/science/article/pii/S0010465500000552>
- Goldwyn EE, Hastings A (2011) The roles of the Moran effect and dispersal in synchronizing oscillating populations. *Journal of Theoretical Biology* 289(1):237–246, doi: 10.1016/j.jtbi.2011.08.033, URL <http://dx.doi.org/10.1016/j.jtbi.2011.08.033>
- Grenfell BT, Wilson K, Finkenstadt BF, Coulson TN, Murray S, Albon SD, Pemberton JM, Clutton-Brock TH, Crawley MJ (1998) Noise and determinism in synchronized sheep dynamics. *Nature* 394(6694):674–677, doi: 10.1038/29291, URL <http://dx.doi.org/10.1038/29291>
- Groner ML, Gettinby G, Stormoen M, Revie CW, Cox R (2014) Modelling the impact of temperature-induced life history plasticity and mate limitation on the epidemic potential of a marine ectoparasite. *PLoS ONE* 9(2):e88465, URL <http://dx.doi.org/10.1371/journal.pone.0088465>
- Hastings A (1993) Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. *Ecology* 74(5):1362–1372, doi: 10.2307/1940066
- Hastings A, Powell T (1991) Chaos in a three species food chain. *Ecology* 72(3):896–903, URL <http://www.jstor.org/stable/1940591>
- Hastings A, Hom CL, Ellner S, Turchin P, Godfray HCJ (1993) Chaos in Ecology: Is Mother Nature a Strange Attractor? *Annual Review of Ecology and Systematics* 24(1):1–33, doi: 10.1146/annurev.es.24.110193.000245, URL <http://www.jstor.org/discover/10.2307/2097171>
- Heggberget TG, Johnsen BO, Hindar K, Jonsson B, Hansen LP, Hvidsten Na, Jensen AJ (1993) Interactions between wild and cultured Atlantic salmon: a review of the Norwegian experience. *Fisheries Research* 18(1-2):123–146, doi: 10.1016/0165-7836(93)90044-8
- Hilborn R, Mangel M (1997) *The Ecological Detective: Confronting Models with Data*, Monographs in Population Biology, vol 28. Princeton University Press
- Holt RD, McPeck MA (1996) Chaotic population dynamics favors the evolution of dispersal. *American Naturalist* 148(4):709–718, doi: 10.2307/2678832, URL <http://www.jstor.org/stable/2556325>
- Igboeli OO, Burka JF, Fast MD (2014) *Lepeophtheirus salmonis*: a persisting challenge for salmon aquaculture. *Animal Frontiers* 4(1):22–32, doi: 10.2527/af.2014-0004, URL <https://dl.sciencesocieties.org/publications/af/abstracts/4/1/22>
- Ives AR, Settle WH (1997) *Metapopulation Dynamics and Pest Control in Agricultural Systems*. *American Naturalist* 149(2):220–246
- Jansen PA, Kristoffersen AB, Viljugrein H, Jimenez D, Aldrin M, Stien A (2012) Sea lice as a density-dependent constraint to salmonid farming. *Proceedings of the Royal Society B: Biological Sciences* 279(1737):2330–2338, doi: 10.1098/rspb.2012.0084, URL <http://rspb.royalsocietypublishing.org/content/279/1737/2330.abstract>
- Johnson SC, Albright LJ (1991a) Development, Growth, and Survival of *Lepeophtheirus salmonis* (Copepoda: Caligidae) Under Laboratory Conditions. *Journal of the Marine Biological Association of the United Kingdom* 71(02):425–436, doi: 10.1017/S0025315400051687, URL <http://dx.doi.org/10.1017/S0025315400051687>

- org/10.1017/S0025315400051687
- Johnson SC, Albright LJ (1991b) The developmental stages of *Lepeophtheirus salmonis* (Krøyer, 1837) (Copepoda: Caligidae). *Canadian Journal of Zoology* 69(4):929–950, URL <http://dx.doi.org/10.1017/S0025315400051687>
- Keeling MJ, Gilligan Ca (2000) Metapopulation dynamics of bubonic plague. *Nature* 407(6806):903–906, doi: 10.1038/35038073
- Kendall BE, Fox GA (1998) Spatial structure, environmental heterogeneity, and population dynamics: analysis of the coupled logistic map. *Theoretical population biology* 54(1):11–37, doi: 10.1006/tpbi.1998.1365
- Kristoffersen AB, Rees EE, Stryhn H, Ibarra R, Campisto JL, Revie CW, St-Hilaire S (2013) Understanding sources of sea lice for salmon farms in Chile. *Preventive Veterinary Medicine* 111(1-2):165–75, doi: 10.1016/j.prevetmed.2013.03.015, URL <http://www.ncbi.nlm.nih.gov/pubmed/23628338>
- Krkošek M, Lewis MA, Morton A, Frazer LN, Volpe JP (2006) Epizootics of wild fish induced by farm fish. *Proceedings of the National Academy of Sciences* 103(42):15,506–15,510, doi: 10.1073/pnas.0603525103, URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1591297&tool=pmcentrez&rendertype=abstract>
- Krkošek M, Bateman A, Probošycz S, Orr C (2010) Dynamics of outbreak and control of salmon lice on two salmon farms in the Broughton Archipelago, British Columbia. *Aquaculture Environment Interactions* 1(2):137–146, doi: 10.3354/aei00014, URL <http://www.int-res.com/abstracts/aei/v1/n2/p137-146/>
- Krkošek M, Connors BM, Morton A, Lewis MA, Dill LM, Hilborn R (2011) Effects of parasites from salmon farms on productivity of wild salmon. *Proceedings of the National Academy of Sciences* 108(35):14,700–14,704, doi: 10.1073/pnas.1101845108, URL <http://www.pnas.org/content/108/35/14700>
- Lande R, Engen Steinar, Sæther B (1999) Spatial Scale of Population Synchrony: Environmental Correlation versus Dispersal and Density Regulation. *The American Naturalist* 154(3):271–281, doi: 10.1086/303240, URL <http://www.jstor.org/stable/10.1086/303240>
- Lees F, Baillie M, Gettinby G, Revie CW (2008) The efficacy of emamectin benzoate against infestations of *Lepeophtheirus salmonis* on farmed Atlantic salmon (*Salmo salar* L) in Scotland, 2002–2006. *PLoS ONE* 3(2), URL <http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0001549>
- Levins R (1969) Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. *Bulletin of the Ecological Society of America* 15(3):237–240, URL <http://besa.oxfordjournals.org/content/15/3/237>
- Liebholt A, Koenig WD, Bjørnstad ON (2004) Spatial synchrony in population dynamics. *Annual Review of Ecology and Systematics* 35:467–490, doi: 10.1146/annurev.ecolsys.34.011802.132516, URL <http://www.annualreviews.org/doi/full/10.1146/annurev.ecolsys.34.011802.132516>
- Liu J, Dietz T, Carpenter SR, Alberti M, Folke C, Moran E, Pell AN, Deadman P, Kratz T, Lubchenco J, Ostrom E, Ouyang Z, Provencher W, Redman CL, Schneider SH, Taylor WW (2007) Complexity of coupled human and natural systems. *Science* 317(5844):1513, doi: 10.1126/science.1144004, URL <http://www.ncbi.nlm.nih.gov/pubmed/17872436>
- Marty GD, Saksida SM, Quinn TJ (2010) Relationship of farm salmon, sea lice, and wild salmon populations. *Proceedings of the National Academy of Sciences* 107(52):22,599–22,604, doi: 10.1073/pnas.1009573108, URL <http://www.pnas.org/content/107/52/22599.abstract>
- McCallum H, Harvell D, Dobson A (2003) Rates of spread of marine pathogens. *Ecology Letters* 6:1062–1067, doi: 10.1046/j.1461-0248.2003.00545.x, URL [onlinelibrary.wiley.com/doi/10.1046/j.1461-0248.2003.00545.x/pdf](http://onlinelibrary.wiley.com/doi/10.1046/j.1461-0248.2003.00545.x/pdf)

- Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-being: Synthesis*, vol 5. Island Press, Washington, DC, doi: 10.1196/annals.1439.003, URL [http://www.who.int/entity/globalchange/ecosystems/ecosys.pdf?delimiter"026E30F\\$nhhttp://www.loc.gov/catdir/toc/ecip0512/2005013229.html](http://www.who.int/entity/globalchange/ecosystems/ecosys.pdf?delimiter)
- Moran PAP (1953) The statistical analysis of the Canadian Lynx cycle II. Synchronization and meteorology. *Australian Journal of Zoology* 1:291–298, doi: 10.1071/ZO9530291, URL <http://www.publish.csiro.au/?paper=ZO9530291>
- Oerke EC (2006) Crop losses to pests. *The Journal of Agricultural Science* 144(01):31, doi: 10.1017/S0021859605005708
- Peacock SJ, Krkošek M, Probošycz S, Orr C, Lewis MA (2013) Cessation of a salmon decline with control of parasites. *Ecological Applications* 23(3):606–620, doi: 10.1890/12-0519.1, URL <http://www.esajournals.org/doi/abs/10.1890/12-0519.1>
- Rae GH (2002) Sea louse control in Scotland, past and present. *Pest Management Science* 58(6):515–520, doi: 10.1002/ps.491, URL <http://onlinelibrary.wiley.com/doi/10.1002/ps.491/abstract>
- Ranta E, Kaitala V, Lindstrom J, Linden H (1995) Synchrony in Population Dynamics. *Proceedings of the Royal Society of London Series B: Biological Sciences* 262(1364):113–118, doi: 10.1098/rspb.1995.0184, URL <http://rspb.royalsocietypublishing.org/content/262/1364/113.abstract>
- Revie CW, Gettinby G, Treasurer JW, Rae GH, Clark N (2002) Temporal, environmental and management factors influencing the epidemiological patterns of sea lice (*Lepeophtheirus salmonis*) infestations on farmed Atlantic salmon *Salmo salar* in Scotland. *Pest Management Science* 58(6):576–584, URL <http://onlinelibrary.wiley.com/doi/10.1002/ps.476/abstract>
- Revie CW, Gettinby G, Treasurer JW, Wallace C (2003) Identifying epidemiological factors affecting sea lice *Lepeophtheirus salmonis* abundance on Scottish salmon farms using general linear models. *Diseases of Aquatic Organisms* 57(1-2):85–95, URL <http://www.int-res.com/abstracts/dao/v57/n1-2/p85-95/>
- Rinaldi S, Candaten M, Casagrandi R (2001) Evidence of peak to peak dynamics in ecology. *Ecology Letters* 4:610–617, URL <http://onlinelibrary.wiley.com/doi/10.1046/j.1461-0248.2001.00273.x/full>
- Rogers LA, Peacock SJ, McKenzie P, DeDominicis S, Jones SRM, Chandler P, Foreman MGG, Revie CW, Krkošek M (2013) Modeling parasite dynamics on farmed salmon for precautionary conservation management of wild salmon. *PLoS ONE* 8(4):e60,096, doi: 10.1371/journal.pone.0060096, URL <http://dx.doi.org/10.1371/journal.pone.0060096>
- Sah P, Paul Salve J, Dey S (2013) Stabilizing biological populations and metapopulations through Adaptive Limiter Control. *Journal of theoretical biology* 320:113–23, doi: 10.1016/j.jtbi.2012.12.014, URL <http://www.sciencedirect.com/science/article/pii/S002251931200642X>
- Samways MJ (1979) Immigration, population growth and mortality of insects and mites on cassava in Brazil. *Bulletin of Entomological Research* 69(03):491–505, URL <http://dx.doi.org/10.1017/S000748530001899X>
- Schaffer WM (1985) Order and chaos in ecological systems. *Ecology* 66(1):93–106, URL <http://www.esajournals.org/doi/abs/10.2307/1941309>
- Silva A (2003) Morphometric variation among sardine (*Sardina pilchardus*) populations from the north-eastern Atlantic and the western Mediterranean. *ICES Journal of Marine Science* 3139(03):1352–1360, doi: 10.1016/S1054, URL <http://icesjms.oxfordjournals.org/content/60/6/1352.short>
- Sprott J (2003) *Chaos and time-series analysis*. Oxford University Press, URL <http://sprott.physics.wisc.edu/chaostsa/>



- Steen H, Ims RA, Sonerud GA, Steen H (1996) Spatial and Temporal Patterns of Small-Rodent Population Dynamics at a Regional Scale. *Ecology* 77(8):2365–2372, URL <http://www.esajournals.org/doi/abs/10.2307/2265738>
- Stien A, Bjørn PA, Heuch PA, Elston DA (2005) Population dynamics of salmon lice *Lepeophtheirus salmonis* on Atlantic salmon and sea trout. *Marine Ecology Progress Series* 290(Kabata 1979):263–275, doi: 10.3354/meps290263, URL <http://dx.doi.org/10.3354/meps290263>
- Sugihara G, May R, Ye H, Hsieh Ch, Deyle E, Fogarty M, Munch S (2012) Detecting Causality in Complex Ecosystems. *Science* 338(6106):496–500, doi: 10.1126/science.1227079, URL <http://www.ncbi.nlm.nih.gov/pubmed/22997134><http://www.sciencemag.org/content/338/6106/496.abstract>
- Tompkins DM, Carver S, Jones ME, Krkošek M, Skerratt LF (2015) Emerging infectious diseases of wildlife: a critical perspective. *Trends in Parasitology* 31(4):149–159, doi: 10.1016/j.pt.2015.01.007, URL <http://linkinghub.elsevier.com/retrieve/pii/S1471492215000197>
- Van Bael S, Pruett-Jones S (1996) Exponential Population Growth of Monk Parakeets in the United States. *The Wilson Bulletin* 108(3):584–588, URL <http://www.jstor.org/stable/4163726>
- Walker PJ, Winton JR (2010) Emerging viral diseases of fish and shrimp. *Veterinary Research* 41(6), doi: 10.1051/vetres/2010022

## A Solution to ODE

The solutions to Eq. (1) are:

$$\begin{aligned} u(t) &= f_u(t, u_0, v_0) \\ &= c_1 \exp\left[\frac{r_{uu} + r_{vv} + \alpha}{2}t\right] + c_2 \exp\left[\frac{r_{uu} + r_{vv} - \alpha}{2}t\right] \end{aligned} \quad (\text{A.1})$$

$$\begin{aligned} v(t) &= f_v(t, u_0, v_0) \\ &= c_1 \left(\frac{r_{vv} - r_{uu} + \alpha}{2r_{uv}}\right) \exp\left[\frac{r_{uu} + r_{vv} + \alpha}{2}t\right] + c_2 \left(\frac{r_{vv} - r_{uu} - \alpha}{2r_{uv}}\right) \exp\left[\frac{r_{uu} + r_{vv} - \alpha}{2}t\right], \end{aligned} \quad (\text{A.2})$$

where

$$c_1 = \frac{2r_{uv}v_0 - u_0(r_{vv} - r_{uu} - \alpha)}{2\alpha} \quad (\text{A.3})$$

$$c_2 = \frac{u_0(\alpha + r_{vv} - r_{uu}) - 2r_{uv}v_0}{2\alpha} \quad (\text{A.4})$$

$$\alpha = \sqrt{(r_{uu} - r_{vv})^2 + 4r_{uv}r_{vu}}. \quad (\text{A.5})$$

To get the time of the next treatment given the growth rates and initial conditions, we first rearrange Eqs (A.1-A.2). We denote the time of the next treatment of  $u$  and  $v$  as  $T_u$  and  $T_v$ , respectively. The equations for  $T_u$  and  $T_v$  are:

$$\begin{aligned} 2\alpha N_{\max} = \exp\left(\frac{r_{uu} + r_{vv}}{2}T_u\right) &\left[\left(\exp\left(\frac{\alpha}{2}T_u\right) - \exp\left(\frac{-\alpha}{2}T_u\right)\right)(2r_{uv}v_0 + u_0(r_{uu} - r_{vv}))\right. \\ &\left. + u_0\alpha\left(\exp\left(\frac{\alpha}{2}T_u\right) + \exp\left(\frac{-\alpha}{2}T_u\right)\right)\right] \end{aligned} \quad (\text{A.6})$$

$$\begin{aligned} 4\alpha r_{uv}N_{\max} = \exp\left(\frac{r_{uu} + r_{vv}}{2}T_v\right) &[(2r_{uv}v_0(r_{vv} - r_{uu}) + 4u_0r_{vu}r_{uv}) \\ &\left(\exp\left(\frac{\alpha}{2}T_v\right) - \exp\left(\frac{-\alpha}{2}T_v\right)\right) + 2r_{uv}v_0\alpha\left(\exp\left(\frac{\alpha}{2}T_v\right) + \exp\left(\frac{-\alpha}{2}T_v\right)\right)]. \end{aligned} \quad (\text{A.7})$$

In Eqs (A.6-A.7),  $T_u$  and  $T_v$  cannot be solved for explicitly, so we used a numerical root finding algorithm to determine  $T_u$  and  $T_v$ .

## B Development of return map

We used the dynamical system described in Eq. (2) to construct a return map that takes the population density  $u$  when  $v$  is treated and returns  $u$  the next time  $v$  is treated. We first consider the scenario where  $u$  is not treated in between consecutive treatments of  $v$ . We denote the time to the next treatment of  $v$  as  $T_{v0}$ . In this case, the resulting population density  $u$  at the next treatment of  $v$  is

$$\phi(u^*) = f_u(T_{v0}, u^*, N_{\min}), \quad (\text{B.1})$$

where  $f_u$  is the solutions to Eq. (1), given in Appendix A. Next, we consider the case where  $u$  is treated once in between treatments of  $v$ . This leads to a return map of the form,

$$\phi(u^*) = f_u(T_{v1}, N_{\min}, f_v(T_{u0}, u^*, N_{\min})), \quad (\text{B.2})$$

where  $T_{u0}$  is the time from the initial treatment of  $v$  to the treatment of  $u$  and  $T_{v1}$  is the subsequent time from the treatment of  $u$  to the next treatment of  $v$ . These two cases can be combined into a single equation as,

$$\phi(u^*) = \underbrace{H(\tilde{T}_0) f_u(T_{v0}, u^*, N_{\min})}_{u \text{ not treated}} + \underbrace{H(\tilde{T}_1) [1 - H(\tilde{T}_0)] f_u(T_{v1}, N_{\min}, f_v(T_{u0}, u^*, N_{\min}))}_{u \text{ treated once}}. \quad (\text{B.3})$$

We can continue in this way to get the equation that includes the possibility for  $u$  being treated twice in between treatments of  $v$ ,

$$\begin{aligned} \phi(u^*) = & \underbrace{H(\tilde{T}_0) f_u(T_{v0}, u^*, N_{\min})}_{u \text{ not treated}} \\ & + \underbrace{H(\tilde{T}_1) [1 - H(\tilde{T}_0)] f_u(T_{v1}, N_{\min}, f_v(T_{u0}, u^*, N_{\min}))}_{u \text{ treated once}} \\ & + \underbrace{H(\tilde{T}_2) [1 - H(\tilde{T}_1)] f_u(T_{v2}, N_{\min}, f_v(T_{u1}, N_{\min}, f_v(T_{u0}, u^*, N_{\min})))}_{u \text{ treated twice}}. \end{aligned} \quad (\text{B.4})$$

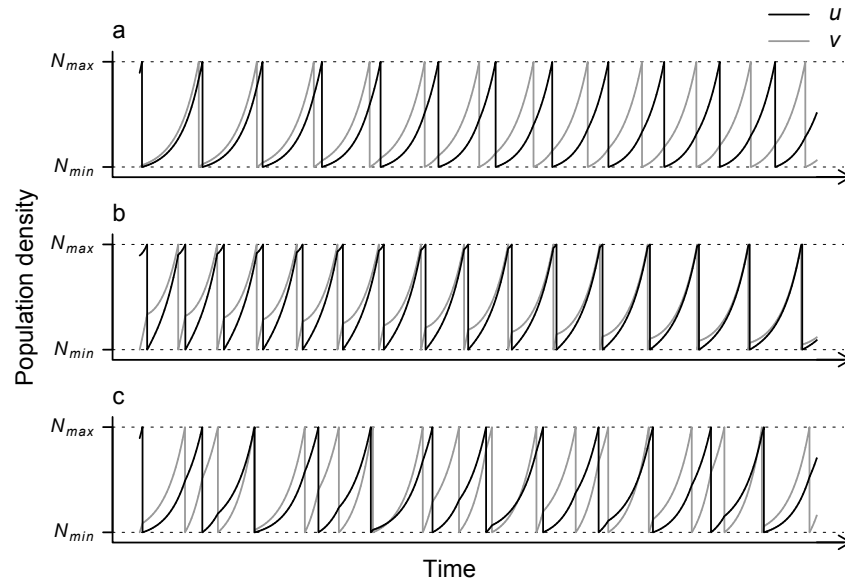
By induction, we arrive at the general equation for the return map, given in (3):

$$\phi(u^*) = \underbrace{[H(\tilde{T}_0)] f_u(T_{v0}, u^*, N_{\min})}_{m=0} + \underbrace{\left[ \sum_{m=1}^{\infty} H(\tilde{T}_m) \prod_{n=0}^{m-1} [1 - H(\tilde{T}_n)] \right] f_u(T_{vm}, N_{\min}, v_{m-1})}_{m \geq 1}. \quad (\text{B.5})$$

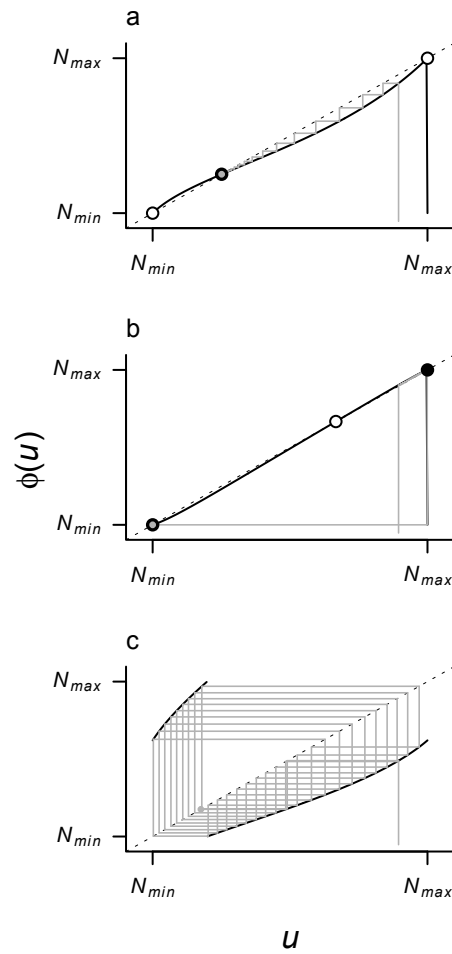
### C Algorithm describing return map

Because Eqs (A.6-A.7) can not be solved for  $T_u$  and  $T_v$ , model analysis by the return map involved simulating successive treatments until  $v$  was treated next. The recursive algorithm we applied to calculate the population density  $u$  when  $v$  was treated next is:

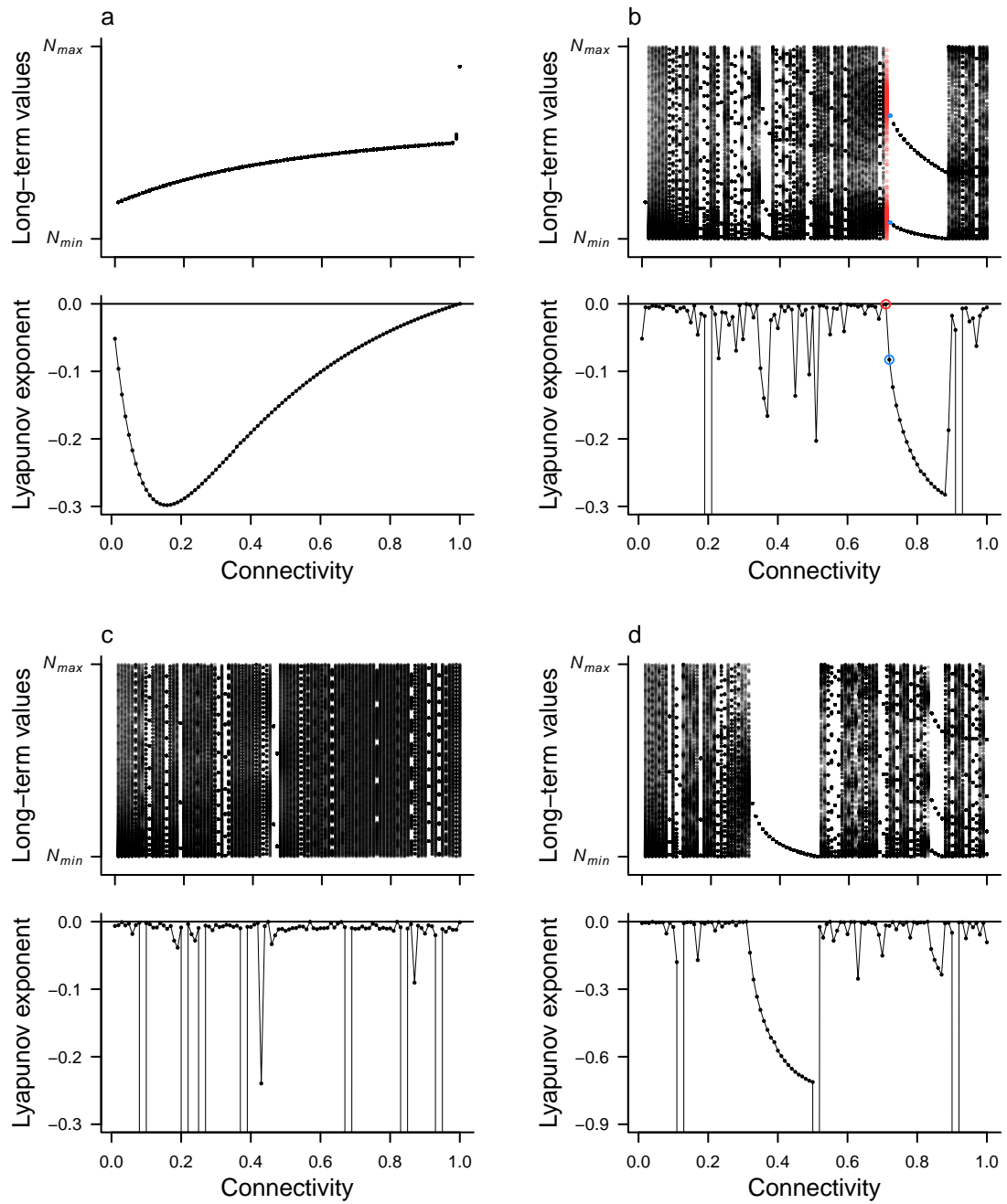
|   |   |
|---|---|
| <pre>function u_next(u, v, R)   evaluate T_u(u, v, R) = Tu   evaluate T_v(u, v, R) = Tv   if (T_u &gt; T_v) then     return f_u(T_v, u, v)   else     v_new = f_v(T_u, u, v)     return u_next(Nmin, v_new, R)   end if</pre> | <p>Calculate the time to the next treatment of <math>u</math> and the time to the next treatment of <math>v</math></p> <p>If the time to treatment of <math>v</math> is less, return <math>u</math> when <math>v</math> is treated.</p> <p>Otherwise, <math>u</math> is treated. Calculate <math>v</math> when <math>u</math> is treated and repeat function with new initial values.</p> |
|---|---|



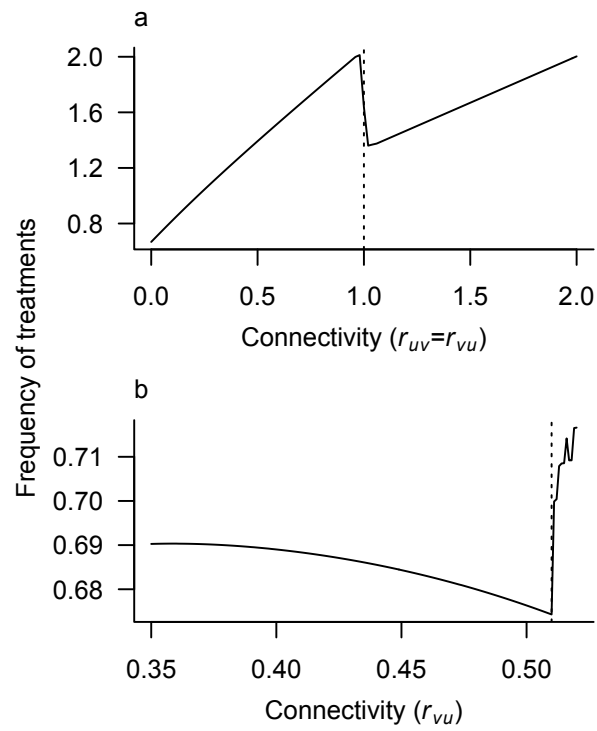
**Fig. 1** Three types of behaviour observed were observed for connected populations subject to control: (a) alternating treatments of populations for equal growth rates of the two populations and connectivity less than the internal growth rates ( $r_{ij}/r_{ii} = 0.1$ ), (b) synchrony in the population dynamics between patches for equal growth rates of the two populations and connectivity greater than the internal growth rates ( $r_{ij}/r_{ii} = 10$ ) and (c) apparently chaotic dynamics where the treatment timing was unpredictable for unequal growth rates of the two populations. Initial conditions were  $u_0 = 2.7$  (black line) and  $v_0 = N_{\min}$  (grey line). The upper and lower horizontal dashed lines indicate the treatment threshold and abundance of parasite immediately after treatment, respectively.



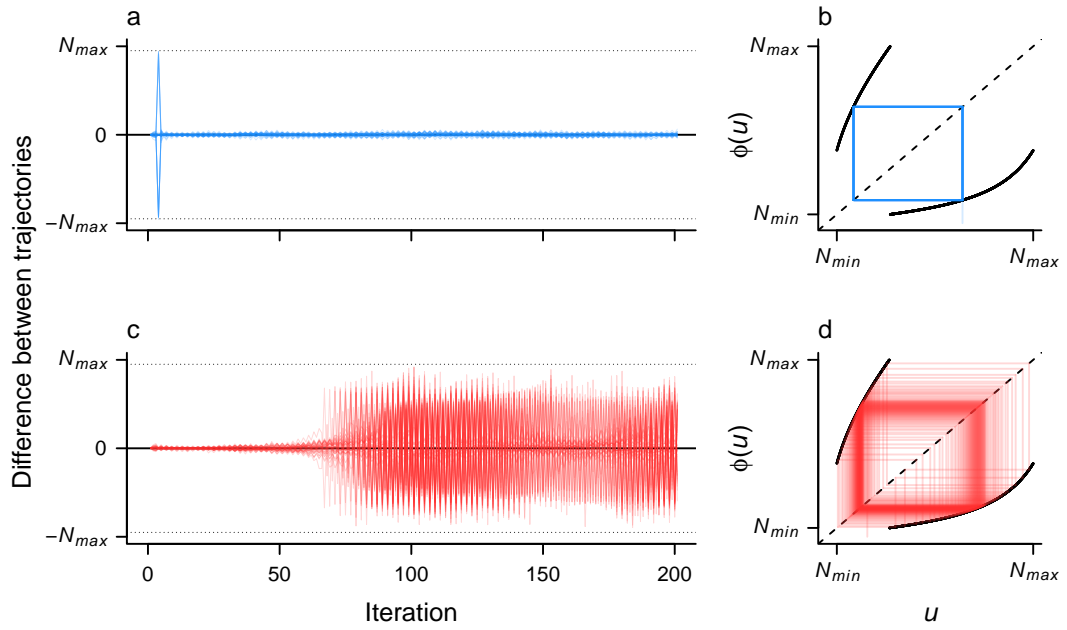
**Fig. 2** Return maps for the population density  $u$  at re-treatment of  $v$  ( $\phi(u^*)$ ) over increasing initial population density,  $u^*$ . (a) For low connectivity, there was a stable equilibrium in  $(N_{min}, N_{max})$  (black point) and unstable equilibria at  $N_{min}$  and  $N_{max}$  (white points). (b) When connectivity was higher than internal growth, there was an unstable equilibrium in  $(N_{min}, N_{max})$  and stable equilibria at  $N_{min}$  and  $N_{max}$ , and the two populations synchronized. (c) For unequal connectivity,  $u$  was treated  $m$  or  $m + 1$  times before  $v$  was treated, yielding a discontinuity in the return map that resulted in cycles. The relative growth rates in each panel correspond to those in Fig. 1. The grey lines show 30 iterations of the return map (i.e., cobwebbing) from  $u^* = 2.7$ , ending at the grey point.



**Fig. 3** Long-term values of  $\phi(u^*)$  and the Lyapunov exponents  $\lambda$  under four different scenarios for changing connectivity (a-d; scenarios A-D in Table 1). In calculating long-term values, for each value of connectivity we plotted the last 500 of 2000 iterations starting at  $u_0^* = 2.7$  (see Fig. S1 for results with other starting values). Red and blue points in (c) indicate the parameter values for stochastic simulations in Fig. 5. Online version in colour.



**Fig. 4** The frequency of treatments over increasing connectivity. (a) In scenario A, the frequency of treatments drops when the connectivity exceeds internal growth rates (dotted line) and populations become synchronized (Table 2), but rises again as connectivity increases further due to increasing total growth rate. (b) In scenario D, the frequency of treatments declines over the region of phase locking (see Fig. 3d) as the stable point approaches  $N_{\min}$ , reducing the impact of the rescue-effect. The minimum frequency of treatments occurs where populations are synchronized at  $r_{vu} + r_{vv} = r_{uv} + r_{uu}$  (i.e.  $r_{vu} = 0.51$ , dotted line; Table 2).



**Fig. 5** The effect of stochasticity differed with small changes in parameters. The difference between two trajectories initially separated by  $\epsilon_0$  remained small for parameters under which the deterministic model showed periodic dynamics (a), but increased for parameters under which the deterministic model showed quasiperiodic dynamics (c). The corresponding deterministic return maps of the fiducial trajectory for scenario B with  $r_{vu} = 0.72$  (b) and  $r_{vu} = 0.71$  (d) (see Fig. 3b). Online version in colour.