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Modelling the harvest of an insect pathogen

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Abstract

Ensuring a sustainable yield is essential for continued survival of a natural resource, however over-exploitation can easily occur. Therefore, understanding how increasing the harvesting rate affects the yield is vital. Harvesting of infected hosts in a host–pathogen system, for example the fungal pathogen *Cordyceps sinensis* which is harvested for medicinal use, has not been explored mathematically in the literature. We present a generalized host–pathogen model in which the infected host is harvested. Two strategies are explored; proportional harvesting at a constant rate and in an open-closed setting (a repeating cycle of a period of harvest followed by a period where the resource is left to recover). We present yield-effort curves for both strategies and find that open-closed harvesting affects the traditional yield-effort curve, with the system able to support a greater range of harvesting rates. Furthermore, host–pathogen systems may exhibit more complex population dynamics than single equation/species models, depending on the eigenvalues of the linearised system. In the open-closed setting we find that if there are complex eigenvalues in the absence of harvesting although small changes in the length of open season have little impact on the maximum sustainable yield, it can dramatically change the harvesting rate needed to achieve this. For proportional harvesting in a constant setting our model shows that if there are real eigenvalues in the absence of harvesting, then resilience–harvest relationship agrees with accepted theory, where as yield initially increases so too does the return time (a measure of the long-term resilience). However, when there are complex eigenvalues we see, counter to intuition, that the return time initially decreases whilst still providing increased yield. We also study the transient (short-term) reactivity, which shows that in both cases harvesting can initially decrease the reactivity. These results show that harvesting can in some instances enhance the ability of host–pathogen systems to respond to perturbations in both the short- and long-term.

Key words: Harvesting strategies; Host–pathogen; Yield; Recovery time; Resilience; *Cordyceps sinensis*

1   Introduction

Harvesting of a biological resource is modelled for many purposes including management of fisheries (Conover and Munch 2002; Yakubu et al. 2011) or forest, (Gustafson 1996) and conservation of populations (Beissinger and Bucher 1992). The vast majority of models applied to systems of interest model the species using a single equation to which a term is added, which represents a harvesting strategy. A classic example of this is Beddington and May (1977), which demonstrated

the existence of an economic threshold at which the yield is maximised for some intermediate harvesting rate (termed maximum sustainable yield (MSY)). Beddington and May (1977) also showed that overexploitation results in a smaller population than that at the MSY and high harvesting effort produces a low average yield with higher variance, and hence higher system recovery times. The implications for harvesting management are clear, and sustainable harvesting strategies must be employed to ensure cost-effectiveness as well as to prevent extinction of the harvested species.

However, most species experience interspecific interactions, and sustainable strategies will be influenced by the type and strength of the interactions. For example, harvesting of prey species can significantly affect predator abundance and may even cause system collapse if the harvesting rate is sufficiently high (Legović et al. 2010; Kar and Ghorai 2011). Whilst harvesting interactions and their effects were analysed other measures such as return time and reactivity, which are important indicators of ecosystem health (Beddington and May 1977; Neubert and Caswell 1997), were not studied. Harvesting within other types of interspecific interactions have been considered, such as competition, (Geček and Legović 2012), mutualism (Legović and Geček 2012) and predator–prey–parasite systems (Bairagi et al. 2009). In contrast, there are no examples in the literature of harvesting in host–pathogen systems, and we aim to address this gap here. Furthermore, simple single species models, such as the Beddington and May (1977) model, exhibit very stable dynamics, where return to the equilibrium after perturbations is monotonic. However, for higher order models (e.g. interacting predator–prey or host–pathogen models) the dynamics may be more complex, which is the focus of this article.

Whilst harvesting in host–pathogen systems may not occur in reality as frequently as in other types of species interactions, there are a number of economically important examples, such as baculovirus collection for biocontrol (Grzywacz et al. 2008; Mushobozi et al. 2005). A particularly important example is harvesting of *Cordyceps sinensis*, which is the motivation for this study. This entomopathogenic fungus infects caterpillars of the ghost moth genus *Thitaordes* (*Hepialiade*) (Cannon et al. 2009; Maczey et al. 2010) by penetrating the host exoskeleton (Cannon et al. 2009) or by host ingestion of the fungal spores (Boesi 2003). After killing the caterpillar, the fungus produces a fruiting body (stromata) which appears above ground to release spores which infect other susceptible hosts (Cannon et al. 2009; Winkler 2008). The fruiting bodies are harvested for medicinal purposes in their native range in the Tibetan Plateau (Negi et al. 2006; Winkler 2008), and this is important to local economies (Weckerle et al. 2010). It is thought that increases in

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harvesting have decreased yield by as much as $30 - -50\%$ in some areas (Negi et al. 2006).

To combat over-exploitation, a number of different harvesting strategies have been investigated in harvesting models. Beddington and May (1977) compared two harvesting strategies: proportional harvesting and constant harvesting. In the former, a constant proportion of the population is harvested at each time, making yield dependent on the harvesting effort and the availability of the resource. In contrast, the constant strategy simply removes a constant number of individuals from the population, which is independent of the population size. Interestingly, these two strategies predict identical MSYs in single species model. However, whilst the proportional harvesting strategy has only one steady state (other than the trivial steady state) under the constant harvesting strategy there are two steady states; one stable and one unstable. After small perturbations the system will return to the stable steady state. However, larger perturbations have different effects; a large perturbation above the stable steady state will cause the system to take a long time to recover, whilst those below the steady state will cause population extinction (Beddington and May 1977). For these reasons, proportional harvesting strategies are advised rather than constant harvesting (Bairagi et al. 2009; Beddington and May 1977; Cooke and Witten 1986; Yakubu et al. 2011).

Despite the relative benefits of a proportional harvesting strategy, over-harvesting may still lead to population extinction and therefore adaptations to this strategy have been developed. One such is open-closed harvesting, by which harvesting occurs during the open period and stops during the closed period, allowing the resource to recover partially or completely. In fisheries management, these closures, varying in time length from weeks to years (Cinner and Aswani 2007), can have an impact on both the size and biomass of fish (Bartlett et al. 2009; McClanahan et al. 2006). The timing of the open period of harvesting can have a great effect on the MSY (Kokko and Lindström 1998), and if harvesting does not start at the beginning of the prescribed open period the overall yield can be decreased (Xu et al. 2005). It has also been shown that if a population has strong Allee effects then harvesting mid-season can make the population more prone to over-exploitation (Cid et al. 2014).

Modelling different harvesting strategies allows us to answer questions regarding yield of the resource, recovery time, resilience and reactivity. In interacting multi-species systems, an understanding of how harvesting affects all species is vital to their continued survival. In predator–prey systems, harvesting either trophic level has implications for the MSY, and so it is necessary to consider the interaction between the two (Beddington and May 1980; Kar and Ghosh 2013). How-

ever, it is unclear how guidance about harvesting from existing modelling studies translates to host–pathogen species interactions.

To this end, we explore the impact of harvesting on a compartmentalized host–pathogen model in which we harvest the infected stages. We apply proportional harvesting over a constant rate and in an open-closed setting to determine the MSY and determine how the different strategies affect the yield that can be attained. We also consider three system measures that are affected by harvesting: recovery time, resilience and reactivity. Using these measures, we find that the results do not always coincide with single species harvesting theory and that harvesting in host–pathogen systems may have beneficial effects, depending on the system interaction strengths and the level of harvesting. Using an open-closed harvesting strategy we find that small changes in the length of open period can have a dramatic impact on the harvesting effort that produces the maximum yield. Finally, we discover that in an open-closed setting it is better to harvest for a long open period at a lower effort than to harvest for a shorter time at a higher effort if we wish to maximize the yield.

2   Materials and methods

We base host–pathogen dynamics on 'Model G' by Anderson and May (1981). This classic compartmentalised differential equation model has three compartments; susceptible hosts, $X(t)$, infected hosts, $Y(t)$ and free-living infective stages of the pathogen, $W(t)$, at time t. The free-living stages of the pathogen are explicit in the model, as infection occurs through this means. In addition to this model, we make additional realistic assumptions to include a rate at which susceptible and infected hosts take up the pathogen (Boots 1999), and density-dependence acting upon the susceptible hosts (Bowers et al. 1993; Caraco and Wang 2008; Dwyer 1994).

We assume that all hosts grow according to the logistic equation in the absence of the fungal pathogen, where r is the intrinsic growth rate of the hosts and k is the carrying capacity of the susceptible hosts. It is important to note that $r = a - b$ where a is the birth rate of hosts and b the natural morality rate. The rate of transmission is modelled by the law of mass action. Infected hosts have an induced mortality rate α, and each dead host produces an average λ spores. Free-living pathogen spores decay in the environment at a constant rate μ.

In many multi–species and predator–prey model systems harvesting occurs at the bottom trophic level, however there are examples of models where harvesting occurs at more than one

trophic level (Beddington and May 1980; Legović and Geček 2012; Kar and Ghosh 2013). Here we investigate the scenario where harvesting occurs at an upper trophic level. Specifically, using *C. sinensis* as our motivation, we assume harvesting occurs in the infected compartment, since it is the fruiting bodies of the fungal pathogen (along with their dead infected host) that are collected for medicinal use. We therefore wish to maximise the yield without eradicating the pathogen, so that (a) local communities are able to benefit economically from selling the fruiting bodies and (b) the fungus can continue to infect the caterpillar so that the fruiting body can be used for medicinal purposes. We denote $H(Y)$ as the rate at which infected hosts are harvested.

The above assumptions lead to the following model and corresponding initial conditions

$$\frac{\mathrm{d}X}{\mathrm{d}t} = rX\left(1 - \frac{X}{k}\right) - \beta XW, \tag{1a}$$

$$\frac{\mathrm{d}Y}{\mathrm{d}t} = \beta XW - (b + \alpha)Y - H(Y), \tag{1b}$$

$$\frac{\mathrm{d}W}{\mathrm{d}t} = \lambda\alpha Y - \mu W, \tag{1c}$$

$$X(0) = x_0, \qquad Y(0) = y_0, \qquad W(0) = w_0. \tag{2}$$

All parameters and their definitions are given in Table 1.

2.1 Harvesting strategies

The model, Eq. (1), will be analysed with the harvesting term $H(Y)$ taking two functional forms, representing two contrasting harvesting strategies. The first is a proportional harvesting strategy (Brauer and Sánchez 1975) which is given by

$$H(Y) = hY. \tag{3}$$

Here, a proportion h of the infected hosts will be harvested at a constant rate, as is commonly assumed (Anderson and May 1980; Beddington and May 1977; Beissinger and Bucher 1992; Legović and Geček 2010; Yakubu et al. 2011).

The second functional form is an open-closed strategy (Capasso et al. 1983; Xu et al. 2005). Harvesting occurs during the open period whilst in the closed period harvesting is stopped. We assume that harvesting commences at the start of the open period and continues until the end. The

harvesting strategy during the open period is proportional harvesting to allow comparison with the previous functional form. This strategy is modelled by

$$H(Y) = \begin{cases} hY & \text{if } nT < t \le (n+p)T, \\ 0 & \text{if } (n+p)T < t \le (n+1)T, \end{cases} \tag{4}$$

where $n = 0, 1, 2, \ldots$ are positive integers, T is the total length of the open-closed period and p is the proportion of time harvesting occurs, $0 \le p \le 1$, i.e. pT is the length of the open period and $(1-p)T$ is the length of the closed period.

2.2 Yield

We measure the success of harvesting through yield. Generally the yield is given by $\bar{Y} = hY^*$ where h is the harvesting rate and Y^* the steady state of infected individuals. However, this does not make sense when the harvested population is fluctuating in time, for example if the attracting equilibrium is unstable, which is possible for certain parameter combinations (Anderson and May 1981; Boots 1999; Bowers et al. 1993). Hence, where the population exhibits fluctuating dynamics we define yield as

$$\bar{Y} = hY_{\text{ave}} = h \lim_{t \to \infty} \frac{1}{t - t_0} \int_{t_0}^{t} Y(\tau) \mathrm{d}\tau, \tag{5}$$

where t_0 is the initial starting time sufficiently large so that any transient behaviour has ceased. That is, the yield is simply the average density of the infected hosts multiplied by the harvesting rate. Note that if the system goes to equilibrium then $Y_{\text{ave}} = Y^*$, and so the standard definition of yield is recovered. Also note that this yield definition may be applied to systems that exhibit chaotic dynamics.

For an open-closed strategy, the periodicity of the harvesting strategy ensures that stable sustainable harvest equilibria are not feasible, and so the population dynamics must vary temporally. Therefore, a suitable temporally varying yield measure must be defined to which open periods contribute and are subsequently averaged across. Hence, we define the yield in the open-closed strategy as

$$\bar{Y} = h \lim_{n \to \infty} \frac{1}{nT} \sum_{i=0}^{n-1} \int_{t_0+iT}^{t_0+(i+p)T} Y(\tau) \mathrm{d}\tau, \tag{6}$$

where n is the number of open-closed periods, t_0 compensates for transient behaviour (as in Eq. (5))

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and T and p define the open periods (as in Eq. (4)).

2.3 System measures

To consider the "health" of the harvested host-pathogen system, we consider three system measures: return time, resilience and reactivity. It is important to note that these measures are only valid for a parameter space where an equilibrium is stable, and thus we restrict the parameters accordingly when considering these measures. Furthermore, since an open-closed harvesting strategy causes non-equilibrium dynamics, we also restrict these measures to the constant proportional harvesting strategy.

2.3.1 Return time and resilience

The return (or recovery) time measures how long a population takes to return to its steady state after a perturbation (Beddington and May 1977; Pimm and Lawton 1977, 1978). Hence, this measure reflects the long-term recovery of the system. Following the definition of Neubert and Caswell (1997), we define the return time, Ret(h), as

$$\text{Ret}(h) = \frac{-1}{\text{Re}(\lambda_1(A))}, \tag{7}$$

where $\lambda_1(A)$ is the dominant eigenvalue of the linearised model (1) at the equilibrium (the Jacobian). Note that since the Jacobian depends on the harvesting rate, h, then the return times also depends on the harvesting rate.

Resilience, Res(h), measure is simply the reciprocal of the return time,

$$\text{Res}(h) = -\text{Re}(\lambda_1(A)). \tag{8}$$

Both these measures account for the variance of long-term system stability, and are dependent on the harvesting rate.

2.3.2 Reactivity

Perturbations in ecological systems can grow significantly before they decay, and this is measured by reactivity, Reac(h), which measures the short-term behaviour. Following Neubert and Caswell

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(1997)

$$\text{Reac}(h) = \lambda_1(H(A)), \tag{9}$$

where $\lambda_1(H(A))$ is the dominant eigenvalue of the Hermitian part of A (i.e. $H(A) = (A + A^T)/2$).

3 Results

There are several model parameters which can be varied, but we concentrate on the host carrying capacity (k). For a host-pathogen system in a natural environment, such as *C. sinensis*, it is difficult to manage the infection process of a pathogen directly. However, it is more likely that one can change the carrying capacity of the host population by managing the environment, for example by rotating grazing of livestock (Cannon et al. 2009).

3.1 Constant proportional harvesting

3.1.1 Analytical results

The host-pathogen model with proportional harvesting generates three steady states; a trivial steady state $(X^*, Y^*, W^*) = (0, 0, 0)$, a pathogen-free steady state $(X^*, Y^*, W^*) = (k, 0, 0)$ and an endemic steady state

$$(X^*, Y^*, W^*) = \left(\frac{\mu}{\lambda\alpha\beta}(b + \alpha + h), \frac{\mu W^*}{\lambda\alpha}, \frac{r}{\beta}\left(1 - \frac{X^*}{k}\right) \right). \tag{10}$$

Linear stability analysis is given in Appendix. The trivial steady state is always unstable, whilst for the pathogen-free steady state to be stable

$$h > \frac{\lambda\alpha\beta k}{\mu} - b - \alpha =: h_{\max}. \tag{11}$$

Hence, if the harvesting rate is sufficiently high $(h > h_{\max})$, then this over-harvesting will cause the pathogen to become extinct. For the endemic steady state to be biologically realistic

$$k > X^* \implies h < h_{\max}, \tag{12}$$

meaning that the pathogen-free steady state is unstable. Therefore the carrying capacity has to be greater than the steady state of the susceptible host population. If the pathogen is present in

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the population this will always be true; the susceptible host population cannot exceed the carrying capacity. It is not possible to determine closed-form stability conditions for the endemic equilibrium. Therefore we need to resort to numerical solutions (see below).

Harvesting at the endemic equilibrium increases the number of susceptible hosts at a rate proportional to the number that would otherwise generate free-living pathogen spores if there was no harvesting. Harvesting decreases the number of infected hosts, hence fewer spores are produced and so the number of free-living pathogen spores also decreases. Therefore there is less pathogenicity and the number of susceptible hosts increases.

3.1.2 Yield

For stable steady states, the maximum sustainable yield (MSY) and its associated harvesting rate (h_{MSY} - the maximal harvesting rate) can be calculated analytically. The yield is given by

$$hY^* = h\frac{\mu W^*}{\lambda\alpha} = h\frac{\mu r}{\lambda\alpha\beta}\left(1 - \frac{\mu}{\lambda\alpha\beta k}(b+\alpha+h)\right) = \frac{\mu}{\lambda\alpha\beta}\left(-\frac{h^2}{k} + h(r-b-\alpha)\right). \tag{13}$$

Solving the derivative of the yield Eq. (13) at zero gives the turning point of the curve, which is the harvesting effort that gives the maximum yield,

$$h_{\mathrm{MSY}} = \frac{1}{2}\left(\frac{\lambda\alpha\beta k}{\mu} - b - \alpha\right) = h_{\max}/2. \tag{14}$$

Hence,

$$\mathrm{MSY} = h_{\mathrm{MSY}}Y^* = \frac{1}{2}\left(\frac{\lambda\alpha\beta k}{\mu} - b - \alpha\right)\left(\frac{\mu r}{\lambda\alpha\beta}\left(1 - \frac{X^*}{k}\right)\right) \tag{15a}$$

$$= \frac{1}{4}\frac{(\lambda\alpha\beta k - b\mu - \alpha\mu)^2 r}{\beta^2\lambda^2\alpha^2 k}. \tag{15b}$$

The analytical expression (15) gives a direct relationship between the MSY and the parameters. Increasing the intrinsic growth rate of the host (r) increases the MSY; a greater growth rate means there is more of the pathogen to harvest and hence the MSY increases. For an endemic steady state to exist, and therefore yield to be produced, the carrying capacity (k) has to be greater than a minimum value, given by

$$k_{\min} = \frac{\mu(b+\alpha)}{\lambda\alpha\beta}. \tag{16}$$

For $k \leq k_{\min}$ the system is at the pathogen-free equilibrium and hence the MSY is not defined. When the MSY is defined ($k > k_{\min}$) there is a linear increase in yield as the carrying capacity increases. A similar situation arises for the virulence of the pathogen (β). If the virulence of the pathogen is less than or equal to

$$\beta_{\min} = \frac{\mu(b + \alpha)}{\lambda \alpha k}. \tag{17}$$

then the endemic steady state is unstable, and the system is at the pathogen-free steady state. As the virulence of the pathogen increases from $\beta_{\min}$ there is an increase in the MSY, which tends towards an asymptote found at

$$\beta = \frac{rk}{4}. \tag{18}$$

Therefore increasing virulence of the pathogen eventually has little effect on the MSY. This is because no matter how virulent the pathogen, the yield is constrained by the number of hosts available. Consequently, as the virulence of the pathogen increases, the MSY tends towards an asymptote which is dependent on the carrying capacity and the intrinsic growth rate of the host. Finally, as the pathogen induced mortality rate (α) increases, the MSY decreases. Although increasing the pathogen induced mortality rate increases the rate of sporulation, it also decreases the proportion of infected hosts in the population, giving a decreased MSY.

The yield can be seen graphically in Fig. 1 as we vary the harvesting rate between zero and $h_{\max}$. Here we consider the yield for two cases; when in the absence of harvesting the system has real eigenvalues (real case) and when it has complex eigenvalues with negative real-part (complex case). For both cases, as the harvesting effort increases so does the yield; harvesting at a greater rate produces more of the resource and hence the yield increases. After the maximum yield is attained harvesting at a greater effort decreases yield; the resource is over-exploited. By over-harvesting the number of infected hosts decline, leading to a decreased yield. Harvesting beyond this point causes extinction of the pathogen due to over-exploitation and the host population goes to carrying capacity. We see that the qualitative behaviour of the curve does not change for either case and the maximal harvesting rate is given by $h_{\mathrm{MSY}} = h_{\max}/2$. However, as the carrying capacity increases and the eigenvalues switch from real to complex, the yield increases according.

Fig. 2(a) shows the different stability regions that occur in the absence of harvesting as the carrying capacity and virulence of the pathogen are changed. As both parameters are increased the stability changes from being disease free, to monotonically stable, through damped oscillations

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until there is instability. If we then include constant proportional harvesting with $h = h_{\mathrm{MSY}}$ in the model we can see in Fig. 2(b) that, other than at the disease-free equilibrium, the system is stable for all the parameter ranges. This can be shown analytically; harvesting at h_{MSY} reduces the second stability condition to

$$h_{\mathrm{MSY}} < \frac{\lambda \alpha \beta k}{\mu} - b - \alpha = h_{\max}, \tag{19}$$

which is always true. Similarly, substituting h_{MSY} into the third stability condition (given in Appendix) results in an expression which is always positive. Therefore, if $k > k_{\min}$ and $\beta > \beta_{\min}$, when harvesting at the maximal harvesting rate the system is always stable, whether there are real or complex eigenvalues in the absence of harvesting.

3.1.3 Recovery time and resilience

Fig. 3(a) shows the recovery time of the system for the real and complex cases. Unlike the yield-effort curves, changing the carrying capacity results in a significant change to the qualitative behaviour of recovery time. For the real case, the recovery graph has the same qualitative behaviour as has been found for single species systems (Beddington and May 1977). For low harvesting rates there is a gradual increase in the recovery time, which continues for moderate harvesting rates, but there is a rapid increase in the recovery time for harvesting rates above h_{MSY}. The complex case gives very different results, by which the unharvested system exhibits damped oscillations to the equilibrium, and this has a pronounced effect on the recovery time. As harvesting is increased the recovery time decreases initially, which suggests that low levels of harvesting may be beneficial. As harvesting increases further a minimum return time is achieved, at which point the eigenvalues become real and the recovery times increase, suggesting that the system will be less able to recover from perturbations as harvesting increases. It should be noted that the minimum return time does not coincide with the MSY.

For the reciprocal of the recovery time, resilience (Fig. 3(b)), we see that in the real case increasing the harvesting rate decreases resilience. In contrast, increasing harvesting in the complex case increases resilience to a maximum, after which harvesting causes the eigenvalues to become real and the resilience decreases. It can clearly be seen that the MSY occurs after the bifurcation.

In Fig. 3(c) we analyse reactivity, a measure of the short term response to perturbations. In

both the real and complex cases initial increases in harvesting at first decrease reactivity until a minimum after which reactivity increases rapidly. This would suggest that low levels of harvesting would make the system less prone to short-term amplified transients.

We demonstrate the generalities of these findings in Fig. 4. Increasing the host carrying capacity increases the yield and destabilises the interaction. Conversely, increasing harvesting first increases yield to the MSY, but this is followed by a decrease in yield and the eventual extinction of the pathogen. Furthermore, increasing harvesting generally acts to stabilise the host–pathogen interaction. Importantly, it should be noted that the MSY only occurs in the monotonically stable region of parameter space. This would suggest that, in general, low level harvesting will increase resilience before the MSY is reached when the host–pathogen system exhibits unstable or damped oscillatory behaviour in the absence of harvesting.

3.2 Open-closed proportional harvesting

We now consider the open-closed strategy as a mitigation against over-harvesting. To recap, this strategy implements a periodic proportional harvest during the open season and no harvest during the closed season, which may allow the pathogen to recover. Since the resultant behaviour fluctuates due to the harvesting strategy we are unable to use the system health measures as we did for constant proportional harvesting. Hence, we use numerical simulations to investigate optimal harvesting strategies.

Fig. 5(a) shows the yield-effort curves for the proportional open-closed harvesting strategy for the real case ($k = 1$). Here, the three curves represent different proportions of open period; $p = 0.2$, $p = 0.5$ and $p = 0.8$. When $p = 0.2$ we see an initial increase in the yield until the MSY is reached. After this there is a gradual decrease in the yield attained, but because of the short open season the decrease is very slow. The short open season allows continued yielding for a greater range of harvesting efforts above the MSY than under constant proportional harvesting (compare Fig. 1). Increasing the proportion of open period ($p = 0.5$ and $p = 0.8$) causes an increase in the MSY, which is also attained at lower harvesting rates. However, this comes at a cost since over-harvesting leads to over-exploitation causing a decreased yield and making the system more prone to population extinction.

Similarly in the complex case ($k = 4$ Fig. 5(b)) increasing the open season proportion increases the MSY and allows for harvesting efforts which would have caused extinction under constant

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proportional harvesting. However, in contrast to the $k = 1$ case, the harvesting rates at which the MSY is attained does not vary greatly with the proportion of the open season (i.e. $h_{\mathrm{MSY}} \approx$ constant $\forall p$).

The MSY is lower than in the constant proportional harvesting case although we used the same parameter values. This is because the closed period does not allow for harvesting, and therefore the yield is less than when harvesting continuously. This is true in both the real and complex cases.

Fig. 6(a) shows the MSY for the proportional open-closed harvesting strategy when the carrying capacity (k) and the proportion of time spent harvesting (p) are varied. As the length of the open season increases so too does the MSY, as a greater proportion of time is spent harvesting. Increasing the carrying capacity also increases the MSY; an increased carrying capacity provides a greater resource. Fig.6(b) shows the corresponding maximal harvesting rates (h_{MSY}). For small carrying capacities the maximum harvesting rate is less than for larger carrying capacities. For small carrying capacities the maximal harvesting rate decreases (according to power laws) with increasing length of open season (see Fig. A1(a) in Appendix when $k = 2.5$). For long open seasons, the maximal harvesting rates are relatively low since harvesting is spread over a long period, with a relatively short period for population recovery. In contrast, for short open seasons the maximal harvesting rates increase since intensive harvesting can occur as the recovery period is relatively long. Fig. 6(b) shows different behaviours for larger carrying capacities, with more variation in the maximal harvesting effort as the length of open period is increased. As the carrying capacity increases the dynamics during the closed period change (as seen in Fig. 2(a)). This means that as the length of open season varies the population density of the infected hosts at the end of the closed season varies (see Fig. A2 and Fig. A1(b) in Appendix). A small change in the length of the open season mean there is either an additional peak or trough in infected host density in the closed season. This either accelerates or decelerates the MSY which in turn increases or decreases the optimal harvesting rate respectively, yielding the oscillatory behaviour in the optimal harvesting rate for large carrying capacities in Fig. 6(b). It is interesting to note that whilst the maximal harvesting rates change dramatically for small changes in the length of the open period, there is little change in the corresponding MSY values (see Fig. A1(c) and (d) for an example when $k = 7$ for greater clarity). In Fig. 6(a) for larger carrying capacities the MSY increases linearly, however the maximal harvesting rates shown in Fig. 6(b) oscillate as the proportion of the open season increases. The oscillations become dampened as the proportion of open season increases and there

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is less difference in the maximal harvesting rates. Therefore, if in the absence of harvesting there are oscillatory dynamics, this has a large impact on the resultant dynamics in the open-closed harvesting strategy, and can hence make it difficult to assess what may be the best harvesting rate.

4 Discussion

We have developed existing theory to model the harvest of an insect-pathogen in a host–pathogen system using two contrasting harvesting strategies. We examined the MSY, and determined how it is affected by variations in parameters relating to carrying capacity, growth rates and virulence of the pathogen. We found that under constant proportional harvesting the return time, and hence resilience, is highly dependent on the eigenvalues of the system in the absence of harvesting. Therefore, harvesting can be beneficial in terms of system resilience if environmental fluctuations occur, both in the short- and long-term. Finally, we have shown that the implementation of a closed season without harvesting supports a greater range of harvesting rates, but a reduced yield is found compared to constant proportional harvesting.

We have shown that constant proportional harvesting can allow for an amount of over-exploitation before extinction of the pathogen, which mirrors findings from single species models (Yakubu et al. 2011) and for a predator–prey model if only the predator is harvested (Legović et al. 2010; Kar and Ghosh 2013). However, in a simple predator–prey model if only the prey is harvested the predator can be driven to extinction before the MSY of the prey has been reached (Legović et al. 2010), thus reducing the system to a single species model. In a more complex predator–prey model with intraspecific competition in the predator growth dynamics, the same can happen however there can be co-existence of both species (Kar and Ghosh 2013). Overharvesting above the MSY leads to the extinction of the predator and again results in the single species model. We also found the host–pathogen system can allow for an amount of over-exploitation under an open-closed harvesting strategy. However, for this strategy we demonstrated a new yield-effort curve which is no longer symmetric around h_{MSY}, as in the constant proportional case. Harvesting over the maximum still decreases yield, as in the constant proportional case and single species models (Beddington and May 1977; Yakubu et al. 2011), but decreases at a slower rate than in these cases as the closed season allows for a period of recovery.

Under constant proportional harvesting we have found that variations in the carrying capacity and other parameters can affect the underlying dynamics of the system. This in turn heavily

affects the health measures of the host–pathogen system. In the real case we have shown that the return time increases with harvesting effort, which is consistent with the literature for the single species model (Beddington and May 1977). In contrast, increasing the carrying capacity gives the complex case, for which we have shown there is an initial decrease in the return time. The resilience analysis complements this result, agreeing with Kristensen et al. (2003), whereby the maximum resilience occurs where the eigenvalues change from complex to real. Their analysis was of a three-compartment aquatic food web model involving Lotka–Volterra dynamics. We have not found any literature on harvested predator–prey type models where the resilience has been calculated. It is interesting to note that in the complex case overharvesting can still result in a faster return time than no harvesting. However, over-harvesting results in decreased yield and hence is still not profitable.

The results described here have implications for choosing an appropriate harvesting strategy. Although an open-closed harvesting strategy is less likely to cause extinction of the host, the yield is less than under a constant proportional strategy. Therefore, fully understanding the interactions between the host, pathogen, harvesting effort and yield is vital in ensuring the resource is used to it's full potential. A cost-benefit analysis may need to be performed to determine if it is imperative the host has time to recover, or, if it can be harvested continually to maximise return. Wildlife and fisheries management often shows ecological advantages of open-closed harvesting (Bartlett et al. 2009; Cinner and Aswani 2007), and therefore the yield needs to be examined in the context of the host–pathogen system being studied.

Our results have shown that understanding how yield, and especially MSY, change under different environmental circumstances is vital, as changing practices may enable a greater harvest or avoid overharvesting. For example, increasing the carrying capacity 4-fold produces around eight times the yield under constant proportional harvesting and 5-10 times the yield under the open-closed harvesting strategy. Thus, farming of yaks and other livestock may increase the occurrence of *C. sinensis*, as they keep the vegetation shorter, which enhances (a) dispersal of spores and (b) finding the fungus for harvest (Cannon et al. 2009; Winkler 2005). Altering where and when the yaks and other livestock graze may therefore influence the carrying capacity, in turn altering the MSY. In an open-closed setting practices such as these to increase the carrying capacity have a positive effect on the MSY, however we have shown that managing the strategy to optimise the harvesting effort is difficult. In this setting a small carrying capacity will reduce the MSY slightly,

however it will be more difficult to determine the optimum harvesting rate to achieve such a yield. The variations in maximal harvesting rates makes exploitation of the resource easier for harvesters; slight changes in practices regarding the amount of time spent harvesting could have great implications for the host–pathogen system if the harvesting rate is not also changed appropriately.

Our results indicate that the health of the harvested host–pathogen system is strongly dependent on the strength of the host–pathogen interaction, and the types of dynamics exhibited (monotonic or oscillatory stability). Furthermore, low levels of harvesting may aid the resilience of the system to perturbations in both the short- and long-term. Moreover, if in the absence of harvesting there are real or complex eigenvalues, harvesting well beyond the MSY would (i) decrease yield and (ii) make the system extremely prone to large scale and long-lived transient behaviours that may be detrimental to people dependent on the harvest. Therefore, the accuracy of life-history parameters are vital, as small changes could change the predicted system eigenvalues and hence alter the measures of short- and long-term health of the system, as well as the predicted MSY. Using bioeconomic models, Hoshino et al. (2014) found that modelling different levels of stage/age-structure complexity, combined with variability of life-history parameters, could have large effects on bioeconomic target reference points, such as MSYs. Our results are in agreement with these findings, but in addition, we have also shown that ecosystem health (resilience and reactivity) could also be affected.

For harvested host-pathogen systems such as *C. sinensis*, it is vital to determine appropriate strategies for harvesting. Alternatives to the measures explored in this paper include no-take areas. Little et al. (2010) established that for fisheries no-take areas can combat population extinction. They benefit the surrounding, harvested areas and hence this idea may also be applicable to host–pathogen systems. Site specific quotas (Beissinger and Bucher 1992) are another alternative which may also assist with sustainable management.

Our study has explored two strategies for harvesting hosts in a host–pathogen system. Using an open-closed strategy means the pathogen is less likely to be driven to extinction as higher levels of harvesting can be supported. However, harvesting at a constant rate can produce a greater yield providing the resource is not overexploited. The environmental conditions are undeniably important, as they affect the underlying dynamics and mean that harvesting can affect the system in different ways. There are six key areas of biological knowledge needed to harvest animals; population size and range, habitat requirements, resilience to human disturbance and habitat changes,

mortality and productivity rates, key factors which regulate populations, and effects of variations on the environment (Beissinger and Bucher 1992). These can be applied to a host–pathogen harvesting model. For example, the *C. sinensis* system is poorly understood (Cannon et al. 2009), and study of the host–pathogen interactions in the field is required to inform a more specific model. However, we have developed a model of harvesting in a host–pathogen system, and shown that frequently some level of harvesting is more beneficial for system stability than no harvesting.

Acknowledgements

Appendix

Linear stability analysis: host–pathogen model with proportional harvesting

The Jacobian matrix for the host–pathogen model with proportional harvesting is given by

$$
J_{(X^*Y^*,W^*)} = \begin{pmatrix} r\left(1 - \frac{2X^*}{k}\right) - \beta W & 0 & -\beta X^* \\ \beta X^* & -(b + \alpha + h) & \beta X^* \\ 0 & \lambda \alpha & -\mu \end{pmatrix}.
$$

At the trivial steady state the characteristic equation is given by

$$
\sigma^3 + \sigma^2(b + \alpha + h + \mu - r) + \sigma(\mu(b + \alpha + h) - r(b + \alpha + h + \mu)) - r\mu(b + \alpha + h) = 0.
$$

A Routh–Hurwitz condition is always violated with this characteristic equation and hence the trivial steady state is unstable.

The characteristic equation for the pathogen-free steady state is given by

$$
\sigma^3 + \sigma^2(r + b + \alpha + h + \mu) + \sigma(r(b + \alpha + h + \mu) + \mu(b + \alpha + h) - \beta k \lambda \alpha) + (r\mu(b + \alpha + h) - r\beta k \lambda \alpha) = 0.
$$

In this case the one Routh–Hurwitz condition is always valid. However for the other conditions

18

to hold then

$$\frac{\mu(b + \alpha + h)}{\beta k} > \lambda\alpha.$$

The characteristic equation for the endemic steady state can be given by

$$\sigma^3 + \sigma^2\left(\frac{rX^*}{k} + b + \alpha + h + \mu\right) + \sigma\left(\frac{rX^*}{k}(b + \alpha + h + \mu)\right) + r\left(1 - \frac{X^*}{k}\right)(b + \alpha + h)\mu = 0.$$

Again one condition is always satisfied, and for the other conditions to be satisfied it is necessary that

$$\lambda\alpha > \frac{\mu(b + \alpha + h)}{\beta k},$$

and

$$(r + b + \alpha + \mu + h)\left(\frac{rX^*}{k}(b + \alpha + h + \mu)\right) - r\left(1 - \frac{X^*}{k}\right)(b + \alpha + h)\mu > 0.$$

464

465

466   *Stability analysis: harvesting at h_{MSY}*

467

The third condition for stability at the endemic equilibrium is

$$(r + b + \alpha + \mu + h_{\mathrm{MSY}})\left(\frac{rX^*}{k}(b + \alpha + h + \mu)\right) - r\left(1 - \frac{X^*}{k}\right)(b + \alpha + h_{\mathrm{MSY}})\mu > 0.$$

468   Let

$$
\begin{aligned}
r_1 &= (r + b + \alpha + \mu + h_{\mathrm{MSY}})\left(\frac{rX^*}{k}(b + \alpha + h + \mu)\right), \\
&= \frac{1}{8}\frac{(2r\mu + b\mu + \alpha\mu + 2\mu^2 + \lambda\alpha\beta k)r(b\mu + \alpha\mu + \lambda\alpha\beta k)(b\mu + \alpha\mu + \lambda\alpha\beta k + 2\mu^2)}{\mu^2\lambda\alpha\beta k}
\end{aligned}
$$

469   and

$$
\begin{aligned}
r_2 &= r\left(1 - \frac{X^*}{k}\right)(b + \alpha + h_{\mathrm{MSY}})\mu, \\
&= -\frac{1}{4}\frac{r(-\lambda\alpha\beta k + \beta\mu + \alpha\mu)(b\mu + \alpha\mu + \lambda\alpha\beta k)}{\lambda\alpha\beta k}
\end{aligned}
$$

19

470 Then condition three is $r_1 - r_2$, given by

$$\frac{1}{8} \frac{1}{\mu^2 \lambda \alpha \beta k} \left(r(b\mu + \alpha\mu + \lambda\alpha\beta k) \left(2r\mu^2 b + 2r\mu^2 \alpha + 2r\mu\lambda\alpha\beta k + 4r\mu^3 + b^2\mu^2 + 2b\mu^2\alpha \right. \right.$$
$$\left. \left. + 2b\mu\lambda\alpha\beta k + 6b\mu^3 + \alpha^2\mu^2 + 2\alpha^2\mu\lambda\beta k + 6\alpha\mu^3 + 2\mu^2\lambda\alpha\beta k + 4\mu^4 + \lambda^2\alpha^2\beta^2 k^2 \right) \right),$$

471 which is always positive. Therefore at the harvesting effort which produces the MSY the third

472 Routh–Hurwitz condition holds and, as the first two do, the system is always stable.

473

474 *Open-closed proportional harvesting*

475

476 Fig. A1(a) shows the maximal harvesting rate (h_{MSY}) as the proportion of open period increases

477 when the carrying capacity is $k = 2.5$. The maximal harvesting rate when $k = 2.5$ decreases

478 according to the power law $f(x) = ax^b + b$, which was fitted using MATLAB, where $a = 0.003543$,

479 $b = -2.175$ and $c = 0.2377$ with corresponding 95% confidence intervals of $(0.00286, 0.004226)$,

480 $(-2.296, -2.054)$ and $(0.2363, 0.2395)$. In this case the R–square value is 0.996 for the best fit. For

481 small carrying capacities the maximal harvesting rate follows a similar trend as the proportion of

482 the open season increases.

483 Fig. A1(b) shows the density of infected hosts as the harvesting begins at the start of the open

484 season, averaged over 50 open-closed seasons. Whilst for small carrying capacities the density

485 of infected hosts does not vary greatly as the proportion of the open season increases, for larger

486 carrying capacities there is more variation, and oscillatory behaviour in the density of infected

487 hosts. This subsequently affects the maximal harvesting rate for larger carrying capacities as the

488 length of open season increases.

489 Fig. A1(c) shows the MSY as the proportion of open period increases when the carrying capacity

490 is $k = 7$. The MSY increases as the proportion of open season increases. For small changes in

491 length of open season there is a small increase in the MSY.

492 Fig. A1(d) shows the maximal harvesting rate (h_{MSY}) as the proportion of open period increases

493 when the carrying capacity is $k = 7$. The maximal harvesting rate shows dampened oscillations as

494 the proportion of open period increases.

495 Fig. A2(a) shows the time series when there are real eigenvalues in the absence of harvesting

496 $(k = 2)$ as the length of the open season is varied. In the absence of harvesting there is a stable

20

equilibrium, meaning that at the end of the closed period the infected hosts density is approximately the same independent of the length of open season.

Fig. A2(b) shows the time series when there are complex eigenvalues in the absence of harvesting with negative real part ($k = 5$) as the length of the open season is varied. In the absence of harvesting there is oscillatory behaviour. This means that the length of the open season has an impact on the infected hosts density at the end of the closed season before harvesting commences.

Fig. A2(c) shows the time series when there are complex eigenvalues in the absence of harvesting with negative real part ($k = 7$) as the length of the open season is varied. In the absence of harvesting there is again oscillatory behaviour. Due to the increased carrying capacity the amplitude of the oscillations is greater than when $k = 2$, again meaning that the length of the open season has an impact on the infected hosts density at the end of the closed period, thus affected the maximal harvesting rate which achieves the MSY.

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605   dynamic implications in the Pacific halibut and Atlantic cod fisheries. *Math. Biosci.*, 232:66–77.

Table 1: Parameter definitions for the mathematical model (1).

Parameter/variable	Definition	Value
X	Density of susceptible hosts	
Y	Density of infected hosts	
W	Density of free-living pathogen spores	
r	Intrinsic growth rate of the host (birth rate - natural death rate).	5
k	Carrying capacity of the susceptible population	
β	Force of infection of the pathogen/virulence of the pathogen	2
b	Natural mortality rate of the host	0.1
α	Pathogen induced mortality rate of the host	0.003
$h(Y)$	Harvesting term; dependent on Y, the density of infected hosts	
$\lambda\alpha$	Rate of sporulation from the infected hosts.	15α
μ	Rate of decay of the pathogen	0.4
T	Total length of open-closed period	100
p	Proportion of time harvesting occurs	0 - 1
n	Total number of open-closed seasons	50
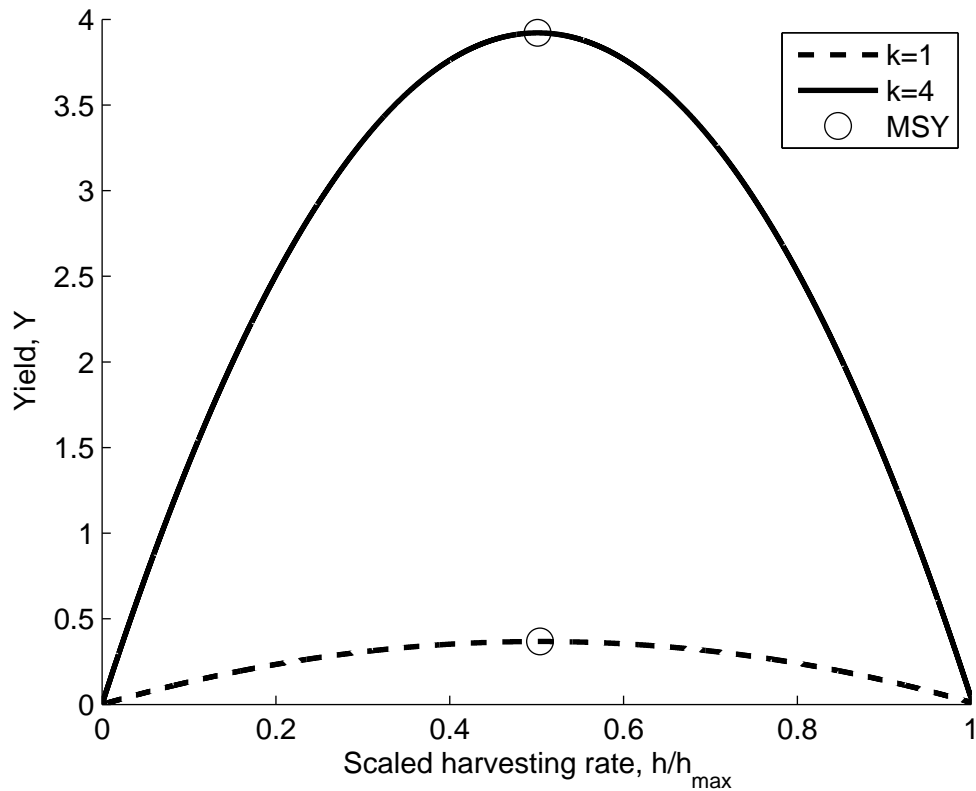
Fig. 1: The scaled yield-effort curve for constant proportional harvesting. The yield is plotted for varied scaled harvesting rates. The dashed line shows the curve when, in the absence of harvesting, all eigenvalues are real ($k = 1$), whilst the solid line shows the curve when, in the absence of harvesting, eigenvalues are complex ($k = 4$) with negative real part. The circles denote the respective MSY points. For $k = 1$ $h_{\mathrm{MSY}} = 0.0610$ and $h_{\mathrm{max}} = 0.1220$ and for $k = 4$ $h_{\mathrm{MSY}} = 0.3985$ and $h_{\mathrm{max}} = 0.7970$ (all to 4 decimal places). All other parameters are given in Table 1.

(a)
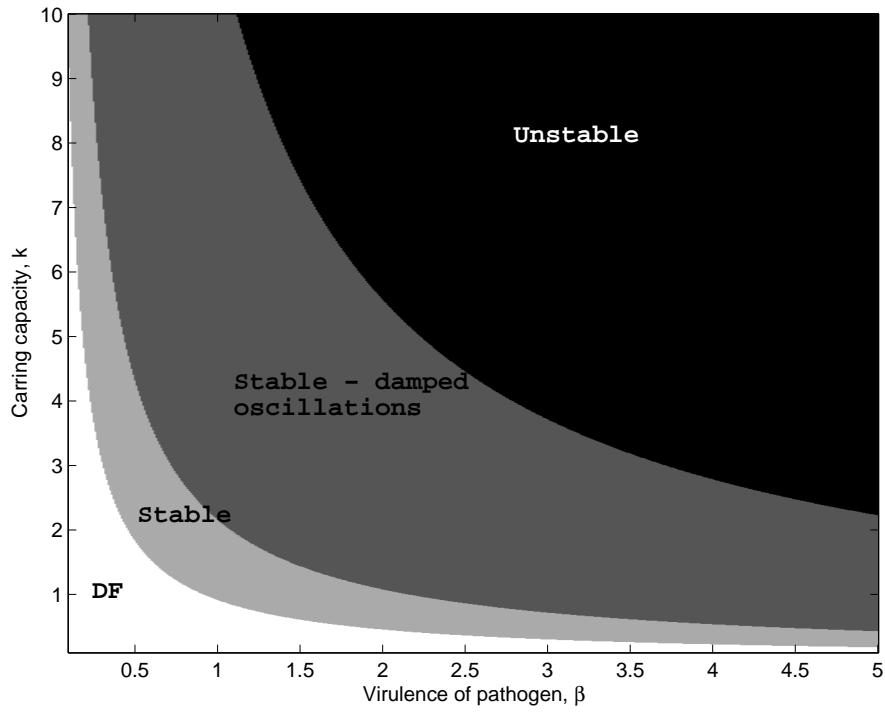
(b)
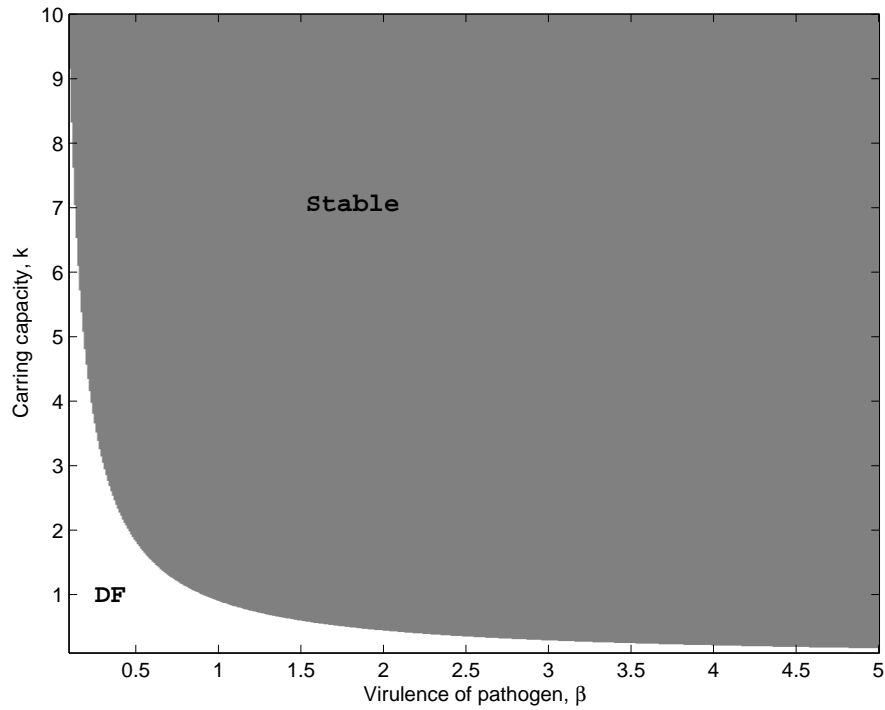
Fig. 2: The stability regions for selected parameters. In (a) we plot the stability regions, as given by the results in Appendix, in the absence of harvesting. In (b) we again plot the stability regions, this time when harvesting is included in the model at the rate of h_{MSY}. All other parameters are given in Table 1.
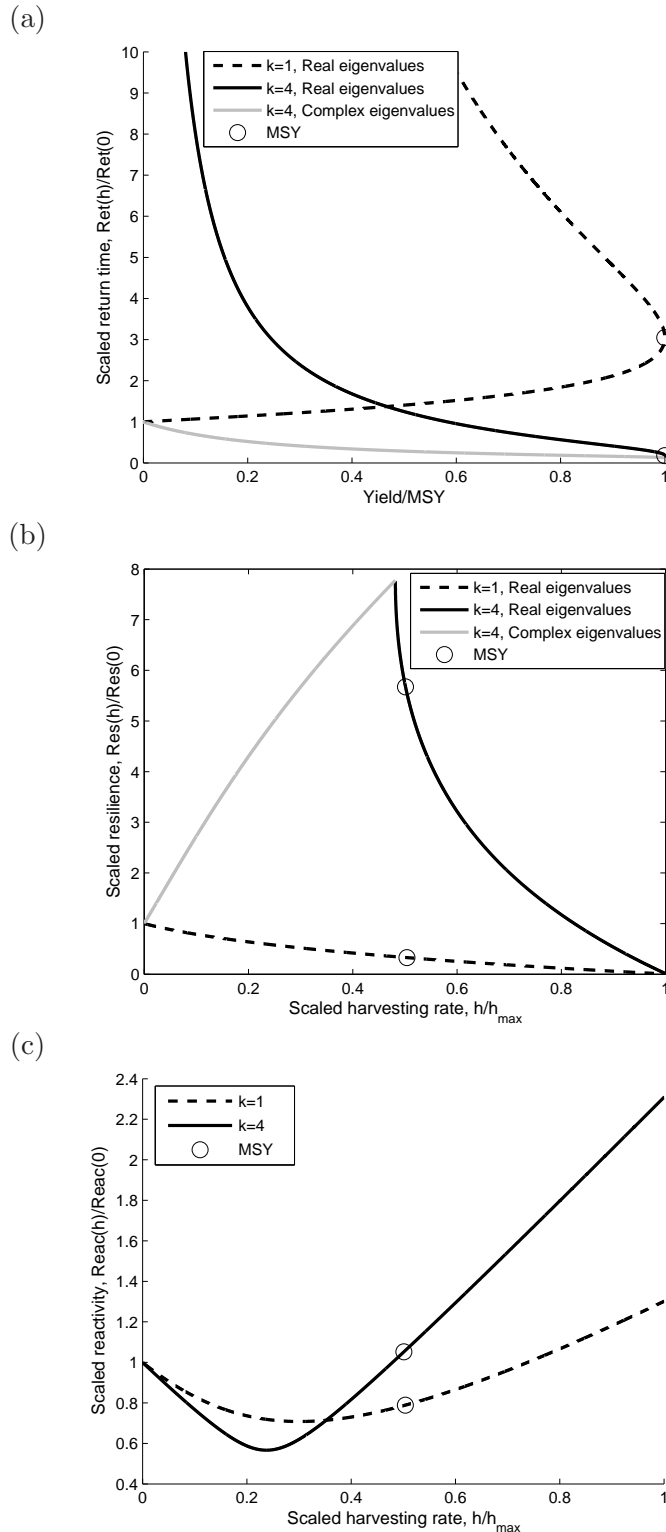
Fig. 3: (a) Scaled return times as a function of yield for proportional harvesting. Two cases are presented: carrying capacity $k = 1$ where the eigenvalues are real in the absence of harvesting (dashed lines); carrying capacity $k = 4$ where the eigenvalues are complex with negative real-part in the absence of harvesting (solid lines: grey, complex eigenvalues and black, real eigenvalues). (b) Resilience of the system for different harvesting rates for the two cases. The lines are as in (a). (c) Reactivity plotted against the scaled harvesting rates for the two cases. The lines are as in (a), but we do not distinguish between complex and real eigenvalues here. All other parameters are given in Table 1.

(a)
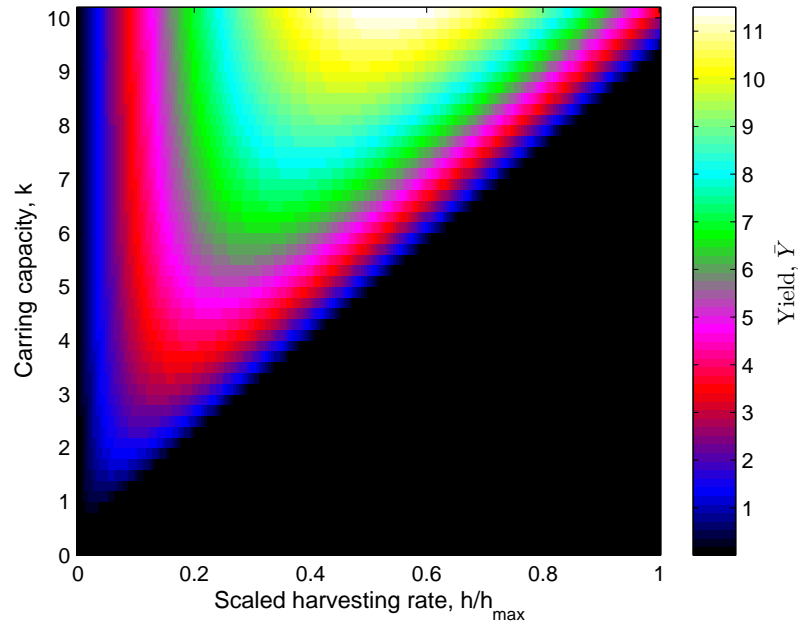
(b)
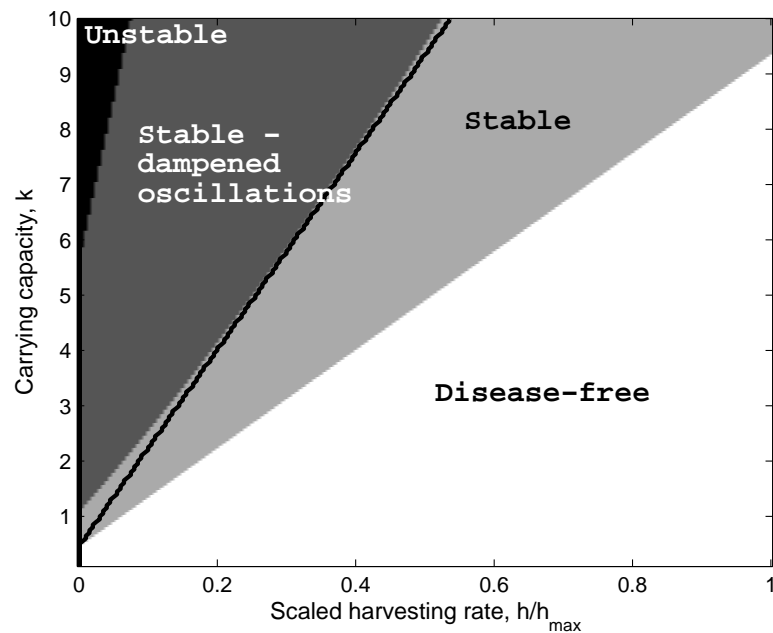
Fig. 4: The yield-effort curves and stability regions for the constant proportional harvesting strategy. In (a) we plot the yield, as calculated by (5), for varying carrying capacities, k, and harvesting rates, h. In (b) we plot the corresponding stability regions, as given by the results in Appendix. The black line is the MSY curve as calculated by the maximum values from (a). All other parameters are given in Table 1.
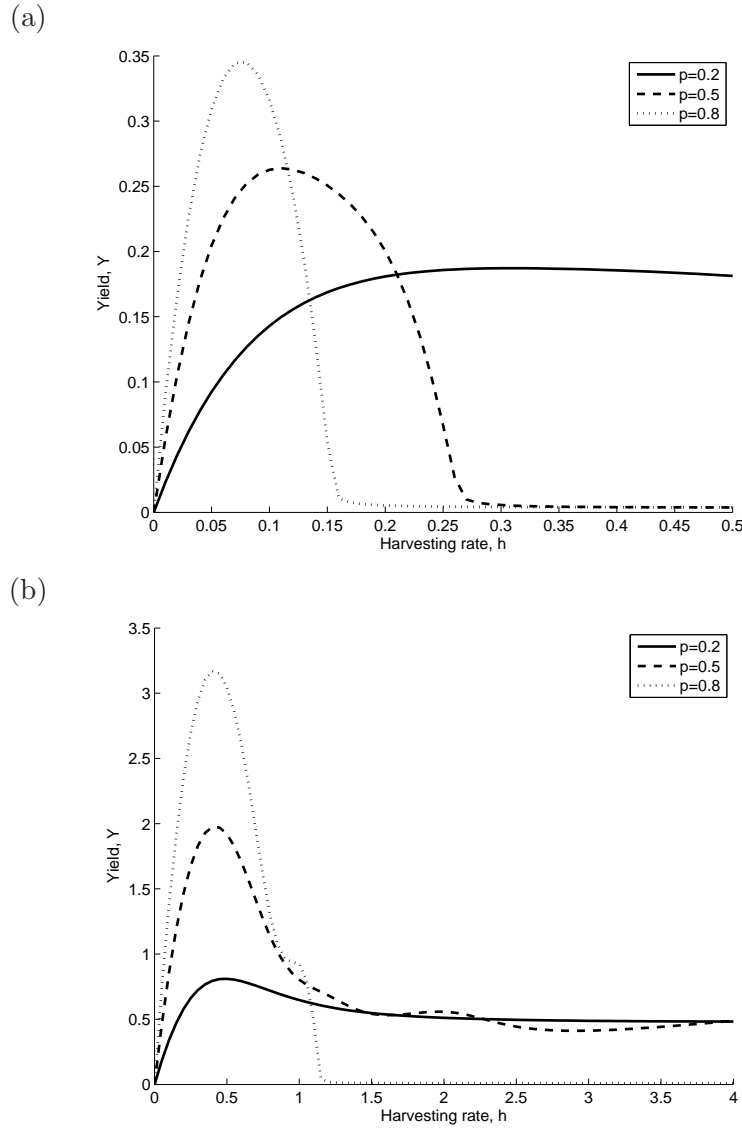
(a)

(b)

Fig. 5: The yield-effort curves for the open-closed harvesting including a proportional harvesting strategy. In these graphs the thick line corresponds to the open period lasting 20% of the open-closed period, the dashed line the open period lasts for 50% of the total time and the dot-dashed line represents when the open period lasts for 80% of the total time. (a) In the absence of harvesting there are negative real eigenvalues ($k = 1$). (b) In the absence of harvesting there are complex eigenvalues with negative real-part ($k = 4$).
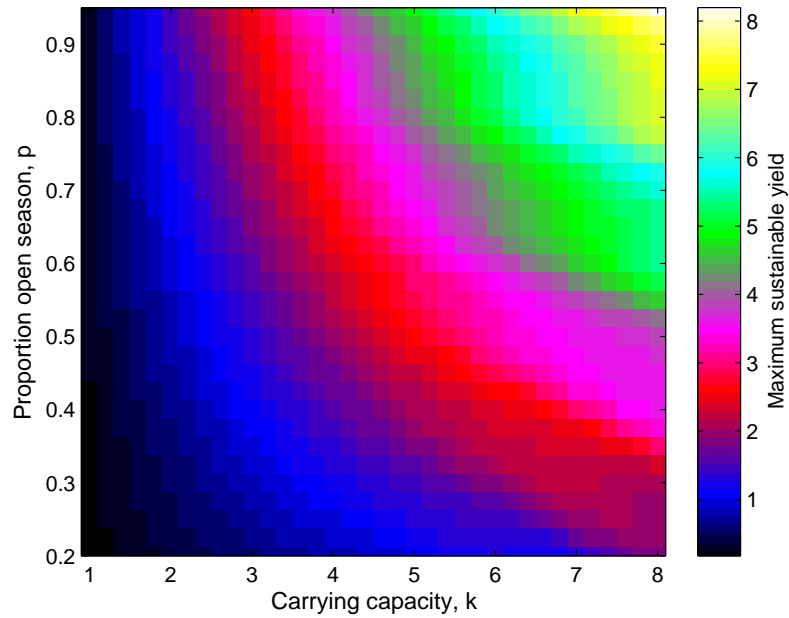
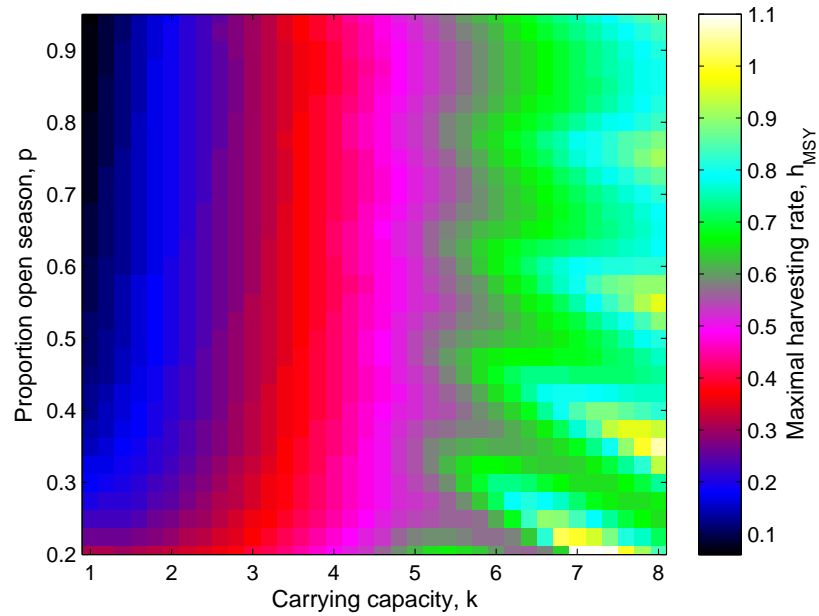Fig. 6: The MSY and h_{MSY} for the open-closed harvesting strategy. In (a) we plot the maximum sustainable yield, found by taking the maximum over a range of harvesting values for varying carrying capacities, k, and proportion of open season, p. In (b) we plot the harvesting effort which corresponds to the MSY, h_{MSY}. All other parameters are given in Table 1.
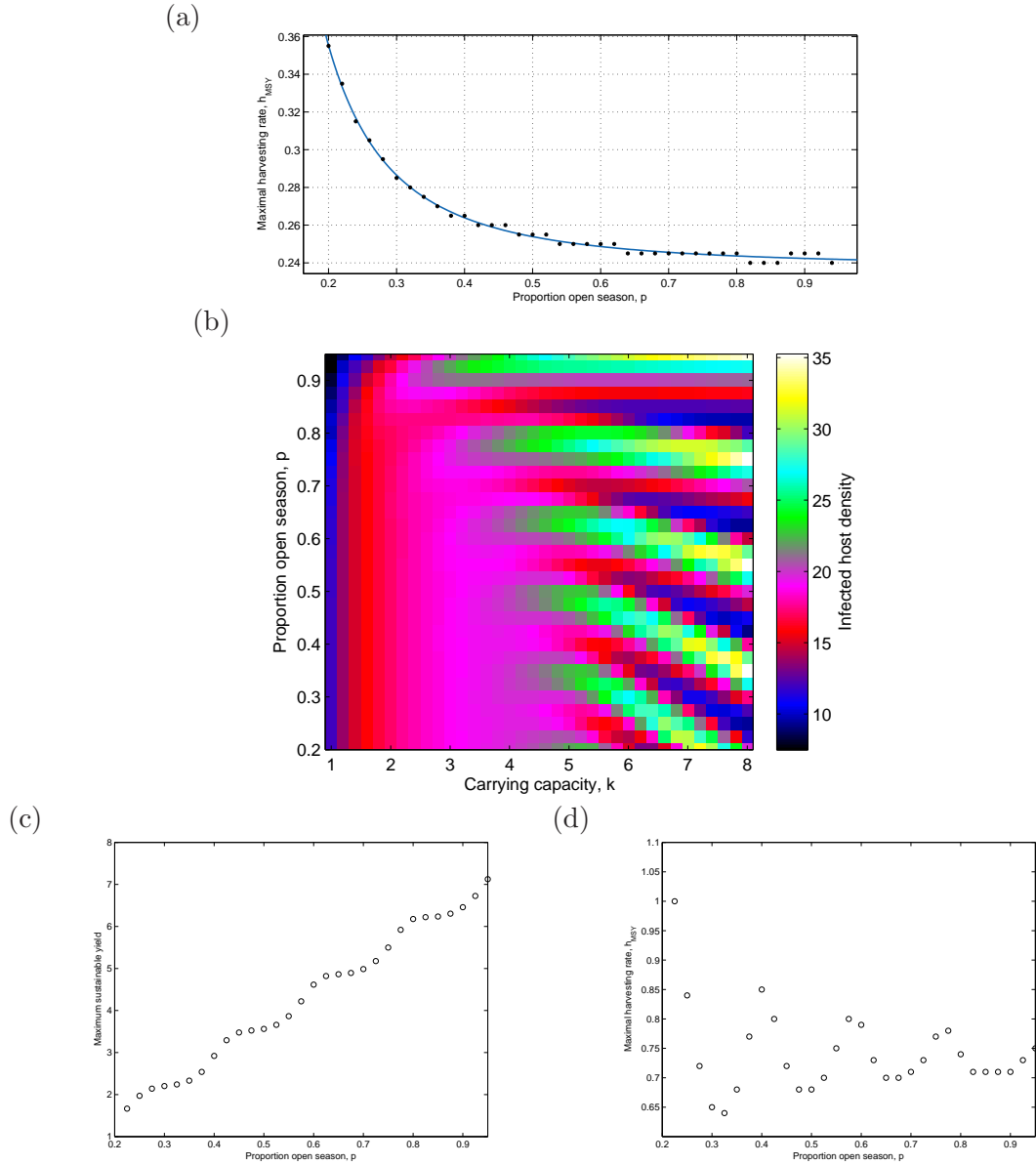
Fig. A1: (a) Maximal harvesting rate as a function of proportion of open season for a carrying capacity size $k = 2.5$. A power law curve has been fitted which is of the form $f(x) = ax^b + c$. (b) The density of infected hosts, averaged over 50 years, at the start of the open season as the carrying capacity and length of open period are varied. (c) MSY as a function of proportion of open season for a carrying capacity size $k = 7$. (d) Maximal harvesting rate as a function of proportion of open season for a carrying capacity of size $k = 7$. All other parameters are given in Table 1.
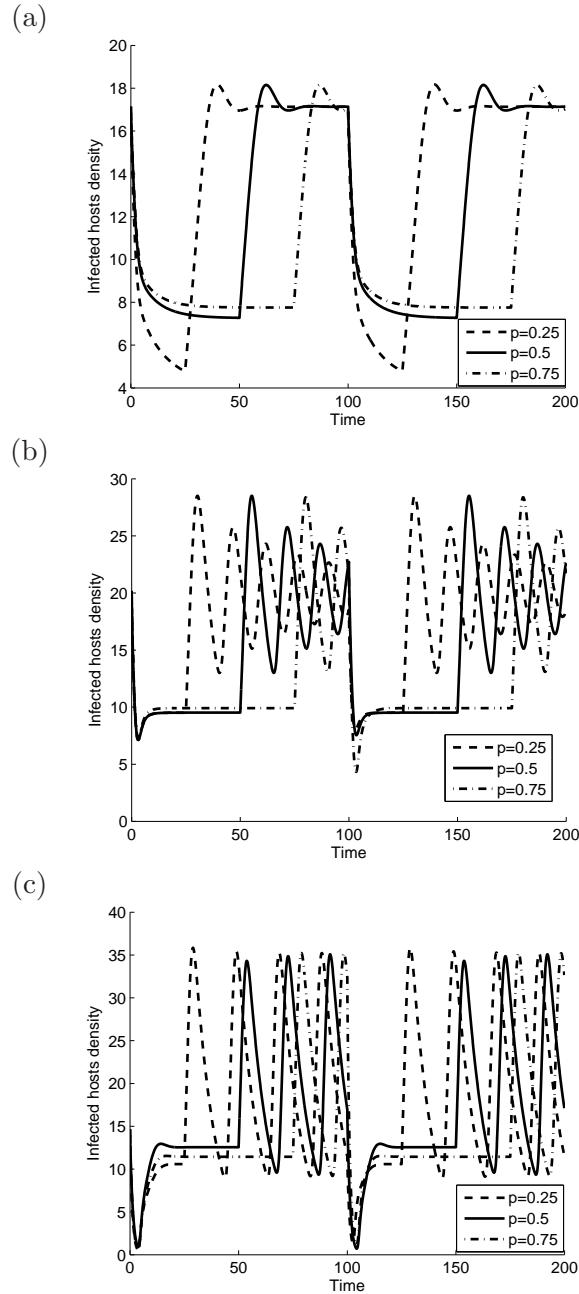
33

Fig. A2: Time series for the open-closed harvesting including a proportional harvesting strategy. In these graphs the thick line corresponds to the open period lasting 20% of the open-closed period, the dashed line the open period lasts for 50% of the total time and the dotted dot-dashed line represents when the open period lasts for 75% of the total time. (a) In the absence of harvesting there are negative real eigenvalues ($k = 2$). (b) In the absence of harvesting there are complex eigenvalues with negative real-part ($k = 5$). (c) In the absence of harvesting there are complex eigenvalues with negative real-part ($k = 7$). All other parameters are given in Table 1.