

## A MODEL OF INFECTIOUS SALMON ANEMIA VIRUS WITH VIRAL DIFFUSION BETWEEN WILD AND FARMED PATCHES

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(Communicated by Shigui Ruan)

**ABSTRACT.** As the practice of aquaculture has increased the interplay between large fish farms and wild fisheries in close proximity has become ever more pressing. Infectious Salmon Anemia virus (ISAv) is a flu-like virus affecting a variety of finfish. In this article, we adapt the standard deterministic within host model of a viral infection to each patch of a two patch system and couple the patches via linear diffusion of the virus. We determine the basic reproductive ratio  $\mathcal{R}^0$  for the full system as well as invariant subsystems. We show the existence of unique positive equilibrium in the full system and subsystems and relate the existence of the equilibrium to the  $\mathcal{R}^0$  values. In particular, we show that if  $\mathcal{R}^0 > 1$ , the virus persists in the environment and is enzootic in the host population; if  $\mathcal{R}^0 \leq 1$ , the virus is cleared and the system asymptotically approaches the disease free equilibrium. We also show that, with positive diffusivity, it is possible for the virus to be excluded when there is a susceptible host population in only one patch, but to persist if there are susceptible host populations in both patches. We analyze the local stability of the equilibria and show the existence of Hopf bifurcations.

**1. Introduction.** Infectious salmon anemia virus (ISAv), is the virus which causes infectious salmon anemia (ISA) with 15 to 100% accumulated mortality over the course of a several months long infection in a farm environment [5]. It is found in all large salmon-producing countries including Norway, Scotland, Ireland, Canada, the United States, and Chile [23]. ISAv is transmitted among finfish horizontally by passive movement of infected seawater [15] and via direct contact with excretions or secretions of infected individuals. Salmon farms consist of a collection of net cages placed in open body of water. It is known that the location of salmon farms among wild salmon migratory routes in British Columbia raises the level of sea lice infection [14]. In this article we investigate the dynamics of an ISAv infection in the setting in which a farm is in close proximity to a wild migratory route. We propose a deterministic 2-patch model which includes both direct host-to-host and environmental transmission of the virus within each patch. The patches are coupled by diffusion of the virus.

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2010 *Mathematics Subject Classification.* Primary: 37N25, 92D30; Secondary: 34A34, 37G15.

*Key words and phrases.* ISA, ISAv, bifurcation, Hopf, stability, nonlinear systems, infectious disease, mathematical biology.

The authors are supported by NSF grant DMS-1411853.

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One of the early models to study HIV transmission in vivo, called the standard model in that area of research, was used by Nowak and May (2000) [16] and by Perelson and Nelson (1999) [17] and has been adapted to infection in a marine environment by Beretta and Kuang (1998) [1]. The model, as it appeared in [1], assumes that the susceptible host population experiences logistic growth, the infection of susceptible host marine bacteria can become infected only as a result of contact with a bacteriophage and results in a nonlinear system of three ordinary differential equations. We adapt this model for a single patch to allow for the susceptible population to be able to become infected by direct contact with an infected individual. We further assume that the change in the density of the viral compartment as a result of infecting a susceptible host is negligible. Finally, we assume the two patches are coupled via linear viral diffusion. The result is a 6-dimensional nonlinear system which is neither cooperative nor competitive.

This article is organized as follows: In Section 2, we introduce the model and describe the underlying assumptions. In Section 3, we develop criteria for the existence of positive equilibria, which we show to be unique whenever they exist, in the full 6-dimensional system as well as in 3 and 4-dimensional subsystems. In Section 4, we appeal to the Butler-McGehee lemma and results from persistence theory [24] to show weak persistence of the virus. We then use results of Thieme [21] to prove uniform strong persistence of the virus. In Section 5, we go on to study the local stability of equilibria and the conditions for the existence of Hopf bifurcations in the subsystems and full system. Finally, in Section 6, we summarize the results and discuss their implications to the real world setting.

**2. Model.** The biological setting motivating the model is a salmon farm in close proximity to a population of wild salmon. We assume that farmed salmon and wild salmon have no direct contact, but that virus present in the environment can pass between patches via diffusion. As a simplifying assumption, we assume that the rate of diffusion is equal whether the virus is diffusing from the farm patch to the wild patch or vice versa. We assume the susceptible fish experience logistic growth as in [1] and the model allows for differing birth and mortality rates in the farmed and wild patches. We assume that infected fish cannot reproduce and experience the same mortality regardless of what patch they are in. We let  $S_F$ ,  $I_F$ ,  $V_F$  represent the densities of susceptible farmed salmon, infected farmed salmon and the virus in the farm patch. Similarly, let  $S_W$ ,  $I_W$ , and  $V_W$  represent densities of susceptible and infected wild salmon and the virus in the wild patch. Then our model is

$$\begin{cases} \dot{S}_F &= S_F(\beta_F - \mu_F S_F) - S_F(I_F + \rho V_F) \\ \dot{I}_F &= S_F(I_F + \rho V_F) - \alpha I_F \\ \dot{V}_F &= k(V_W - V_F) - \omega V_F + \delta I_F \\ \dot{S}_W &= S_W(\beta_W - \mu_W S_W) - S_W(I_W + \rho V_W) \\ \dot{I}_W &= S_W(I_W + \rho V_W) - \alpha I_W \\ \dot{V}_W &= k(V_F - V_W) - \omega V_W + \delta I_W \end{cases} \quad (1)$$

where  $\beta_F$ ,  $\beta_W$  are the respective birth rates of salmon in the farmed and wild compartments,  $\mu_F$ ,  $\mu_W$  are the respective mortality rates of healthy salmon in the farmed and wild compartments,  $\alpha$  is the mortality rate of infected salmon,  $\rho$  is the rate of mass action infection via contact with the virus in the environment,  $k$  is the rate of diffusion,  $\omega$  is the rate of viral clearing and  $\delta$  is the rate of virus shedding.

All of the aforementioned parameters are assumed to be positive except  $k$  which is assumed to be non-negative.

By scaling  $V_F, V_W$  and relabeling  $\rho\delta = \delta$  we have

$$\begin{cases} \dot{S}_F &= S_F(\beta_F - \mu_F S_F) - S_F(I_F + V_F) \\ \dot{I}_F &= S_F(I_F + V_F) - \alpha I_F \\ \dot{V}_F &= k(V_W - V_F) - \omega V_F + \delta I_F \\ \dot{S}_W &= S_W(\beta_W - \mu_W S_W) - S_W(I_W + V_W) \\ \dot{I}_W &= S_W(I_W + V_W) - \alpha I_W \\ \dot{V}_W &= k(V_F - V_W) - \omega V_W + \delta I_W \end{cases} \quad (2)$$

An important feature of system (2) is that it is dissipative, that is there is a bounded set  $B \subset \mathbb{R}^6$  so that  $\varphi_t(x) \in B$  for all large  $t$  and for all  $x \in \mathbb{R}^6$  [18]. This is an important feature because it implies that the system satisfies the compactness assumption  $\mathbf{C}_{4.1}$  and the hypothesis of Theorem 4.5 of Thieme [21]. This result is the key to extending weak persistence to uniform strong persistence of the system.

**Proposition 1.** *All nonnegative solutions of system (2) are uniformly bounded in forward time for all  $k \geq 0$ .*

The dynamics of system (2) and the techniques we employ to understand them rely heavily on understanding the dynamics on the boundary. We therefore analyze invariant boundary (sub)systems along with the full system (2). These subsystems also have important biological relevance in their own right, which will be discussed in section 6.

The proofs of results for the various subsystems are, in many instances, similar to the proof for the full system. In such cases, results will be offered without proof to avoid repetition.

**3. Existence and uniqueness of equilibria.** Since the two patches are coupled only by viral diffusion, in the case when  $k = 0$  system (2) uncouples into two 3-dimensional invariant subsystems which are identical up to choice of parameters and are given by

$$\begin{cases} \dot{S} &= S(\beta - \mu S) - S(I + V) \\ \dot{I} &= S(I + V) - \alpha I \\ \dot{V} &= -\omega V + \delta I \end{cases} \quad (3)$$

We first identify boundary equilibria by examining the flow on invariant subsets of the boundary  $\partial\mathbb{R}_+^3$ .

**Proposition 2.** *System (3) admits boundary equilibria  $(0, 0, 0)$  and  $DFE_3 = (\frac{\beta}{\mu}, 0, 0)$ . The equilibrium at the origin is always a saddle rest point.*

By analyzing the next-generation matrix of system (3) we are able to determine the basic reproductive ratio  $\mathcal{R}_3^0$ , where the second subscript 3 represents the dimension of the subsystem.

**Lemma 3.1.** *The basic reproductive ratio for system (3) is*

$$\mathcal{R}_3^0 = \frac{(\delta + \omega)\beta}{\alpha\omega\mu}.$$

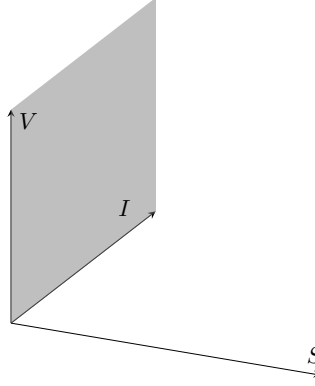


FIGURE 1. The invariant boundary set  $B$  is the shaded region together with the  $S$ -axis.

**Proposition 3.** *There exists a unique positive endemic equilibrium  $E_3 = (\bar{S}, \bar{I}, \bar{V})$  of (3) if and only if  $\mathcal{R}_3^0 > 1$ . If  $\mathcal{R}_3^0 \leq 1$ , then solutions with positive initial conditions approach  $DFE_3$ .*

When the viral diffusivity is positive, that is  $k > 0$ , system (2) admits two four dimensional invariant boundary subspaces, namely  $\{S_W = I_W = 0\}$  and  $\{S_F = I_F = 0\}$ . These subspaces are exactly those in which fish are present in only one patch. The analysis of dynamics in both patches is identical up to renaming the parameters. The dynamics of (2) in either subspace is determined by

$$(4) \quad \begin{cases} \dot{S} &= S(\beta - \mu S) - S(I + V_1) \\ \dot{I} &= S(I + V_1) - \alpha I \\ \dot{V}_1 &= k(V_2 - V_1) - \omega V_1 + \delta I \\ \dot{V}_2 &= k(V_1 - V_2) - \omega V_2. \end{cases}$$

**Proposition 4.** *System (4) admits boundary equilibria  $\vec{0} = (0, 0, 0, 0)$  and  $DFE_4 = (\frac{\beta}{\mu}, 0, 0, 0)$ . The equilibrium at the origin is always a saddle rest point.*

We now derive the basic reproductive ratios for each of these invariant 4-dimensional subsystems and examine the criteria for the existence of positive equilibria there. We will do this, as before, by examining the next generation matrix. First, we define

$$S(k) = \frac{\alpha\omega(2k + \omega)}{\omega(2k + \omega) + \delta(k + \omega)} \quad (5)$$

**Lemma 3.2.** *The basic reproductive ratio for system (4) is given by  $\mathcal{R}_4^0 = \frac{\beta}{\mu S(k)}$ , where  $S(k)$  is given by (5).*

From (5) we see that  $S(k)$  is a monotonically increasing continuous function of  $k$  and that  $S(0) = \bar{S} = \frac{\alpha\omega}{\delta + \omega}$ , the density of susceptible fish at the unique endemic equilibrium of system (3),  $E_3$ . Let  $K = \frac{\beta}{\mu}$  be the carrying capacity of the logistic growth function for susceptible fish. Then  $K$  is the density of susceptible fish

at  $DFE_3$  and  $DFE_4$ . Then  $\mathcal{R}_4^0 = \frac{K}{S(k)}$  is a monotonically decreasing continuous function of  $k$  and  $\mathcal{R}_4^0(0) = \mathcal{R}_3^0$ .

**Proposition 5.** *There exists a unique positive endemic equilibrium  $E_4 = (S', I', V_1', V_2')$  for system (4) if and only if  $\mathcal{R}_4^0 > 1$ . If  $\mathcal{R}_4^0 \leq 1$ , then solutions with positive initial conditions asymptotically approach  $DFE_4$ .*

The 4-dimensional subsystem (4) corresponds to the biological case where fish are present in one patch only. If we reinterpret this setting from the perspective of the virus, we can look upon the two patches as one containing a resource necessary for reproduction and the other as being devoid of resources. Mathematically, it is possible that  $\mathcal{R}_3^0 > 1$  and for some sufficiently large  $k$ ,  $\mathcal{R}_4^0 < 1$ . Thus, it is possible that in one patch, the resource is sufficient to sustain the virus, but as diffusion increases, the virus spends time in a patch without any resource. In this barren patch the virus still experiences exponential decay due to viral clearing. Thus, the patch is a sink for the virus. When  $\mathcal{R}_4^0 < 1$  the susceptible fish in the non-barren patch is not a rich enough resource to overcome the deleterious effects of being coupled to the sink patch.

From the perspective of susceptible fish, if the rate of diffusion can be increased so that  $\mathcal{R}_4^0$  decreases below 1, then increasing diffusion prevents the invasion of the virus. In this light, it is natural to label this phenomenon wash-out.

When referring to the 4-dimensional subspace of system (2) inhabited by susceptible type  $i$ ,  $i = F, W$  we will write  $\mathcal{R}_i^0 = \frac{\beta_i}{\mu_i S(k)} = \frac{K_i}{S(k)}$  and  $E_i$  for the boundary equilibrium corresponding to  $E_4$ .

Now, we turn our attention to the full 6-dimensional system (2). We begin by identifying the boundary equilibria. System (2) admits two non-trivial equilibria on the boundary corresponding to the 4-dimensional subsystem (4) with fish in only one patch, namely

$$E_F = (S_F^*, I_F^*, V_F^*, 0, 0, V_W^*) \quad \text{and} \quad E_W = (0, 0, V_F', S_W', I_W', V_W').$$

**Corollary 1.**  *$E_i$  exists if and only if  $\mathcal{R}_i^0 > 1$  for  $i = F$  or  $W$ .*

*Proof.* Suppose without loss of generality that  $S_W = I_W = 0$ . Then (2) becomes,

$$\begin{cases} \dot{S}_F &= S_F(\beta_F - \mu_F S_F) - S_F(I_F + V_F) \\ \dot{I}_F &= S_F(I_F + V_F) - \alpha I_F \\ \dot{V}_F &= k(V_W - V_F) - \omega V_F + \delta I_F \\ \dot{S}_W &= 0 \\ \dot{I}_W &= 0 \\ \dot{V}_W &= k(V_F - V_W) - \omega V_W \end{cases} \quad (6)$$

which corresponds to the invariant subsystem (4) by identifying  $(S, I, V_1, V_2, \beta, \mu)$  with  $(S_F, I_F, V_F, V_W, \beta_F, \mu_F)$ . Thus,  $(S_F^*, I_F^*, V_F^*, 0, 0, V_W^*)$  exists if and only if  $\mathcal{R}_F^0 > 1$ .  $\square$

**Proposition 6.** *In the case that  $I_j = V_j = 0$  for  $j = F$  or  $W$  the model becomes uncoupled and there exists a nonnegative disease free equilibrium  $E_0 = (K_F, 0, 0, K_W, 0, 0)$ .*

*Proof.* When  $I_F = V_F = I_W = V_W = 0$ , the system uncouples and in both compartments it is reduced to the logistic model

$$\dot{S} = S(\beta_j - \mu_j S) \quad (7)$$

This system admits the following four boundary equilibria in addition to those mentioned above,

$$\begin{aligned} \mathcal{E}_{00} &= (0, 0, 0, 0, 0, 0) & \mathcal{E}_{10} &= \left(\frac{\beta_F}{\mu_F}, 0, 0, 0, 0, 0\right) \\ \mathcal{E}_{01} &= \left(0, 0, 0, \frac{\beta_W}{\mu_W}, 0, 0\right) & \mathcal{E}_{11} &= \left(\frac{\beta_F}{\mu_F}, 0, 0, \frac{\beta_W}{\mu_W}, 0, 0\right). \end{aligned}$$

Relative to the invariant subspace  $I_F = V_F = I_W = V_W = 0$ ,  $\mathcal{E}_{00}$  is a repeller,  $\mathcal{E}_{10}$  and  $\mathcal{E}_{01}$  are saddles, and  $\mathcal{E}_{11}$  attracts all positive solutions. We refer to  $\mathcal{E}_{11}$  as the disease free equilibrium, which we relabel  $E_0$ .  $\square$

Our next result is the derivation of the basic reproductive ratio,  $\mathcal{R}^0$ , for the full system (2). Recall that  $K_F$  and  $K_W$  are the disease-free equilibrium densities of susceptible fish in the farm and wild patches respectively.

**Lemma 3.3.** *The basic reproductive ratio for system (2) is given by*

$$\mathcal{R}_{FW}^0 = \frac{1}{2} \left( \mathcal{R}_F^0 + \mathcal{R}_W^0 + \sqrt{(\mathcal{R}_F^0 - \mathcal{R}_W^0)^2 + 4K_F K_W C^2} \right)$$

where  $C = \frac{\delta k}{\alpha \omega (2k + \omega)}$ . Furthermore,  $\mathcal{R}_{FW}^0 > \max(\mathcal{R}_F^0, \mathcal{R}_W^0)$ .

*Proof.* The Jacobian matrix of (2) evaluated at the  $E_0$  has the form

$$J = \begin{bmatrix} -\beta_F & -\frac{\beta_F}{\mu_F} & -\frac{\beta_F}{\mu_F} & 0 & 0 & 0 \\ 0 & \frac{\beta_F}{\mu_F} - \alpha & \frac{\beta_F}{\mu_F} & 0 & 0 & 0 \\ 0 & \delta & -(k + \omega) & 0 & 0 & k \\ 0 & 0 & 0 & -\beta_W & -\frac{\beta_W}{\mu_W} & -\frac{\beta_W}{\mu_W} \\ 0 & 0 & 0 & 0 & \frac{\beta_W}{\mu_W} - \alpha & \frac{\beta_W}{\mu_W} \\ 0 & 0 & k & 0 & \delta & -(k + \omega) \end{bmatrix},$$

and it admits two negative eigenvalues  $-\beta_F$ ,  $-\beta_W$ , and the remaining four eigenvalues come from the  $4 \times 4$  submatrix  $J_0$ , corresponding to the infectious compartments. To derive the basic reproductive ratio  $\mathcal{R}_{FW}^0$ , we consider the following decomposition

$$J_0 = \begin{bmatrix} \frac{\beta_F}{\mu_F} & \frac{\beta_F}{\mu_F} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{\beta_W}{\mu_W} & \frac{\beta_W}{\mu_W} \\ 0 & 0 & 0 & 0 \end{bmatrix} - \begin{bmatrix} \alpha & 0 & 0 & 0 \\ -\delta & k + \omega & 0 & -k \\ 0 & 0 & \alpha & 0 \\ 0 & -k & -\delta & k + \omega \end{bmatrix} = F - V.$$

Then direct calculation reveals that

$$V^{-1} = \begin{bmatrix} \frac{1}{\alpha} & 0 & 0 & 0 \\ \frac{\delta}{\alpha \omega} \left( \frac{k + \omega}{2k + \omega} \right) & \frac{1}{\omega} \left( \frac{k + \omega}{2k + \omega} \right) & \frac{\delta}{\alpha \omega} \left( \frac{k}{2k + \omega} \right) & \frac{1}{\omega} \left( \frac{k}{2k + \omega} \right) \\ 0 & 0 & \frac{1}{\alpha} & 0 \\ \frac{\delta}{\alpha \omega} \left( \frac{k}{2k + \omega} \right) & \frac{1}{\omega} \left( \frac{k}{2k + \omega} \right) & \frac{\delta}{\alpha \omega} \left( \frac{k + \omega}{2k + \omega} \right) & \frac{1}{\omega} \left( \frac{k + \omega}{2k + \omega} \right) \end{bmatrix}$$

and the non-zero eigenvalues of  $FV^{-1}$  are the eigenvalues of the  $2 \times 2$  matrix

$$\begin{bmatrix} \frac{\beta_F}{\mu_F} \left( \frac{1}{\alpha} + \frac{\delta(k + \omega)}{\alpha \omega (2k + \omega)} \right) & \frac{\beta_F}{\mu_F} \frac{\delta k}{\alpha \omega (2k + \omega)} \\ \frac{\beta_W}{\mu_W} \frac{\delta k}{\alpha \omega (2k + \omega)} & \frac{\beta_W}{\mu_W} \left( \frac{1}{\alpha} + \frac{\delta(k + \omega)}{\alpha \omega (2k + \omega)} \right) \end{bmatrix} = \begin{bmatrix} \frac{\beta_F}{\mu_F} \frac{S(k)}{\alpha \omega (2k + \omega)} & \frac{\beta_F}{\mu_F} \frac{\delta k}{\alpha \omega (2k + \omega)} \\ \frac{\beta_W}{\mu_W} \frac{\delta k}{\alpha \omega (2k + \omega)} & \frac{\beta_W}{\mu_W} \frac{S(k)}{\alpha \omega (2k + \omega)} \end{bmatrix}.$$

Thus,  $p(\lambda) = \lambda^2 - \frac{1}{S(k)}\left(\frac{\beta_F}{\mu_F} + \frac{\beta_W}{\mu_W}\right)\lambda + \frac{\beta_F\beta_W}{\mu_F\mu_W}\left(\frac{1}{S(k)^2} - \frac{\delta^2 k^2}{\alpha^2 \omega^2 (2k+\omega)^2}\right)$  and the largest root is given by

$$\begin{aligned}\lambda_1 &= \frac{1}{2} \left( \frac{1}{S(k)} \left( \frac{\beta_F}{\mu_F} + \frac{\beta_W}{\mu_W} \right) \right. \\ &\quad \left. + \sqrt{\frac{1}{S(k)^2} \left( \frac{\beta_F}{\mu_F} + \frac{\beta_W}{\mu_W} \right)^2 - 4 \frac{\beta_F\beta_W}{\mu_F\mu_W S(k)^2} + 4 \frac{\beta_F\beta_W}{\mu_F\mu_W} \frac{\delta^2 k^2}{\alpha^2 \omega^2 (2k+\omega)^2}} \right) \\ &= \frac{1}{2} \left( \frac{1}{S(k)} \left( \frac{\beta_F}{\mu_F} + \frac{\beta_W}{\mu_W} \right) + \sqrt{\frac{1}{S(k)^2} \left( \frac{\beta_F}{\mu_F} - \frac{\beta_W}{\mu_W} \right)^2 + 4 \frac{\beta_F\beta_W}{\mu_F\mu_W} \frac{\delta^2 k^2}{\alpha^2 \omega^2 (2k+\omega)^2}} \right) \\ &= \frac{1}{2} (\mathcal{R}_F^0 + \mathcal{R}_W^0) + \sqrt{(\mathcal{R}_F^0 - \mathcal{R}_W^0)^2 + 4K_F K_W C^2}.\end{aligned}$$

Finally, we have that

$$\begin{aligned}\mathcal{R}_{FW}^0 &> \frac{1}{2} (\mathcal{R}_F^0 + \mathcal{R}_W^0 + \sqrt{(\mathcal{R}_F^0 - \mathcal{R}_W^0)^2}) \\ &= \frac{1}{2} \left( (\mathcal{R}_F^0 + \mathcal{R}_W^0) + |\mathcal{R}_F^0 - \mathcal{R}_W^0| \right) \\ &= \max(\mathcal{R}_F^0, \mathcal{R}_W^0).\end{aligned}$$

□

**Proposition 7.** *If  $\mathcal{R}_{FW}^0 \leq 1$ , then  $E_0$  attracts all positive solutions of (2).*

*Proof.* First, suppose that  $\mathcal{R}_{FW}^0 < 1$ , then  $J_0$  is a quasi-positive irreducible Hurwitz matrix, and by the Perron-Frobenius theorem, there exist  $v^T > 0$  and  $\lambda > 0$  such that  $v^T J_0 = -\lambda v^T$ . For any  $\varepsilon > 0$ , there exists  $t_0$  such that  $S_F(t) < \frac{\beta_F}{\mu_F} + \varepsilon$ ,  $S_W(t) < \frac{\beta_W}{\mu_W} + \varepsilon$  for all  $t > t_0$ . Consider an auxiliary function  $W := v^T x$ , where  $x = (I_F, V_F, I_W, V_W)^T$ . Then

$$\dot{W} < v^T \left( J_0 + \begin{bmatrix} \varepsilon & \varepsilon & 0 & 0 \\ 0 & 0 & \varepsilon & \varepsilon \\ 0 & 0 & \varepsilon & \varepsilon \\ 0 & 0 & 0 & 0 \end{bmatrix} \right) x < -\lambda W + \varepsilon (v_1(I_F + V_F) + v_3(I_W + V_W)) \leq (-\lambda + \varepsilon r)W,$$

for some  $r > 0$ . If  $\varepsilon > 0$  is sufficiently small, we have that  $W(t) \rightarrow 0$ , which implies that the corresponding solution converges to the  $E_0$ .

Now, suppose that  $\mathcal{R}_{FW}^0 = 1$ , then there exists  $v^T > 0$  such that  $v^T J_0 = (0, 0, 0, 0)$ . Consider an auxiliary function

$$W = v_1 \int_{\frac{\beta_F}{\mu_F}}^{S_W} \frac{\tau - \frac{\beta_F}{\mu_F}}{\tau} d\tau + v_3 \int_{\frac{\beta_W}{\mu_W}}^{S_F} \frac{\tau - \frac{\beta_W}{\mu_W}}{\tau} d\tau + v^T x.$$

A direct calculation shows that

$$\dot{W} = -v_1 \mu_F (S_F - \frac{\beta_F}{\mu_F})^2 - v_3 \mu_W (S_W - \frac{\beta_W}{\mu_W})^2 \leq 0.$$

An application of LaSalle's Invariance Principle concludes the proof. □

In Lemma 3.3 we give a lower bound  $\mathcal{R}_{FW}^0$  so that if either  $\mathcal{R}_F^0$  or  $\mathcal{R}_W^0 > 1$ , then  $\mathcal{R}_{FW}^0 > 1$ . We can now give a kind of upper bound for  $\mathcal{R}_{FW}^0$ . Suppose that  $\mathcal{R}_3^0 < 1$  in both farm and wild patches when  $k = 0$ . Then there exists  $v_1, v_2$  such that

$$(v_1, 1) \begin{bmatrix} K_F - \alpha & K_F \\ \delta & -\omega \end{bmatrix} < 0 \quad \text{and} \quad (v_2, 1) \begin{bmatrix} K_W - \alpha & K_W \\ \delta & -\omega \end{bmatrix} < 0.$$

Then letting  $J_0$  be as the proof of Lemma 3.3 we have

$$(v_1, 1, v_2, 1)J_0 = \left( (v_1, 1) \begin{bmatrix} K_F - \alpha & K_F \\ \delta & -\omega \end{bmatrix}, (v_2, 1) \begin{bmatrix} K_W - \alpha & K_W \\ \delta & -\omega \end{bmatrix} \right) < 0.$$

Thus, by arguments similar to those in Proposition 7, if  $\mathcal{R}_3^0 < 1$  in both patches when  $k = 0$ , then  $\mathcal{R}_{FW}^0 < 1$  for any  $k$ .

In the remainder of this section, we derive sufficient conditions for the existence of a positive equilibrium and prove that it is unique whenever exists.

**Proposition 8.** *There exists a unique positive equilibrium,  $E_{FW} = (\overline{S}_F, \overline{I}_F, \overline{V}_F, \overline{S}_W, \overline{I}_W, \overline{V}_W)$  for the full system (2) if and only if  $E_0$  is unstable and either*

- i) (a)  $\beta_W < \frac{\omega(2+\frac{\omega}{k})+\delta(1+\frac{\omega}{k})}{\delta}\beta_F + \mu_W S(k)$  and;
- (b)  $\beta_F < (1 + \frac{\omega}{k} + \frac{\delta}{k})^2 \frac{\omega(2+\frac{\omega}{k})+\delta(1+\frac{\omega}{k})}{\delta}\beta_W + \mu_F S(k)$  or;
- ii) (a)  $\beta_F < \frac{\omega(2+\frac{\omega}{k})+\delta(1+\frac{\omega}{k})}{\delta}\beta_W + \mu_F S(k)$  and;
- (b)  $\beta_W < (1 + \frac{\omega}{k} + \frac{\delta}{k})^2 \frac{\omega(2+\frac{\omega}{k})+\delta(1+\frac{\omega}{k})}{\delta}\beta_F + \mu_W S(k)$ ,

where  $S(k)$  is given by (5).

*Proof.* For ease of notation we omit the bars. At equilibrium,  $\dot{S}_j = 0$  and  $\dot{I}_j = 0$  for  $j = F, W$ . Thus,  $\dot{S}_j + \dot{I}_j = (S_j + I_j) = 0$ . Hence,

$$I_j = \frac{1}{\alpha} S_j (\beta_i - \mu_i S_j)$$

where  $i = 1 \iff j = F$  and  $i = 2 \iff j = W$ . Substituting into the  $\dot{I}_j = 0$  equation yields,

$$V_j = \frac{1}{\alpha} (\beta_i - \mu_i S_j) (\alpha - S_j)$$

with  $i$  a function of  $j$  as before. Note that  $I_j, V_j > 0 \iff S_j < \min(\alpha, \frac{\beta_i}{\mu_i})$ . Now we substitute the expressions for  $V_j$  into the equation  $\dot{V}_j = 0$  and obtain the relations

$$(\beta_W - \mu_W S_W)(\alpha - S_W) = (\beta_F - \mu_F S_F) \left[ \alpha \left(1 + \frac{\omega}{k}\right) - \left(1 + \frac{\omega}{k} + \frac{\delta}{k}\right) S_F \right] \quad (8)$$

$$(\beta_F - \mu_F S_F)(\alpha - S_F) = (\beta_W - \mu_W S_W) \left[ \alpha \left(1 + \frac{\omega}{k}\right) - \left(1 + \frac{\omega}{k} + \frac{\delta}{k}\right) S_W \right] \quad (9)$$

Relations (8) and (9) define monotonically increasing curves in the  $(S_F, S_W)$ -plane.

Solving both (8) and (9) for  $\frac{\beta_F - \mu_F S_F}{\beta_W - \mu_W S_W}$  yields

$$\frac{\alpha \left(1 + \frac{\omega}{k}\right) - \left(1 + \frac{\omega}{k} + \frac{\delta}{k}\right) S_W}{\alpha - S_F} = \frac{\alpha - S_W}{\alpha \left(1 + \frac{\omega}{k}\right) - \left(1 + \frac{\omega}{k} + \frac{\delta}{k}\right) S_F}.$$

That is,

$$\frac{\alpha \left(1 + \frac{\omega}{k}\right) - \left(1 + \frac{\omega}{k} + \frac{\delta}{k}\right) S_W}{\alpha - S_W} = \frac{\alpha - S_F}{\alpha \left(1 + \frac{\omega}{k}\right) - \left(1 + \frac{\omega}{k} + \frac{\delta}{k}\right) S_F}, \quad (10)$$

a hyperbola. In the square  $[0, \alpha] \times [0, \alpha]$ , in the  $(S_F, S_W)$ -plane, (10) has an upper branch with endpoints  $(\alpha, \widehat{S})$  and  $(\widehat{S}, \alpha)$ , where  $\widehat{S} = \alpha \frac{1+\frac{\omega}{k}}{1+\frac{\omega}{k}+\frac{\delta}{k}}$ , and a lower branch with endpoints  $(0, S(k))$  and  $(S(k), 0)$ .

From equation (8) and for  $S_W < \min(\alpha, \frac{\beta_W}{\mu_W})$ , we must have  $S_F < \min(S(k), \frac{\beta_F}{\mu_F})$  for solutions to be positive and feasible. Similarly, from (9) we have that  $S_F <$



$\min(\alpha, \frac{\beta_W}{\mu_W})$ . Thus, any intersection between (8) and (10) or (9) and (10) must occur on the lower branch of (10). Consider (8) and let

$$\varphi(S_F, S_W) = (\beta_W - \mu_W S_W)(\alpha - S_W) - (1 + \frac{\omega}{k} + \frac{\delta}{k})(\beta_F - \mu_F S_F)(\widehat{S} - S_F)$$

Since (8) (resp. (9)) can have at most one intersection with (10) in this range, (8) and (10) have a unique intersection if and only if  $\varphi(0, S(k))\varphi(S(k), 0) < 0$ , where

$$\begin{aligned}\varphi(0, S(k)) &= (\beta_W - \mu_W S(k))(\alpha - S(k)) - (1 + \frac{\omega}{k} + \frac{\delta}{k})\beta_F \widehat{S} \\ \varphi(S(k), 0) &= \beta_W \alpha - (1 + \frac{\omega}{k} + \frac{\delta}{k})(\beta_F - \mu_F S(k))(\widehat{S} - S(k))\end{aligned}$$

If  $\varphi(0, S(k)) > 0$  and  $\varphi(S(k), 0) < 0$  then

(a)  $\beta_W > \frac{\omega(2+\frac{\omega}{k})+\delta(1+\frac{\omega}{k})}{\delta}\beta_F + \mu_W S(k) > \beta_F$  and;

(b)  $\beta_F > (1 + \frac{\omega}{k} + \frac{\delta}{k})^2 \frac{\omega(2+\frac{\omega}{k})+\delta(1+\frac{\omega}{k})}{\delta}\beta_W + \mu_F S(k) > \beta_W$ ,

a contradiction. Thus, for (8) and (10) to have a unique intersection, we must have  $\varphi(0, S(k)) < 0$  and  $\varphi(S(k), 0) > 0$ . This holds if and only if

(a)  $\beta_W < \frac{\omega(2+\frac{\omega}{k})+\delta(1+\frac{\omega}{k})}{\delta}\beta_F + \mu_W S(k)$  and;

(b)  $\beta_F < (1 + \frac{\omega}{k} + \frac{\delta}{k})^2 \frac{\omega(2+\frac{\omega}{k})+\delta(1+\frac{\omega}{k})}{\delta}\beta_W + \mu_F S(k)$ .

Consider (9) and let  $\psi(S_F, S_W) = (\beta_F - \mu_F S_F)(\alpha - S_F) - (1 + \frac{\omega}{k} + \frac{\delta}{k})(\beta_W - \mu_W S_W)(\widehat{S} - S_W)$ . Then we see via similar arguments that (9) and (10) have a unique intersection if and only if  $\psi(S(k), 0) < 0$  and  $\psi(0, S(k)) > 0$  if and only if

(a)  $\beta_F < \frac{\omega(2+\frac{\omega}{k})+\delta(1+\frac{\omega}{k})}{\delta}\beta_W + \mu_F S(k)$  and;

(b)  $\beta_W < (1 + \frac{\omega}{k} + \frac{\delta}{k})^2 \frac{\omega(2+\frac{\omega}{k})+\delta(1+\frac{\omega}{k})}{\delta}\beta_F + \mu_W S(k)$ .

□

The previous result gives necessary and sufficient conditions for the existence of the unique positive equilibrium with thresholds in the  $S_F, S_W$  plane. This is the clearest formulation with respect to the endemic equilibrium itself, since the values of  $I_F, V_F, I_W$  and  $V_W$  are determined by  $S_F$  and  $S_W$ . Next, we recast the result in terms of the stability with respect to the interior of the boundary equilibria  $EE_F$  and  $EE_W$  lying in 4-dimensional faces of the boundary.

**Corollary 2.** *There exists a unique positive equilibrium  $E_{FW}$  if and only if  $E_0$  is unstable,  $\beta_W - V_W^* > 0$  when evaluated at  $E_F$  and  $\beta_F - V_F^* > 0$  when evaluated at  $E_W$ .*

*Proof.* The Jacobian of system (2) evaluated at  $E_F$  has the form

$$J = \begin{bmatrix} -\mu_F S(k) & -S(k) & -S(k) & 0 & 0 & 0 \\ \beta_F - \mu_F S(k) & S(k) - \alpha & S(k) & 0 & 0 & 0 \\ 0 & \delta & -(k + \omega) & 0 & 0 & k \\ 0 & 0 & 0 & \beta_W - V_W^* & 0 & 0 \\ 0 & 0 & 0 & V_W^* & -\alpha & 0 \\ 0 & 0 & k & 0 & \delta & -(k + \omega) \end{bmatrix}.$$

It is clear that  $\beta_W - V_W^*$  is a positive eigenvalue of  $J$  with associated eigenvector pointing into  $\mathbb{R}_+^6$ . A similar statement holds for  $\beta_F - V_F^*$  by symmetry. Let  $Q =$

$\frac{\delta k}{\omega(2k+\omega)+\delta(k+\omega)}$ . Then  $V_W^* = Q(\beta_F - \mu_F S(k))$  and  $\varphi(S(k), 0) = \alpha(\beta_W - \frac{1}{\gamma}(\beta_F - \mu_F S(k)))$ . Thus,

$$\varphi(S(k), 0) > 0 \iff \beta_W - Q(\beta_F - \mu_F S(k)) > 0 \iff \beta_F < \frac{1}{Q}\beta_W + \mu_F S(k),$$

which correspond to  $i)(b)$  and  $ii)(a)$  of Proposition 8, respectively. Similarly,  $V_F' = Q(\beta_W - \mu_W S(k))$  and,

$$\psi(0, S(k)) > 0 \iff \beta_F - Q(\beta_W - \mu_W S(k)) > 0 \iff \beta_W < \frac{1}{Q}\beta_F + \mu_W S(k)$$

which correspond to  $i)(a)$  and  $ii)(b)$  of Proposition 8, respectively.  $\square$

This result implies that the endemic equilibrium undergoes a transcritical bifurcation the positive equilibrium of one of the 4-dimensional invariant boundary subsystems as  $(S_F, S_W)$  crosses the on of the linear constraints given in Proposition 8.

The stability of the  $E_0$  is given by the value of  $\mathcal{R}^0$  as compared to the threshold value 1. That is  $\mathcal{R}^0 < 1 \iff E_0$  is stable and  $\mathcal{R}^0 > 1 \iff E_0$  is unstable. By Lemma 3.3  $\mathcal{R}_{FW}^0$  is given as a function of  $\mathcal{R}_F^0$  and  $\mathcal{R}_W^0$ , each of which is a function of  $\beta_i, \mu_i$  and  $S(k)$  for  $i = F$  or  $W$ . Therefor we can recast our previous results regarding the local stability of equilibria in terms of the location of  $(\mathcal{R}_F^0, \mathcal{R}_W^0)$  with respect to 3 constraints

**Theorem 3.4.** *There exists a unique positive equilibrium if and only if  $\mathcal{R}_{FW}^0 > 1$ ,  $\mathcal{R}_W^0 > \frac{\mu_F}{\mu_W}Q(\mathcal{R}_F^0 - 1)$  and  $\mathcal{R}_F^0 > \frac{\mu_W}{\mu_F}Q(\mathcal{R}_W^0 - 1)$ , where  $Q$  is as in the previous Corollary.*

*Proof.* By Lemma 3.3, if either  $\mathcal{R}_F^0 > 1$  or  $\mathcal{R}_W^0 > 1$  then  $\mathcal{R}_{FW}^0 > 1$ . If both  $\mathcal{R}_F^0 < 1$  and  $\mathcal{R}_W^0 < 1$  then by the proof of Lemma 3.3  $\mathcal{R}_0^0 > 1$  iff and only if  $p(1) < 0$  where  $p(\lambda) = \lambda^2 - (\mathcal{R}_F^0 + \mathcal{R}_W^0)\lambda + \mathcal{R}_F^0 \mathcal{R}_W^0 - \frac{\beta_F \beta_W}{\mu_F \mu_W} \frac{\delta^2 k^2}{\alpha^2 \omega^2 (2k + \omega)^2}$ . Then the equation  $p(1) = 0$  gives

$$\begin{aligned} 1 - \mathcal{R}_F^0 + \mathcal{R}_W^0 + \mathcal{R}_F^0 \mathcal{R}_W^0 &= \frac{\beta_F \beta_W}{\mu_F \mu_W} \frac{\delta^2 k^2}{\alpha^2 \omega^2 (2k + \omega)^2} \\ 1 - \mathcal{R}_F^0 + \mathcal{R}_W^0 + \mathcal{R}_F^0 \mathcal{R}_W^0 &= \frac{\beta_F \beta_W}{\mu_F \mu_W} \frac{S(k)^2}{S(k)^2} \frac{\delta^2 k^2}{\alpha^2 \omega^2 (2k + \omega)^2} \\ 1 - \mathcal{R}_F^0 + \mathcal{R}_W^0 + \mathcal{R}_F^0 \mathcal{R}_W^0 &= \mathcal{R}_F^0 \mathcal{R}_W^0 Q^2 \\ \frac{1}{\mathcal{R}_F^0 \mathcal{R}_W^0} - \frac{1}{\mathcal{R}_W^0} - \frac{1}{\mathcal{R}_F^0} + 1 &= Q^2 \\ \left(1 - \frac{1}{\mathcal{R}_F^0}\right) \left(1 - \frac{1}{\mathcal{R}_W^0}\right) &= Q^2 \end{aligned}$$

a hyperbola in the  $\mathcal{R}_F^0, \mathcal{R}_W^0$ -plane. Thus, it follows that  $\mathcal{R}_0^0 > 1$  if  $(\mathcal{R}_F^0, \mathcal{R}_W^0)$  lies above the lower branch of this hyperbola. The lower branch of the hyperbola passes through the points  $(0, 1)$ ,  $(1, 0)$  and  $(\frac{1}{1+Q}, \frac{1}{1+Q})$ . These coordinate pairs correspond to the points  $(0, S(k))$ ,  $(S(k), 0)$  and  $(\frac{S(k)}{1+Q}, \frac{S(k)}{1+Q})$  in the  $\frac{\beta_F}{\mu_F}, \frac{\beta_W}{\mu_W}$  plane. Considering (10) in the  $\frac{\beta_F}{\mu_F}, \frac{\beta_W}{\mu_W}$ -plane corresponds to the first two coordinate pairs,  $(0, S(k))$  and  $(S(k), 0)$ . Solving for the intersection of the lower branch with the line  $\frac{\beta_F}{\mu_F} = \frac{\beta_W}{\mu_W}$  results in the final point. Hence, being above the lower branch also corresponds to

$(\frac{\beta_F}{\mu_F}, \frac{\beta_W}{\mu_W})$  being above the lower branch of (10), that is to the disease free equilibrium being unstable.

Now, suppose  $\mathcal{R}_W^0 > \frac{\mu_F}{\mu_W} Q \mathcal{R}_F^0 - \frac{\mu_F}{\mu_W} Q$ . Then

$$\begin{aligned} \frac{\beta_W}{\mu_W S(k)} > \frac{\mu_F}{\mu_W} Q \frac{\beta_F}{\mu_F S(k)} - \frac{\mu_F}{\mu_W} Q &\iff \frac{\mu_W \beta_W}{\mu_W \mu_F S(k)} > Q \left( \frac{\beta_F}{\mu_F S(k)} - 1 \right) \\ &\iff \beta_W > \frac{\delta k}{\omega(2k + \omega) + \delta(k + \omega)} (\beta_F - \mu_F S(k)) \end{aligned}$$

That is,  $\beta_W - V_W^*$  is a positive eigenvalue of the boundary equilibrium corresponding to the 4-dimensional subsystem (4) with fish in only the farmed patch. Suppose also that  $\mathcal{R}_W^0 < \frac{\mu_F}{\mu_W} Q \mathcal{R}_F^0 + 1$ . Then

$$\begin{aligned} \frac{\beta_W}{\mu_W S(k)} < \frac{1}{Q} \frac{\mu_F \beta_F}{\mu_F \mu_W S(k)} + 1 &\iff \frac{\beta_W}{\mu_W S(k)} - 1 < \frac{1}{Q} \frac{\beta_F}{\mu_F S(k)} \\ &\iff \frac{\delta k}{\omega(2k + \omega) + \delta(k + \omega)} (\beta_W - \mu_W S(k)) < \beta_F \end{aligned}$$

That is,  $\beta_F - V_F'$  is a positive eigenvalue of the boundary equilibrium corresponding to the 4-dimensional subsystem with fish in only the wild patch. Then the result follows by Corollary 2.

If  $\mathcal{R}_0^0 < 1$  then  $i \mathcal{R}_{0,4} < 1$  for  $i = 1, 2$  and  $\frac{\beta_F}{\mu_F} < S(k) < \alpha$  and  $\frac{\beta_W}{\mu_W} < S(k) < \alpha$ . Let

$$x = \begin{bmatrix} I_F \\ V_F \\ I_W \\ V_W \end{bmatrix}. \text{ Then } \dot{x} = Ax \text{ where } A \text{ is the submatrix of the Jacobian corresponding}$$

to viral compartments. Let  $A^0$  be formed by replacing  $S_F$  with  $\frac{\beta_F}{\mu_F}$  and  $S_W$  with  $\frac{\beta_W}{\mu_W}$ . Then  $A^0$  is quasi-positive and irreducible. Since  $\mathcal{R}_0^0 < 1$ ,  $DFE$  is locally stable. Thus, there exists  $\lambda > 0$  and  $v^T > 0$  such that  $v^T A^0 = -\lambda v^T$ . Let  $W = v^T x$ . Let  $\varepsilon_F, \varepsilon_W > 0$ ,  $S_F < \frac{\beta_F}{\mu_F} + \varepsilon_F$ ,  $S_W < \frac{\beta_W}{\mu_W} + \varepsilon_W$  and  $\varepsilon = \max(\varepsilon_F, \varepsilon_W)$ . Then

$$\dot{W} = v^T Ax < v^T \left( A^0 + \begin{bmatrix} \varepsilon_F & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & \varepsilon_W & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \right) x < (-\lambda + \varepsilon) v^T x = (-\lambda + \varepsilon) W.$$

Hence,  $W \rightarrow 0$  for  $\varepsilon$  sufficiently small and the statement follows by the comparison principle.  $\square$

It is evident from region II of Figure 2 that when both 4-dimensional subsystems are sinks for the virus,  $\mathcal{R}_{FW}^0 > 1$  is sufficient for there to exist the positive  $E_{FW}$ . However, if one of those subsystems is a reservoir for the virus additional conditions given in Theorem 3.4 must be met to assure the existence of the positive  $E_{FW}$ .

**4. Persistence.** Having established conditions for the existence of equilibria in the full system (2) as well as in the 3 and 4-dimensional subsystems, (3) and (4), respectively, we now turn our attention to the question of whether the virus goes extinct or whether it persists. We will view the flow of the system as a semidynamical system on a metric space. There is a rich theory of persistence in dynamical systems [2], [3], [6], [7], [8], [12], [13], [21], and [24].

Let  $X$  be the positive orthant of  $\mathbb{R}_+^n$  together with its boundary and let  $\varphi : \mathbb{R} \times X \rightarrow X$  be the solution to the (sub)system under consideration ( $n=3, 4$  or  $6$  for system (3), (4), or (2), respectively). Then the flow  $\varphi$  can be considered a semidynamical

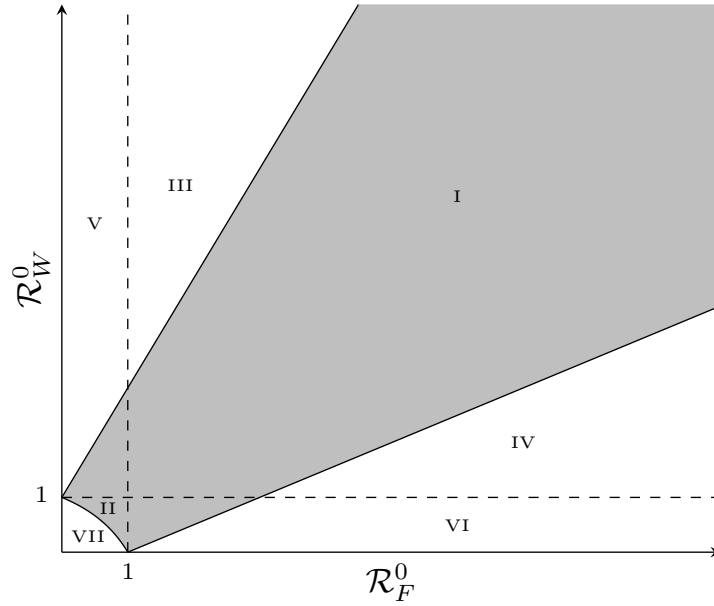


FIGURE 2. In regions I and II, the positive equilibrium  $E_{FW}$  exists. In region III,  $E_F$  is unstable W.R.T. the interior and  $E_W$  is stable W.R.T.. In region V,  $E_F$  DNE while  $E_W$  is stable W.R.T the interior. Regions IV and VI are the symmetric opposites of regions III and V, respectively.

system on  $X$  such that  $\forall x \in X, t \mapsto \varphi(t, x) = \varphi_t(x)$  with the properties  $\varphi(0, x) = x$  and  $\varphi_t \circ \varphi_s = \varphi_{t+s}$ , the group property.

Suppose that  $X = X_1 \sqcup X_2$  the union of disjoint sets  $X_1$  and  $X_2$  and that  $\varphi$  is a continuous semiflow on  $X_1$ . For any  $x \in X$  and  $Y \subset X$  we define  $d(x, Y) = \inf_{y \in Y} d(x, y)$  to be the distance between the point  $x$  and the set  $Y$ . Following Thieme (1993) [21], let  $Y_2$  be a subset of  $X_2$ .

We say that  $Y_2$  is *weak repeller* for  $X_1$  if

$$\limsup_{t \rightarrow \infty} d(\varphi_t(x_1), Y_2) > 0 \quad \forall x_1 \in X_1.$$

We say that  $Y_2$  is a *uniform weak repeller* for  $X_1$  if there exists  $\varepsilon > 0$  such that

$$\limsup_{t \rightarrow \infty} d(\varphi_t(x), Y_2) > \varepsilon \quad \forall x_1 \in X_1.$$

We say that  $Y_2$  is a *strong repeller* or a *uniform strong repeller* for  $X_1$  if  $\limsup$  is replaced by  $\liminf$  in the above definitions. In our case,  $X_2$  will be a closed subset of the boundary of  $X$  where the virus goes extinct in forward time and  $X_1$  will be its complement. The dynamical system  $\varphi$  is called (*uniformly*) *weakly* or (*uniformly*) *strongly persistent* if  $X_2$  is a (uniform) weak or (uniform) strong repeller for  $X_1$ .

Recall, a subset  $M \subset X$  is called *forward invariant* if and only if  $\varphi_t(M) \subset M$  for all  $t > 0$ , *backward invariant* if and only if  $\varphi_t(M) \subset M$  for all  $t < 0$  and *fully invariant* if and only if it is both forward and backward invariant. A compact invariant subset  $M \subset Y \subset X$  is called and *isolated compact invariant set* in  $Y$  if there is an open

subset  $U \subset X$  such that there is no invariant set  $\tilde{M}$  with  $M \subset \tilde{M} \subset U \cap Y$  except  $M$ .  $U$  is called an *isolating neighborhood* of  $M$ .

Still following [21], we define

$$\Omega(Y_2) = \bigcup_{y \in Y_2} \omega(y), \text{ where } Y_2 = \{x \in X_2 : \varphi_t(x) \in X_2 \forall t > 0\}.$$

We say that a finite covering  $M = \bigcup_{k=1}^m M_k$  in  $X_2$  is *isolated* if the sets  $M_k$  are pairwise disjoint subsets of  $X_2$ , which are isolated compact invariant sets in  $X$ .

A set  $M \subset X_2$  is said to be *chained* (in  $X_2$ ) to another (not necessarily distinct) set  $N \subset X_2$ ,  $M \mapsto N$ , if there exists  $y \in X_2 \setminus (M \cup N)$  and a full orbit through  $y$  such that  $\alpha(y) \subset M$  and  $\omega(y) \subset N$ .

A finite covering  $M = \bigcup_{k=1}^m M_k$  is called *cyclic* if, after possible renumbering,  $M_1 \mapsto M_1$  or  $M_1 \mapsto M_2 \mapsto \dots \mapsto M_k \mapsto M_1$  for some  $k \in \{2, \dots, m\}$ . If  $M$  is not cyclic, it is called *acyclic*.

Now that we have established the necessary definitions we will show first that when  $\mathcal{R}_{FW}^0 > 1$  the boundary set corresponding to the eventual extinction of the virus is a weak repeller for its complement and then by a result of Thieme [21] this boundary set is in fact a uniform strong repeller. This implies that in cases where there are initially positive densities of both susceptible and infected individuals or initially positive densities of both susceptible individuals and virus in the environment that the virus will persist.

The basic reproductive ratio  $\mathcal{R}_{FW}^0$  is defined in the context of epidemiology as the expected number of new cases of infection caused by a typical infected individual [11]. Then  $\mathcal{R}_{FW}^0 > 1$  implies that a typical infected individual will more than replace themselves. Thus, if the system is at rest in the disease free equilibrium,  $E_0$ , and  $\mathcal{R}_{FW}^0 > 1$ , if a small number of infected individuals are introduced, they will invade. This in turn implies that the linearization of system evaluated at  $E_0$  indicates growth in at least one direction, i.e. the Jacobian has at least one eigenvalue  $\lambda_d$  with  $\text{Re}(\lambda_d) > 0$ . The proof we provide here for weak persistence rests on the fact that  $E_0$  is a saddle whose unstable manifold enters the interior, when  $\mathcal{R}_{FW}^0 > 1$ . By appealing to a powerful result due to Thieme [21] we can extend from weak persistence to uniform strong persistence.

**Proposition 9.** *If  $\mathcal{R}_{FW}^0 > 1$ , then system (2) is weakly persistent.*

*Proof.* If  $X = \overline{\mathbb{R}_+^6}$  and  $X_2 = \{S_F = S_W = 0\} \cup \{I_F = V_F = I_W = V_W = 0\}$ , then  $X_2$  is fully invariant with respect to  $\varphi$ , the flow of system (2) and  $X_1 = X \setminus X_2$  is forward invariant. Since (2) is dissipative, we may restrict and relabel  $X = [0, C]^6$ ,  $X_2 = X_2 \cap [0, C]^6$ , and  $X_1 = X \setminus X_2$  for some  $C > 0$ . Then  $X_1$  and  $X_2$  are disjoint, forward invariant sets and  $X_2$  is compact. By the forward invariance of  $X_2$ ,  $Y_2 = X_2$  direct examination of the flow on  $X_2$  shows that  $\Omega(X_2) = \{\mathcal{E}_{00}, \mathcal{E}_{10}, \mathcal{E}_{01}, E_0\}$ . Suppose for the sake of contradiction that there exists  $x_1 \in X_1$  such that  $\limsup_{t \rightarrow \infty} d(\varphi_t(x_1), X_2) = 0$ . Then there exists  $x_2 \in X_2$  with  $x_2 \in \omega(x_1)$  and therefore  $\omega(x_2) \subset \omega(x_1)$ . By the invariance of  $X_1$  and repeated applications the Butler-McGehee Lemma, we may assume without loss of generality that  $\omega(x_2) = \{E_0\}$ . By appealing once more to the invariance of  $X_1$  and the Butler-McGehee Lemma, we have that there exists  $q_1, q_2 \in \omega(x_1)$  with  $q_1 \in W^s(E_0)$  and  $q_2 \in W^u(E_0)$ . However,  $W^u(E_0) \setminus \{E_0\} \cap X_2 = \emptyset$ . This contradicts the assumption  $\limsup_{t \rightarrow \infty} d(\varphi_t(x_1), X_2) = 0$ . Thus,  $X_2$  is a weak repeller for  $X_1$  and  $\varphi$  is weakly persistent.  $\square$

**Lemma 4.1.** *Consider system (2) and suppose  $\mathcal{R}_{FW}^0 > 1$ ,  $M_1 = \mathcal{E}_{00}$ ,  $M_2 = \mathcal{E}_{10}$ ,  $M_3 = \mathcal{E}_{01}$  and  $M_4 = E_0$ . Then  $M = \bigcup_{i=1}^4 M_i$  is an acyclic isolated covering for  $\Omega(X_2)$  in  $X_2$ .*

*Proof.* It is clear that  $M$  is an isolated cover for  $\Omega(X_2)$ . If  $y = (y_1, 0, 0, 0, 0)$  for  $0 < y_1 < \frac{\beta_F}{\mu_F}$ , then  $\alpha(y) = M_1$  and  $\omega(y) = M_2$  so  $M_1 \mapsto M_2$ . Similarly,  $M_1 \mapsto M_3$ . Now,  $W^u(M_j) \cap X_2 \subset W^s(M_4)$  for  $j = 2, 3$ . Thus,  $M_2 \mapsto M_4$ , but  $M_2 \not\mapsto M_1$  and  $M_2 \not\mapsto M_3$ . Similarly,  $M_3 \mapsto M_4$ , but  $M_3 \not\mapsto M_1$  and  $M_3 \not\mapsto M_2$ . Since  $W^u(E_0) \setminus \{E_0\} \cap X_2 = \emptyset$ ,  $M_4$  is not chained to any other element of the covering  $M$ . Thus,  $M$  is acyclic.  $\square$

**Theorem 4.2.** *System (2) is uniformly strongly persistent if and only if  $\mathcal{R}_{FW}^0 > 1$ .*

*Proof.* Let  $X$ ,  $X_1$ ,  $X_2$ ,  $M_1$ ,  $M_2$ ,  $M_3$  and  $M_4$  be as defined in Proposition 9 and Lemma 4.1. Then  $\Omega(X_2) = \{\mathcal{E}_{00}, \mathcal{E}_{10}, \mathcal{E}_{01}, E_0\}$ ,  $X = X_1 \sqcup X_2$ , a disjoint union,  $X_2$  is compact, and  $M = \bigcup_{k=1}^4 M_k$  is an acyclic isolated covering with each  $M_k$  a weak repeller for  $X_1$ . Assumption  $C_{4.1}$  of Thieme (1993) [21] is satisfied by the compactness of  $X$ . Thus, by Theorem 4.5 [21],  $\varphi$  is uniformly strongly persistent. By Proposition 7, if  $\mathcal{R}_{FW}^0 \leq 1$  then solutions with positive initial conditions converge to  $E_0 \in X_2$ .  $\square$

**Remark 1.** It is possible, in a manner similar to the arguments above, to prove persistence results of the form *the  $n$ -dimensional invariant subsystem is uniformly strongly persistent if and only if  $\mathcal{R}_n^0 > 1$  for  $n = 3, 4$ .*

The next result is in keeping with the discussion following the the proof of Proposition 5.

**Corollary 3.** *Suppose there is a positive constant  $k^*$  such that  $S(k^*) = \frac{\beta}{\mu}$ . Then the virus will persist in system (4) for all  $k \in [0, k^*]$  and will go extinct for  $k > k^*$ .*

*Proof.*  $\mathcal{R}_4^0$  is decreasing in  $k$  and equal to 1 for  $k = k^*$ .  $\square$

**Corollary 4.** *If  $\mathcal{R}_i^0 > 1$  for  $i = F$  or  $W$ , then system (2) is uniformly strongly persistent.*

*Proof.* By Lemma 3.3,  $\max(\mathcal{R}_F^0, \mathcal{R}_W^0) > 1$  implies that  $\mathcal{R}_{FW}^0 > 1$ . The statement follows by the previous Theorem.  $\square$

**Remark 2.** In the invariant subsystems, persistence and the existence of a unique endemic equilibrium coincide, whereas in the context of the full system, it is possible that there is no positive equilibrium, but the system is uniformly strongly persistent. This is a result of the fact that our boundary set is a proper subset of the boundary. While persistence with respect to this boundary set still corresponds to the viral compartments being bounded away from zero, it does not preclude converging to an invariant subsystem of lower dimension. The virus is allowed to migrate between patches via diffusion, but the fish are restricted to their birth patch. Thus, the system can be uniformly strongly persistent even while the fish in one patch go extinct.

If a 4-dimensional subsystem is uniformly strongly persistent we will say that the patch relative to the susceptible class is a reservoir for the virus. If the disease free equilibrium in a 4-dimensional subsystem is globally asymptotically stable, then we will say the patch relative to the susceptible class is a sink for the virus. Thus, if either 4-dimensional subspace is a reservoir for the virus, then  $\mathcal{R}_{FW}^0 > 1$  and the virus persists in the full system whether or not a susceptible host is present

in the complementary patch. However, it is clear from Figure 2 that even if both 4-dimensional subsystems are sinks for the virus, it is still possible for  $\mathcal{R}_{FW}^0 > 1$  and hence, the virus will persist in the full system (2). In this way, local patch dynamics strongly influence the persistence of the system.

**5. Bifurcations and the existence of limit cycles.** Even in the 3-dimensional invariant subsystem, the endemic equilibrium is not guaranteed to be locally stable. Assuming that all other parameters are fixed, we show that if the rate of viral shedding,  $\delta$ , is sufficiently large, then the endemic equilibrium may undergo a Hopf bifurcation. We treat the growth rate,  $\beta$ , as the bifurcation parameter with the bifurcation point a function of the remaining parameters. A similar result is given by DeLeenheer and Smith (2003) [19] for the standard model for HIV with growth function  $f_1(T)$ . The main difference between that model and the 3-dimensional subsystem (3) is the addition in (3) of the possibility of infection due to direct contact with an infected individual. Since oscillatory behavior occurs even without infection via direct contact, we can deduce that its introduction is not the underlying cause of oscillations in (3). In [19], the carrying capacity is shown to be the bifurcation parameter. The carrying capacity in subsystem (3) is  $\frac{\beta}{\mu}$ . Thus, increasing  $\beta$  has the effect of increasing the carrying capacity. We now give conditions under which it is precisely increasing  $\beta$  that leads to a Hopf bifurcation and oscillatory behavior in system (3).

**Proposition 10.** *If  $\mathcal{R}_3^0 > 1$  then there exist  $\delta_{crit}$  and  $\beta_{crit}$  such that if  $\delta > \delta_{crit}$  then  $E_3$  undergoes a Hopf bifurcation as  $\beta$  increases through  $\beta_{crit}$ .*

*Proof.*

$$J_{E_3} = \begin{bmatrix} \beta - 2\mu\bar{S} - \bar{I} - \bar{V} & -\bar{S} & -\bar{S} \\ \bar{I} + \bar{V} & \bar{S} - \alpha & \bar{S} \\ 0 & \delta & -\omega \end{bmatrix} = \begin{bmatrix} -\mu\bar{S} & -\bar{S} & -\bar{S} \\ \beta - \mu\bar{S} & \bar{S} - \alpha & \bar{S} \\ 0 & \delta & -\omega \end{bmatrix}$$

and  $\bar{S} = \frac{\alpha\omega}{\omega + \delta} < \alpha$  implies each of the diagonal entries are negative. The characteristic polynomial is given by

$$p(\lambda) = \lambda^3 + a_1\lambda^2 + a_2\lambda + a_3$$

Where,

$$a_1 = \alpha + \omega + (\mu - 1)\bar{S} > 0, \quad a_2 = \bar{S}(\beta + (\alpha + \omega - 2\bar{S})\mu) > 0, \quad \text{and} \quad a_3 = \alpha\omega(\beta - \mu\bar{S}) > 0.$$

Then  $a_1a_2 - a_3 = (\alpha - \bar{S} + \omega + \mu\bar{S})\bar{S}(\beta + (\alpha - \bar{S} + \omega - \bar{S})\mu) - \alpha\omega(\beta - \mu\bar{S})$  is linear in  $\beta$  with coefficient

$$\bar{S}(\alpha - \bar{S} + \omega + \mu\bar{S}) - \alpha\omega = \bar{S}(\alpha + \omega + (\mu - 1)\bar{S}) - \bar{S}(\omega + \delta) = \bar{S}(\alpha + (\mu - 1)\bar{S} - \delta).$$

**Claim 1.**  $\alpha + (\mu - 1)\bar{S} - \delta < 0 \iff \delta > \frac{\alpha - \omega + \sqrt{(\alpha - \omega)^2 + 4\mu\alpha\omega}}{2}$ .

*Proof of Claim.*

$$\begin{aligned} \alpha + (\mu - 1)\bar{S} - \delta &< 0 \\ \alpha + (\mu - 1)\frac{\alpha\omega}{\delta + \omega} - \delta &< 0 \\ \delta^2 + \delta(\omega - \alpha) - \mu\alpha\omega &> 0 \end{aligned}$$

Since by assumption  $\delta > 0$ , we have that the last inequality holds if and only if

$$\delta > \frac{\alpha - \omega + \sqrt{(\alpha - \omega)^2 + 4\mu\alpha\omega}}{2}. \quad \square$$

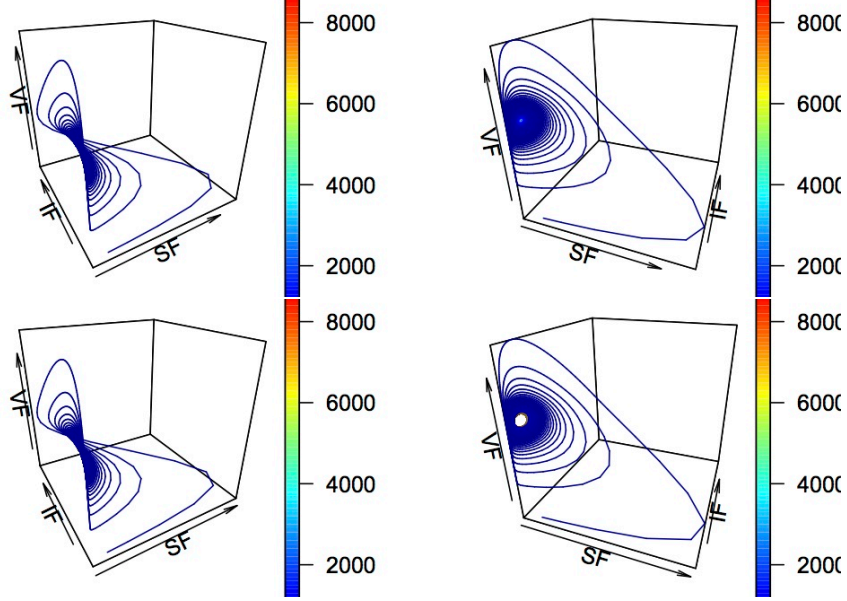


FIGURE 3. Consider system (3) with  $\mu = 1.2$ ,  $\alpha = 1.5$ ,  $\omega = 0.2$  and  $\delta = 1.7$ . Then  $\delta > \delta_{crit} \approx 1.69$  and  $\beta_{crit} \approx 19.21$ . Figure (a) shows that for  $\beta = 19$ , the simulation of the flow through  $(S, I, V) = (1, 1, 1)$  converges to the positive equilibrium  $(\bar{S}, \bar{I}, \bar{V})$ . Figure (b) shows that for  $\beta = 20$ , the simulation for the flow through  $(S, I, V)$  appears to converge to a positive limit cycle.

By Claim 1 the hypothesis on  $\delta$  implies that  $\alpha + (\mu - 1)\bar{S} - \delta < 0$ . Thus,  $a_1 a_2 - a_3$  is decreasing linear function of  $\beta$ . If we consider  $\bar{S}$  to be fixed then the  $\beta$  is bounded below by  $\mu\bar{S}$ , the threshold where  $\mathcal{R}_3^0 = 1$ . Thus, we consider  $a_1 a_2 - a_3$  for  $\beta \in (\mu\bar{S}, \infty)$ . Now,

$$\begin{aligned}
 0 &= a_1 a_2 - a_3 \\
 0 &= (\alpha - \bar{S} + \omega + \mu\bar{S})\bar{S}(\beta + (\alpha - \bar{S} + \omega - \bar{S})\mu) - \alpha\omega(\beta - \mu\bar{S}) \\
 0 &= [\bar{S}(\alpha - \bar{S} + \omega + \mu\bar{S}) - \alpha\omega]\beta + \mu\bar{S}(\alpha - \bar{S} + \omega - \bar{S})(\alpha - \bar{S} + \omega + \mu\bar{S}) + \mu\bar{S}\alpha\omega \\
 0 &= [\bar{S}((\mu - 1)\bar{S} + \alpha - \delta)]\beta + \mu\bar{S}[(\alpha - \bar{S} + \omega - \bar{S})(\alpha - \bar{S} + \omega + \mu\bar{S}) + \alpha\omega]
 \end{aligned}$$

Letting  $\alpha - \bar{S} + \omega = \Delta$  yields,

$$\beta_{crit} = \mu \frac{-(\Delta + \mu\bar{S})(\Delta - \bar{S}) - \alpha\omega}{(\mu - 1)\bar{S} + \alpha - \delta} = \mu \frac{(\Delta + \mu\bar{S})(\Delta - \bar{S}) + \alpha\omega}{\delta - \alpha + (1 - \mu)\bar{S}}$$

Thus,  $a_1 a_2 - a_3 > 0$  for  $\beta \in (\mu\bar{S}, \beta_{crit})$ ,  $a_1 a_2 - a_3 = 0$  for  $\beta = \beta_{crit}$  and  $a_1 a_2 - a_3 < 0$  for  $\beta > \beta_{crit}$ .  $\square$

In Section 3 we saw that the density of susceptible fish at the endemic equilibrium in the 4-dimensional system (4) is given by  $S(k)$ , a continuous function of  $k$ . Furthermore,  $S(0)$  is the density of susceptible fish at the endemic equilibrium of the 3-dimensional system (3). Since the equilibrium densities in all compartments can be written as a function of the density of susceptible fish, increasing  $k$  through zero is a perturbation of  $E_3$  from the 3-dimensional face of  $\mathbb{R}_+^4$  into the interior.



We noted that perturbing system (4) by increasing  $k$  gradually from  $k = 0$  has the effect of continuously and monotonically decreasing  $\mathcal{R}_4^0$ . In fact, in the next result, we see that perturbing  $k$  away from zero perturbs the Hopf periodic orbit shown in Proposition 10 into the interior of  $\mathbb{R}_+^4$ .

**Theorem 5.1.** *Suppose that  $\mathcal{R}_3^0 > 1$  and  $\delta$  is sufficiently large. Then there exists a continuous function  $\beta^*(k)$  such that  $E_4$  undergoes a Hopf bifurcation as  $\beta$  increases through  $\beta^*(k)$  for all  $k$  sufficiently small.*

*Proof.* Consider the linearization of (4) at  $E_4$  given by

$$J = \begin{bmatrix} -\mu S & -S & -S & 0 \\ \beta - \mu S & S - \alpha & S & 0 \\ 0 & \delta & -(k + \omega) & k \\ 0 & 0 & k & -(k + \omega) \end{bmatrix} = \begin{bmatrix} -\mu S & -S & -S & 0 \\ \beta - \mu S & S - \alpha & S & 0 \\ 0 & \delta & -\omega & 0 \\ 0 & 0 & -\omega & -k \end{bmatrix} + \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & -k & k \\ 0 & 0 & k & -k \end{bmatrix} = A + B$$

where  $S$  is taken to be the density of susceptibles at  $E_4$ . Denote that the upper block of  $A$  as  $J_3$  and note  $J_3$  coincides with the Jacobian of system (3) evaluated at the unique positive equilibrium of that system. The characteristic polynomial of  $J$  is

$$p(\lambda) = \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4,$$

Let  $q(\lambda)$  be the characteristic polynomial of  $J_3$ . When  $k = 0$  then  $p(\lambda) = (\lambda + \omega)q(\lambda)$  and Proposition 10 implies that when  $\beta = \beta_{crit}$   $E_4$  admits a pair of purely imaginary eigenvalues and the Routh-Hurwitz Criterion  $a_1a_2a_3 - a_3^2 - a_1^2a_4 = 0$ . Let

$$f(\beta, k) = a_1a_2a_3 - a_3^2 - a_1^2a_4 \quad (11)$$

and

$$\frac{\partial a_1}{\partial \beta} = 0; \quad \frac{\partial a_2}{\partial \beta} = S; \quad \frac{\partial a_3}{\partial \beta} = (2k + 2\omega + \delta)S; \quad \frac{\partial a_4}{\partial \beta} = \alpha\omega(2k + \omega)$$

Then  $f(\beta_{crit}, 0) = 0$  and

$$\begin{aligned} \frac{\partial f}{\partial \beta}(\beta_{crit}, 0) &= a_1a_3 \frac{\partial a_2}{\partial \beta} + a_1a_2 \frac{\partial a_3}{\partial \beta} - 2a_3 \frac{\partial a_3}{\partial \beta} - a_1^2 \frac{\partial a_4}{\partial \beta} \\ &= (\alpha\omega + 2S\omega)(\alpha - S + \mu S)(\mu S(\alpha - S + \omega) + S(\beta_{crit} - \mu S)) \\ &\quad + \alpha\omega S(\alpha - S + \mu S)(\beta_{crit} - \mu S) + 2S\omega^2(\mu S(\alpha - S + \omega) + S(\beta_{crit} - \mu S)) \\ &\quad + S\omega^2(\alpha - S + \omega + \mu S)(\alpha - S + 2\omega + \mu S) - 2\alpha^2\omega^2(\beta_{crit} - \mu S) - \alpha\omega^3(\alpha - S + 2\omega + \mu S) \\ &= a - b(\beta_{crit} - \mu S) - c(\alpha - S + 2\omega + \mu S). \end{aligned}$$

The coefficient of  $\beta_{crit} - \mu S$  is  $b = 2S^2(\delta + 2\omega)(\alpha - S + \mu S - \delta)$  and the coefficient of  $\alpha - S + 2\omega + \mu S$  is  $c = S\omega^2(\alpha - S + \mu S - \delta)$ . Clearly  $\frac{\partial f}{\partial \beta}(\beta_{crit}, 0) > 0$  whenever  $\delta < \alpha - S + \mu S$ . However, by hypothesis we have that  $\delta > \delta_{crit}$  which, by Claim 1 is equivalent to  $\delta > \alpha - S + \mu S$ . Nevertheless, there exists  $\epsilon$  small so that for  $\alpha - S + \mu S < \delta < \alpha - S + \mu S + \epsilon$ ,  $\frac{\partial f}{\partial \beta}(\beta_{crit}, 0) > 0$ . Letting  $\delta \rightarrow \infty$  we have that  $S \rightarrow 0$  and  $\delta S \rightarrow \alpha\omega$  so that  $\frac{\partial f}{\partial \beta}(\beta_{crit}, 0) \rightarrow -2(\alpha\omega)^2\beta_{crit} - (\alpha\omega)\omega^2(\alpha + 2\omega) < 0$ . Thus,  $\frac{\partial f}{\partial \beta}(\beta_{crit}, 0)$  changes sign. However, for  $\delta > \delta_{crit}$ ,  $\frac{\partial f}{\partial \beta}(\beta_{crit}, 0)$  is monotone. Thus, for all but finitely many  $\delta > \delta_{crit}$ ,  $\frac{\partial f}{\partial \beta}(\beta_{crit}, 0) \neq 0$ . We may increase  $\delta_{crit}$  to avoid these finitely many singular cases. Hence, for  $\delta > \delta_{crit}$ , we have that  $f(\beta_{crit}, 0) = 0$  and  $\frac{\partial f}{\partial \beta}(\beta_{crit}, 0) \neq 0$ . Thus, by the Implicit Function Theorem, there is a neighborhood  $U$  of  $k = 0$  such that  $\beta^*(k)$  is a continuous function of  $k$  defined on  $U$ ,  $\beta^*(0) = \beta_{crit}$

and  $f(\beta^*(k), k) = 0$  for  $k \in U$ . It follows by continuity that  $E_4$  changes from stable to unstable and admits a Hopf orbit as  $\beta$  increases through  $\beta^*(k)$ .  $\square$

Theorem 5.1 shows that the birth rate of susceptible fish,  $\beta$ , is a bifurcation parameter for the Hopf bifurcation. However, in the hypothesis we also require that  $\delta$  is sufficiently large. The parameter  $\delta$  is the rate of viral shedding and represents the positive feedback in the viral compartment due to infection. In this sense,  $\delta$  can be likened to a birth rate for the virus. The next result describes the dependence of local stability of  $E_4$  on the rate of viral shedding,  $\delta$ .

**Proposition 11.** *If  $\mathcal{R}_4^0 > 1$  and  $\alpha^2 < 4k^2 + \omega(2k + \omega)(2\omega + \frac{\alpha(\alpha+\beta)}{(k+\omega)^2} + \frac{\alpha}{k+\omega})$ , then the equilibrium  $E_4$  of system (4) is stable for  $\delta$  small and unstable as  $\delta \rightarrow \infty$ .*

*Proof.* At  $E_4$   $S' = S(k) = \alpha \frac{\omega(2k+\omega)}{\omega(2k+\omega)+\delta(k+\omega)}$ ,  $I' = \frac{1}{\alpha}(\alpha - S')(\beta - \mu S')$ ,  $V_1' = \frac{1}{\alpha} S'(\beta - \mu S')$ , and  $V_2' = \frac{k}{\alpha(k+\omega)} S'(\beta - \mu S')$ . Then the characteristic polynomial of the Jacobian evaluated at equilibrium is

$$p(\lambda, k) = a_4(k)\lambda^4 + a_3(k)\lambda^3 + a_2(k)\lambda^2 + a_1(k)\lambda + a_0(k)$$

where

$$\begin{aligned} a_4(k) &= 1 \\ a_3(k) &= 2k + \mu S(k) + \alpha - S(k) + 2\omega \\ a_2(k) &= 2k(\mu S(k) + (\alpha - S(k)) + \omega) \\ &\quad + \mu S(k)(\alpha - S(k) + 2\omega) + 2\omega(\alpha - S(k)) + \omega^2 - \delta S(k) + S(k)(\beta - \mu S(k)) \\ a_1(k) &= 2k(\mu S(k)(\alpha - S(k) + \omega) + S(k)(\beta - \mu S(k))) \\ &\quad + \mu S(k)(\omega^2 + 2\omega(\alpha - S(k)) - \delta S(k)) + (2\omega + \delta)S(k)(\beta - \mu S(k)) \\ a_0(k) &= 2k(\alpha\omega(\beta - \mu S(k))) \\ &\quad + \alpha\omega^2(\beta - \mu S(k)) \end{aligned}$$

$S(k)$  increases from  $\frac{\alpha\omega}{\omega+\delta}$  to  $\frac{2\alpha\omega}{2\omega+\delta}$  as  $k$  increases from 0 to  $\infty$ . We may write  $p(\lambda, k) = P(\lambda, k) + kQ(\lambda, k)$ , where the dependence of  $P$  and  $Q$  on  $k$  comes from the fact that  $S(k)$  depends on  $k$ . First let us consider the case when  $k = 0$ . Then  $p(\lambda, 0) = P(\lambda, 0)$  and the Jacobian evaluated at positive equilibrium admits an eigenvalue  $-\omega$  associated to the eigenvector  $e_4$ . Thus,  $p(\lambda, 0) = (\lambda + \omega)q(\lambda, 0)$  with

$$\begin{aligned} q(\lambda, 0) &= \lambda^3 + (\mu S(0) + \alpha - S(0) + \omega)\lambda^2 + (\mu S(0)(\alpha - S(0) + \omega) \\ &\quad + S(0)(\beta - \mu S(0)))\lambda + S(0)(\beta - \mu S(0))(\omega + \delta). \end{aligned}$$

Letting  $\delta \rightarrow 0$ ,  $S(0) \rightarrow \alpha$  and  $q(\lambda, 0) = \lambda^3 + (\mu\alpha + \omega)\lambda^2 + (\mu\alpha\omega + \alpha(\beta - \mu\alpha))\lambda + \alpha\omega(\beta - \mu\alpha)$  is Hurwitz. Thus, by continuity, for  $\delta$  and  $k$  small, the positive equilibrium is locally stable. Letting  $\delta \rightarrow \infty$ ,  $S(0) \rightarrow 0$ ,  $\delta S(0) \rightarrow \alpha\omega$  and  $q(\lambda, 0) = \lambda^3 + (\alpha + \omega)\lambda^2 + \beta\alpha\omega$ , which is not Hurwitz. Thus, in the limiting case where  $\delta$  approaches infinity and for  $k$  small, the positive equilibrium is unstable.

We once again let  $\delta$  be fixed and positive. Note

$$p(\lambda, k) = P(\lambda, k) + kQ(\lambda, k) = 0 \iff Q(\lambda) + \frac{1}{k}P(\lambda, k) = 0.$$

Let  $U$  be a bounded open set which contains all the zeros of  $Q$ . Note that  $U$  may be chosen to such that  $\forall k \geq 0$   $Q(\lambda, k) = 0 \implies \lambda \in U$ . Then on  $\partial U$  we have that there exist  $m, M \in \mathbb{R}$  such that  $Q(\lambda, k) \geq m$  and  $\frac{P(\lambda, k)}{k} \leq \frac{M}{k}$ . Then there exists  $K > 0$

such that for all  $k \geq K$  we have  $m > \frac{M}{k}$ . Then by Rouché's Theorem,  $Q(\lambda, k)$  and  $Q(\lambda, k) + \frac{1}{k}P(\lambda, k)$  have the same number of zeros in  $U$  for all  $k \geq K$ . Since  $P(\lambda, k)$  is quartic and  $\frac{P(\lambda_i, k)}{k} \rightarrow 0$  as  $k \rightarrow \infty$  for  $\lambda_i$  bounded, there exists  $\lambda_j$  unbounded in  $k$  such that  $p(\lambda_j, k) = 0$ . Consider

$$\frac{1}{k^4}p(k\nu(k)) = \nu^4 + 2\nu^3 + \frac{1}{k}(l.o.t.) = f(\nu, \frac{1}{k}).$$

Then  $\frac{1}{k}$  is a parameter which goes to zero as  $k \rightarrow \infty$ ,  $f(-2, 0) = 0$  and  $\frac{\partial f}{\partial \nu}(-2) \neq 0$ . Then by the Implicit Function Theorem there exists  $\varphi : [0, \infty) \rightarrow \mathbb{R}$  such that  $\varphi(0) = -2$  and  $f(\varphi(\frac{1}{k}), \frac{1}{k}) \equiv 0$ . Hence,  $\lambda_j = k\nu = -2k$  is the unbounded root of  $p$  and is always non-positive.

Let  $k \rightarrow \infty$ , and let  $S_\infty = \lim_{k \rightarrow \infty} S(k) = \frac{2\alpha\omega}{2\omega + \delta}$ . Then,  $p(\lambda, \infty)$  has one root given by  $k\varphi(\frac{1}{k})$  and the remaining roots are the roots of  $Q(\lambda, \infty)$  with

$$\frac{1}{2}Q(\lambda, \infty) = \lambda^3 + (\mu S_\infty + \alpha - S_\infty + \omega)\lambda^2 + (\mu S_\infty)(\alpha - S_\infty + \omega) + S_\infty(\beta - \mu S_\infty)\lambda + \alpha\omega(\beta - \mu S_\infty)$$

Letting  $\delta \rightarrow 0$  we have  $S_\infty \rightarrow \alpha$  and  $Q(\lambda, \infty) = \lambda^3 + (\mu\alpha + \omega)\lambda^2 + (\mu\alpha\omega + \alpha(\beta - \mu\alpha))\lambda + \alpha\omega(\beta - \mu\alpha)$  is Hurwitz and the positive equilibrium is locally stable. Letting  $\delta \rightarrow \infty$  we have  $S_\infty \rightarrow 0$  and  $Q(\lambda, \infty) = \lambda^3 + (\alpha + \omega)\lambda^2 + \beta\alpha\omega$ , which is not Hurwitz.

Now let  $k > 0$  be finite. Letting  $\delta \rightarrow 0$  we have  $p(\lambda) = \lambda^4 + a_3\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0$  with

$$\begin{aligned} a_3 &= 2k + \mu\alpha + 2\omega \\ a_2 &= 2k(\mu\alpha\omega) + 2\mu\alpha\omega + \omega^2 + \alpha(\beta - \mu\alpha) \\ a_1 &= 2k(\mu\alpha\omega + \alpha(\beta - \mu\alpha)) + \mu\alpha\omega^2 + 2\alpha\omega(\beta - \mu\alpha) \\ a_0 &= 2k\alpha\omega(\beta - \mu\alpha) + \alpha\omega^2(\beta - \mu\alpha) \end{aligned}$$

each of which are positive when  $\mathcal{R}_4 > 1$ . Direct computation verifies that  $a_3a_2a_1 - (a_1^2 + a_3^2a_0) > 0$ . Thus, when  $\delta \rightarrow 0$  the positive equilibrium is stable.

Letting  $\delta \rightarrow \infty$  we have  $p(\lambda) = \lambda^4 + a_3\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0$  with

$$\begin{aligned} a_3 &= \alpha + 2(k + \omega) \\ a_2 &= 2\alpha(k + \omega) + \omega(2k + \omega) - \alpha\omega \frac{2k + \omega}{k + \omega} > 2\alpha(k + \omega) + \omega(2k + \omega) - \alpha(k + \omega) > 0 \\ a_1 &= \beta\alpha\omega \frac{2k + \omega}{k + \omega} \\ a_0 &= \beta\alpha\omega(2k + \omega) \end{aligned}$$

Direct computation shows that  $a_3a_2a_1 - (a_1^2 + a_3^2a_0) =$

$$\alpha^2 - 4k^2 - \omega(2k + \omega) \left( 2\omega + \frac{\alpha(\alpha + \beta)}{(k + \omega)^2} + \frac{\alpha}{k + \omega} \right).$$

Thus, if the hypotheses hold,  $p(\lambda)$  is not Hurwitz and the equilibrium is unstable.  $\square$

In the comments preceding Proposition 5 we noted that  $\mathcal{R}_4^0$  is decreasing in  $k$ . Therefore, as  $k$  decreases, it has a stabilizing effect on  $DfE_4$ . In the following result, we define parameters  $\Delta_1$  and  $\Delta_2$  as a function of other parameters and partition the  $\Delta_1, \Delta_2$  plane to determine how increasing  $k$  affects the stability of the disease free equilibrium of the full system (2),  $E_0$ .

**Proposition 12.** *Let  $\Delta_1 = \frac{\beta_F}{\mu_F} - \alpha$  and  $\Delta_2 = \frac{\beta_W}{\mu_W} - \alpha$ . Then,*

- i) If  $(\Delta_1, \Delta_2) \in R_1$ , the region of the  $\Delta_1, \Delta_2$ -plane bounded  $\Delta_1 = -\frac{\delta\beta_F}{\omega\mu_F}$ ,  $\Delta_2 = -\frac{\delta\beta_W}{\omega\mu_W}$  and the lower branch of the hyperbola  $1 = -\frac{\delta\beta_F}{2\omega\mu_F\Delta_1} - \frac{\delta\beta_W}{2\omega\mu_W\Delta_2}$ , then the stability of the disease free equilibrium changes from unstable to stable as  $k \rightarrow \infty$ .
- ii) If  $(\Delta_1, \Delta_2) \in R_2$ , the region of the  $\Delta_1, \Delta_2$ -plane bounded  $\Delta_1 = -\frac{\delta\beta_F}{\omega\mu_F}$ ,  $\Delta_2 = -\frac{\delta\beta_W}{\omega\mu_W}$  and the upper branch of the hyperbola  $1 = -\frac{\delta\beta_F}{2\omega\mu_F\Delta_1} - \frac{\delta\beta_W}{2\omega\mu_W\Delta_2}$ , then the disease free equilibrium remains unstable, but the nature of the stability changes.

*Proof.* The Jacobian of system (2) evaluated at the  $E_0$  is

$$J_{E_0} = \begin{bmatrix} -\beta_F & -\frac{\beta_F}{\mu_F} & -\frac{\beta_F}{\mu_F} & 0 & 0 & 0 \\ 0 & \frac{\beta_F}{\mu_F} - \alpha & \frac{\beta_F}{\mu_F} & 0 & 0 & 0 \\ 0 & \delta & -(k + \omega) & 0 & 0 & k \\ 0 & 0 & 0 & -\beta_W & -\frac{\beta_W}{\mu_W} & -\frac{\beta_W}{\mu_W} \\ 0 & 0 & 0 & 0 & \frac{\beta_W}{\mu_W} - \alpha & \frac{\beta_W}{\mu_W} \\ 0 & 0 & k & 0 & \delta & -(k + \omega) \end{bmatrix}$$

Then  $-\beta_F$  and  $-\beta_W$  are eigenvalues and the remaining eigenvalues are the eigenvalues of the lower dimensional Jacobian

$$J^* = \begin{bmatrix} \Delta_1 & \frac{\beta_F}{\mu_F} & 0 & 0 \\ \delta & -(k + \omega) & 0 & k \\ 0 & 0 & \Delta_2 & \frac{\beta_W}{\mu_W} \\ 0 & k & \delta & -(k + \omega) \end{bmatrix}$$

where  $\Delta_1 = \frac{\beta_F}{\mu_F} - \alpha$  and  $\Delta_2 = \frac{\beta_W}{\mu_W} - \alpha$ . Then,

$$|J^*| = [2\Delta_1\Delta_2\omega + \Delta_1\delta\frac{\beta_W}{\mu_W} + \Delta_2\delta\frac{\beta_F}{\mu_F}]k + (\omega\Delta_1 + \delta\frac{\beta_F}{\mu_F})(\omega\Delta_2 + \delta\frac{\beta_W}{\mu_W})$$

is a linear function of  $k$ . Since the constant coefficient corresponds to the product of the eigenvalues of the uncoupled system, it follows from Proposition 3 that the lines  $\Delta_1 = -\frac{\delta\beta_F}{\omega\mu_F}$  and  $\Delta_2 = -\frac{\delta\beta_W}{\omega\mu_W}$  split the  $\Delta_1, \Delta_2$ -plane into 4 quadrants with  $E_0$  stable in  $QIII$ ,  $E_0$  having one positive eigenvalue in  $QII$  and  $QIV$  and two positive eigenvalues in  $QI$  where the labeling  $I, II, III, IV$  is done counterclockwise with  $QI = \{(\Delta_1, \Delta_2) : \Delta_1 > -\frac{\delta\beta_F}{\omega\mu_F}, \Delta_2 > -\frac{\delta\beta_W}{\omega\mu_W}\}$ .

Furthermore, analyzing the null set of the coefficient of  $k$  in  $|J^*|$  yields the hyperbola given by

$$1 = -\frac{\delta\beta_F}{2\omega\mu_F\Delta_1} - \frac{\delta\beta_W}{2\omega\mu_W\Delta_2}$$

where  $2\Delta_1\Delta_2\omega + \Delta_1\delta\frac{\beta_W}{\mu_W} + \Delta_2\delta\frac{\beta_F}{\mu_F} < 0$  between the branches and positive outside them. Thus, the determinant changes sign as  $k \rightarrow \infty$  in  $R_1$  and  $R_2$ . First we consider  $R_1$ .

Let  $k^* = \frac{-(\Delta_1\omega + \delta\frac{\beta_F}{\mu_F})(\Delta_2\omega + \delta\frac{\beta_W}{\mu_W})}{2\Delta_1\Delta_2\omega + \Delta_1\delta\frac{\beta_W}{\mu_W} + \Delta_2\delta\frac{\beta_F}{\mu_F}}$ , the critical value of  $k$  for which  $|J^*| = 0$ .

Consider the characteristic polynomial of  $J^*$  given by

$$p(\lambda, k) = \lambda^4 + a_3\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0$$

where  $a_1 = a_1(k) = [2\Delta_1\Delta_2 - 2\omega(\Delta_1 + \Delta_2) - \delta(\frac{\beta_F}{\mu_F} + \frac{\beta_W}{\mu_W})]k + \Delta_1(\Delta_2\omega + \frac{\beta_W}{\mu_W}) + \Delta_2(\Delta_1\omega + \frac{\beta_F}{\mu_F}) - \omega(\Delta_1\omega + \delta\frac{\beta_F}{\mu_F} + \Delta_2\omega + \delta\frac{\beta_W}{\mu_W})$  and  $a_0(k) = |J^*|$ . Then,

$$\frac{\partial p}{\partial k}(0, k^*) = 2\Delta_1\Delta_2\omega + \Delta_1\delta\frac{\beta_W}{\mu_W} + \Delta_2\delta\frac{\beta_F}{\mu_F} > 0 \quad \text{in } R_1$$

Let  $e = (\Delta_1\omega + \delta\frac{\beta_F}{\mu_F})$  and  $f = (\Delta_2\omega + \delta\frac{\beta_W}{\mu_W})$ .

$$\begin{aligned} & -(2\Delta_1\Delta_2 - e - f - \Delta_1\omega - \Delta_2\omega)ef + (\Delta_1f + \Delta_2e)^2 - \omega(\Delta_1f + \Delta_2e)(e + f) \\ &= -(2\Delta_1\Delta_2 - e - f - \Delta_1\omega - \Delta_2\omega)ef + \Delta_1^2f^2 + 2\Delta_1\Delta_2ef \\ & \quad + \Delta_2^2e^2 - \omega(\Delta_1f^2 + \Delta_2e^2) - \omega(\Delta_1 + \Delta_2)ef \\ &= (\Delta_2^2 - \Delta_2\omega + f)e^2 + (\Delta_1^2 - \Delta_1\omega + e)f^2 \\ &= \Delta_2^2 - \Delta_2\omega + \Delta_2\omega + \delta\frac{\beta_W}{\mu_W}e^2 + (\Delta_1^2 - \Delta_1\omega + \Delta_1\omega + \delta\frac{\beta_F}{\mu_F})f^2 \\ &= (\Delta_2^2 + \delta\frac{\beta_W}{\mu_W})e^2 + (\Delta_1^2 + \delta\frac{\beta_F}{\mu_F})f^2 > 0 \end{aligned}$$

Thus,  $a_1(k^*) > 0$  for any  $(\Delta_1, \Delta_2)$  which implies that  $\frac{\partial p}{\partial \lambda}(0, k^*) > 0$ . Hence,  $\frac{\partial \lambda}{\partial k} < 0$  for  $(\Delta_1, \Delta_2) \in R_1$  and the change of sign as  $k \rightarrow \infty$  indicates that the principle eigenvalue becomes negative, proving (i).

In  $R_2$ ,  $|J^*| = Ak + B$  where  $A < 0$  and  $B > 0$  changes sign as  $k \rightarrow \infty$ . Then  $\frac{\partial p}{\partial k}(0, k^*) = A < 0$ . Since  $\frac{\partial p}{\partial \lambda} > 0$ , we have that  $\frac{\partial \lambda}{\partial k} > 0$  and the sign change indicates that an additional eigenvalue becomes positive. Since  $|J^*|$  has two negative eigenvalues and two positive eigenvalues for  $k = 0$  as indicated by Proposition 3, there is no change of stability.  $\square$

**Theorem 5.2.** *Suppose that there exists a Hopf periodic orbit,  $\Gamma$  in the patch- $i$  dominated 4-dimensional subsystem (4). Let  $\beta_j^* = \bar{V}_j$ . Then there exists  $\varepsilon > 0$  such that if  $\beta_j = \beta_j^* - \varepsilon$ , then  $E_i$  is an attractor with respect to the interior of  $\mathbb{R}_+^6$  while  $\Gamma$  is a repeller with respect to the interior of  $\mathbb{R}_+^6$ .*

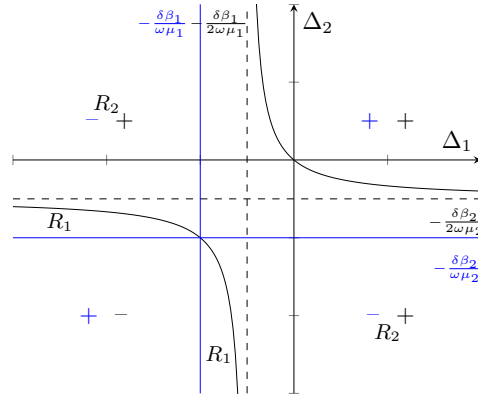


FIGURE 4. The set  $\det J_{E_0} = 0$  in the  $\Delta_1, \Delta_2$ -plane.

*Proof.* We have that  $\overline{S_i} = \frac{\alpha\omega(2k+\omega)}{\omega(2k+\omega)+\delta(k+\omega)}$  and  $Q = \frac{\delta k}{\omega(2k+\omega)+\delta(k+\omega)}$ . From system (4), after taking averages we have,

$$\begin{cases} \langle \dot{S}_i \rangle &= \langle S_i(\beta_i - \mu_i S_i - I_i - V_i) \rangle \\ \langle \dot{I}_i \rangle &= \langle I_i(S_i - \alpha) \rangle + \langle V_i S_i \rangle \\ \langle \dot{V}_i \rangle &= k(\langle V_j \rangle - \langle V_i \rangle) - \omega \langle V_i \rangle + \delta \langle I_i \rangle \\ \langle \dot{V}_j \rangle &= k(\langle V_i \rangle - \langle V_j \rangle) - \omega \langle V_j \rangle. \end{cases} \quad (12)$$

From  $\langle \dot{V}_j \rangle = 0$  we have that

$$\langle V_i \rangle = \frac{k+\omega}{k} \langle V_j \rangle. \quad (13)$$

Since  $\langle \dot{V}_i \rangle = 0$ , substituting (13) into the expression for  $\langle \dot{V}_i \rangle$  and solving for  $\langle I_i \rangle$  yields,

$$\langle I_i \rangle = \frac{\omega(2k+\omega)}{\delta k} \langle V_j \rangle. \quad (14)$$

Note that  $\langle \dot{S}_i \rangle = 0$  implies that  $\langle \frac{\dot{S}_i}{S_i} \rangle = 0$ , thus,  $\beta_i - \mu_i \langle S_i \rangle - \langle I_i \rangle - \langle V_i \rangle = 0$ . That is

$$\beta_i - \mu_i \langle S_i \rangle = \langle I_i \rangle + \langle V_i \rangle.$$

Substituting (13) and (14) after simplification yields,

$$\beta_i - \mu_i \langle S_i \rangle = \frac{1}{Q} \langle V_j \rangle. \quad (15)$$

Now,  $\langle \dot{S}_i + \dot{I}_i \rangle = \langle \dot{S}_i \rangle + \langle \dot{I}_i \rangle = \langle S_i(\beta_i - \mu_i S_i) \rangle - \alpha \langle I_i \rangle = 0$ . After substituting (14) and applying Jensen's Inequality, we have

$$\langle S_i \rangle (\beta_i - \mu_i \langle S_i \rangle) > \frac{\alpha\omega(2k+\omega)}{\delta k} \langle V_j \rangle.$$

By substituting (15) we have that  $\frac{1}{Q} \langle S_i \rangle \langle V_j \rangle > \frac{\alpha\omega(2k+\omega)}{\delta k} \langle V_j \rangle$ , which simplifies to

$$\langle S_i \rangle > \overline{S_i}. \quad (16)$$

Finally, applying (16) to (15) we have that  $\langle V_j \rangle = Q(\beta_i - \mu_i \langle S_i \rangle) < Q(\beta_i - \mu_i \overline{S_i}) = \overline{V_j}$ , or simply put

$$\langle V_j \rangle < \overline{V_j}. \quad (17)$$

Letting  $\varepsilon = \frac{\overline{V_j} - \langle V_j \rangle}{2} > 0$  completes the proof.  $\square$

Let  $\Gamma$  refer to the Hopf orbit contained in the invariant boundary set  $\{S_j = I_j = 0\}$  as above.

**Theorem 5.3.** *Suppose that  $\Gamma$  exists as in the previous theorem. Then as  $\beta_j$  is increased through the value  $\beta_j^* = \langle V_j \rangle$ ,  $\Gamma$  bifurcates into a periodic orbit in the first octant.*

*Proof.* It suffices to consider a branch of solutions  $\overline{F}(S_j, I_j; \beta_j)$  with

$$D_{(S_j, I_j)} \overline{F} = \begin{bmatrix} 1 - e^{\tau_0(\beta_j - \langle V_j \rangle)} & 0 \\ -\frac{\partial P_1}{\partial S_j}(0, 0; \beta_j) & 1 - e^{-\alpha\tau_0} \end{bmatrix}.$$

When  $\beta_j = \beta_j^*$ ,  $D_{(S_j, I_j)} \overline{F}$  becomes

$$D_{(S_j, I_j)} \overline{F} = \begin{bmatrix} 0 & 0 \\ -\frac{\partial P_1}{\partial S_j}(0, 0; \beta_j^*) & 1 - e^{-\alpha\tau_0} \end{bmatrix},$$

which has one dimensional null space spanned by

$$\bar{u} = \left( \frac{1 - e^{-\alpha\tau_0}}{\frac{\partial P_1}{\partial S_j}(0, 0; \beta_j^*)}, 1 \right)^T.$$

Since the column space of  $D_{(S_j, I_j)} \bar{F}(0, 0; \beta_j^*)$  has dimension 1, the condition

$$D_{(S_j, I_j), \beta_j} \bar{F}(0, 0; \beta_j^*) \bar{u} \notin \text{Range} (D_{(S_j, I_j)} \bar{F}(0, 0; \beta_j^*))$$

follows from the fact that the left hand side is of the form  $(\tau_0, 0)^T$  while

$$D_{(S_j, I_j)} \bar{F}(0, 0; \beta_j^*) \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 0 \\ (1 - e^{-\alpha\tau_0})y - \frac{\partial P_1}{\partial S_j}(0, 0; \beta_j^*)x \end{pmatrix}.$$

Thus, there exists a branch of solutions

$$\begin{pmatrix} S_j \\ I_j \end{pmatrix} = \rho \bar{u} + o(\rho)$$

$$\beta_j = \beta_j^* + \rho \tilde{\beta}_j + o(\rho)$$

where  $\rho$  is a scalar. Note that  $\bar{v} = (1, 0)$  is a left eigenvector for the eigenvalue 0. Then

$$\bar{v} D_{(S_j, I_j), \beta_j} \bar{F}(0, 0; \beta_j^*) \bar{u} = \tau_0 > 0$$

implies that this branch of solutions represents a periodic solution which move into the interior of the positive orthant.  $\square$

**6. Discussion.** We have shown that this relatively simple system exhibits very rich dynamics. The 4-dimensional subsystem (4) is a perturbation of the 3-dimensional subsystem (3) in that the disease free equilibrium, positive equilibrium and periodic orbit of the 4-dimensional subsystem are all shown to be continuations of their 3-dimensional counterparts. This is not surprising when we consider the biological setting each subsystem represents. The 3-dimensional subsystem represents one patch inhabited by one susceptible fish population while the 4-dimensional subsystem represents two patches inhabitable by the virus but only one containing a susceptible fish population. We have shown that this second patch acts as a sink for the virus and that  $\mathcal{R}_4^0$  is a decreasing function of the diffusion rate which couples the patch containing fish with the sink patch. Under the right conditions, it is possible for the virus to persist in one uncoupled patch, but to go extinct when that patch is coupled strongly to a patch with no susceptible inhabitants. This indicates that, in certain cases, partitioning the habitat may serve as protection against infection.

We have stated  $\mathcal{R}_4^0$  is a decreasing function of  $k$ . Thus, increasing diffusion can reduce risk of infection, but we need a practical way to implement this as a strategy in a real farm. Consider the mean residence time in a patch, given by  $\frac{1}{k}$ . Then increasing the rate of diffusion is akin to decreasing mean residence time. Furthermore, mean residence time is positively correlated with patch size. Therefore, these results indicate that reducing patch size would decrease the ability of the virus to invade. Of course, reducing patch size also reduces the number of fish per patch, so there is a trade-off for implementing this as a strategy. In this work we have assumed, as a simplification, that farm and wild patches are of equal size. We recognize that this is not the case and suggest that we can discard this assumption by allowing for differing rates of diffusion between patches.

We also saw in Figure 3.4, Region II the positive coexistence equilibrium  $E_{FW}$  exists even when the single species equilibria  $E_F$  and  $E_W$  do not. This is a striking

result as illustrated by the following example. Suppose that a Salmon farm is constructed in a wild Salmon migratory route. Suppose that, initially, there are no fish in either the farm or wild patches. During the course of migration, fish enter the wild patch, but  $\mathcal{R}_W^0 < 1$  and the virus cannot invade. Suppose that the fish leave the wild patch and that the farm is populated with fish. Then  $\mathcal{R}_F^0 < 1$  and the virus does not invade. However, when fish return to the wild patch,  $\mathcal{R}_{FW}^0 > 1$  and the virus invades in both patches. This is not always possible, though. Indeed, if the virus cannot invade either patch in absence of diffusion (3-dimensional, 1-patch system (3)), then  $\mathcal{R}_{FW}^0 < 1$  and the virus cannot invade for any rate of diffusion.

One of the most interesting features of the dynamics of this systems is more interesting mathematically than biologically. It was noted that the 4-dimensional boundary equilibrium exchanges stability with the unique equilibrium which enters the interior of  $\mathbb{R}_+^6$  and becomes  $E_{FW}$ . It was shown that, when the Hopf orbit exists in the boundary, it exchanges stability with a periodic orbit that enters the interior of  $\mathbb{R}_+^6$ . The interesting feature, stated in Theorem 5.2 is that the periodic solution bifurcates into the interior before the positive equilibrium does. That is, there is a parameter regime in which the system admits a positive periodic solution, but no positive equilibrium.

**Acknowledgments.** We would like to acknowledge the support from NSF grant DMS-1411853. The authors would like to thank the referees for their helpful suggestions.

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