MATH3070 Assignment 1

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Question 1

We have two models,

$$R(X) = aXe^{-bX}; \qquad H(x) = \begin{cases} rX & X < k/r \\ k & X \geq k/r \end{cases}$$

for parameters a, b, r, $k > 0$. We're given that the domain of each function is $[0, \infty)$.

(a) We want to find the proliferation and all biologically meaningful equilibria for the model $R(X)$. The proliferation is given by the derivative at $X = 0$, and so

$$R'(X) = ae^{-bx} - abXe^{-bX}$$
$$\Rightarrow R'(0) = a - 0 = a$$

Now, we have equilibria when $X_t = X_{t+1} = R(X_t)$.

$$\Rightarrow X^* = aX^*e^{-bX^*}$$

and so we have one solution at $X^* = 0$. Removing X^* as a factor from each side, we then obtain

$$1 = ae^{-bX^*}$$
$$-bX^* = -\ln(a)$$
$$X^* = \frac{\ln(a)}{b}$$

as another solution. This is biologically meaningful when $\ln(a) > 0$, or $a > e^0 = 1$, otherwise the equilibrium will be negative and not physical for a system that describes a population or biomass.
To determine the stability of these equilibria, we note that an equilibrium X^* is stable when $|F'(X^*)| < 1$ (for discrete time models), and $F'(X) = R'(X)$ in this case. So, for $X^* = 0$,

$$R'(0) = ae^{-b \times 0} - 0 = a$$

and so $X^* = 0$ is only stable when $a < 1$, and is unstable otherwise. Since $a > 0$, we can omit the absolute value signs.
For the other equilibrium $X^* = \ln(a)/b$,

$$R'(\ln(a)/b) = ae^{-\ln(a)} - a\ln(a)e^{-\ln(a)}$$
$$= \frac{a}{a} - \frac{a\ln(a)}{a}$$
$$= 1 - \ln(a)$$

And so the equilibrium $X^* = \ln(a)/b$ is stable only when $|1 - \ln(a)| < 1$, i.e. for $0 < \ln(a) < 2$, or $1 < a < e^2$, and is unstable otherwise.

(b) Now we seek the proliferation and equilibria of the model $H(X)$. As before, the proliferation is given by $H'(0)$,

$$H'(X) = \begin{cases} r & X < k/r \\ 0 & X \geq k/r \end{cases} \tag{1}$$

and so $H'(0) = r$, since both k and $r > 0$, and so $X = 0 \not\geq k/r$ for any k, r.
As for the equilibria, we once again use the fact that $X_t = X_{t+1} = H(X_t)$ at equilibrium. Since this is a piecewise

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function, we must look at each of the cases.

Case I: $X < k/r$. In this case, we have $X_t = rX_t$. Naturally, we have a solution for $X^* = 0$. Dividing both sides by X_t, we also find a family of degenerate solutions when $r = 1$.

Case II: $X \geq k/r$. In this case, we obtain $X_{t+1} = k \geq k/r$ if $r \geq 1$. The solution $X^* = k$ follows naturally. If $r < 1$, we get that $k \not\geq k/r$ in which we fall back to the first case with equilibrium $X^* = 0$.

To assess stability of the equilibria, once again note that $|H'(X^*)| < 1$ is the criteria for a stable equilibrium. Looking at equation (1), we see that the derivative doesn't actually rely on the value of X_t, but really only the parameter r. Hence, we note that $X^* = k$ is stable for $r > 1$ (since $H'(k) = 0$), and $X^* = 0$ is stable for $r < 1$ (since $H'(0) = r$). As in part (a), we can omit the absolute value signs since the parameters are strictly positive.

(c) Now, we aim to rewrite the model $R(X)$ in terms of the parameters r and k that describe the model $H(X)$. As a first step, we want the proliferation to match between the models, so we set $a = r$. Next, we want the equilibria to match between the two models. The $X^* = 0$ equilibrium matches already, so we only need to assess the positive case

$$k = \frac{\ln(a)}{b} = \frac{\ln(r)}{b} \implies b = \frac{\ln(r)}{k}$$

In terms of the other parameters, we can now write the model $R(X)$ in the form

$$R(X) = aXe^{-bX} = rXe^{-X\ln(r)/k} \tag{2}$$

Just to be safe, we can then check the equilibrium to make sure it matches. By the same process as in (a), we obtain $X^* = 0$ as expected. Then we get $X^* = k\ln(r)/\ln(r) = k$ – exactly what we want!

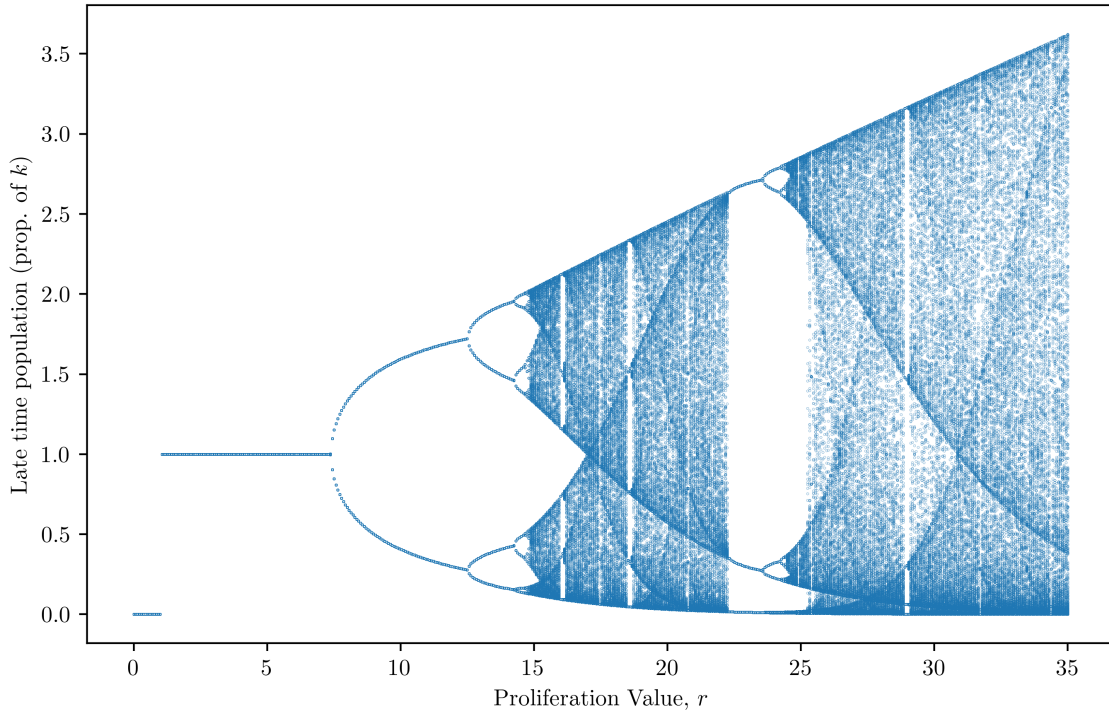(d) Our orbit diagram for the model $R(X)$ described by equation (2) is shown in Figure 1.

Figure 1: We observe the expected stability in the late time populations (or more generally, equilibria) as a function of r. Notably, we see the equilibrium $X^* = 0$ for $r < 1$, a stable equilibrium at $X^* = k$ for $1 < r < e^2$, and unstable for higher values of r up to $r = 35$ in this plot. The code that generates this is a part of the file `Q1.py`, submitted with this document in Blackboard.

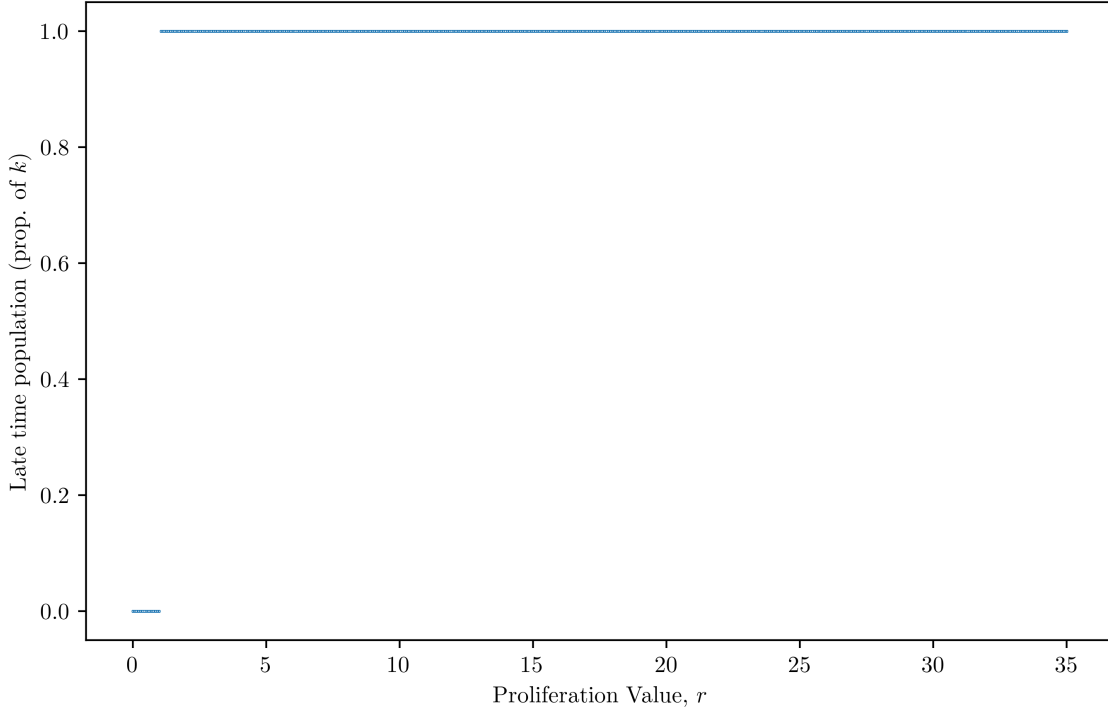(e) The bifurcation diagram for the model $H(X)$ is shown in Figure 2.

Figure 2: We observe the two expected equilibria for the model $H(X)$ at 0 and k, according to the stability conditions described in part (b). The domain of r values was chosen to be the same as Figure 1 so that comparisons could be made across the same domain.

(f) Now, we want to derive the optimal escapement for the system $H(X)$, where $S_t = X_t - h_t$. A theorem given in class states that if $H(S) = X_{t+1} = H(X_t - h_t)$ is smooth (i.e. it's infinitely continuously differentiable), and $H(S) > S$, then $H'(S^*) = 1$ yields the optimal escapement. Unfortunately, we can't use this theorem, since the first derivative of $H(X)$ is discontinuous.

Alternatively, we can look at the increase in the escapement at an initial and subsequent timestep, and maximise this with respect to escapement. That is, we want to maximise the harvest such that

$$\frac{d\left[H(S) - S\right]}{dS} = 0$$

This increase is given as

$$H(S) - S = \begin{cases} rS - S & S < k/r \\ k & S \geq k/r \end{cases}$$

And so differentiating with respect to the escapement gives

$$\frac{d\left[H(S) - S\right]}{dS} = \begin{cases} r - 1 & S < k/r \\ 0 & S \geq k/r \end{cases}$$

Hence, $S \geq k/r$ gives an equilibrium for the function. We want the maximum harvest, which implies the lowest escapement while still maintaining the $S \geq k/r$ condition and so we take the equality. That is, the optimal equilibrium escapement is

$$S = \frac{k}{r}$$

(g) Using the code attached with this document, we computed the optimal equilibrium escapement for the model $R(X)$ (with $r = 2$) as $S \simeq 0.454$. Since the function $R(X)$ is infinitely continuously differentiable, we're able to use the theorem that states $R'(S^*) = 1$ and a root finding algorithm to numerically find S^*.

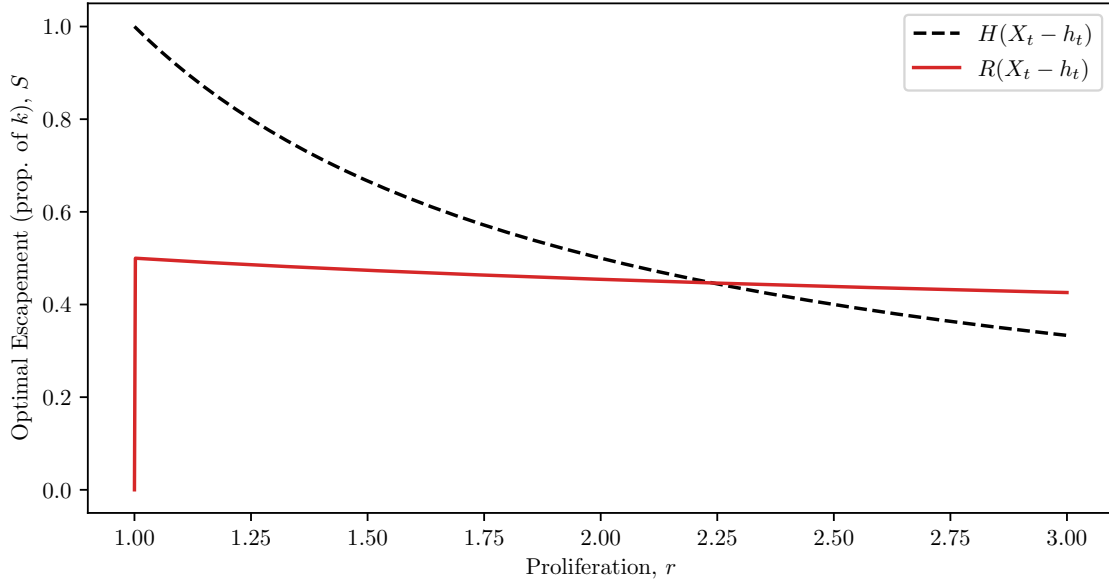(h) The optimal escapements for each of the models $R(X)$ and $H(X)$ are shown in Figure 3.

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Figure 3: We see a steeper slope in the optimal escapement for $H(S)$ than for $R(S)$. Close to $r = 1$ we see essentially a step function for $R(S)$, corresponding to the same region as the instability we mentioned in part (a).

(i) One might prefer the model $H(X)$ due to its wider domain of stability across proliferation values, as seen in the comparison between figures 1 and 2. While $R(X)$ is stable for $1 < r < e^2$, $H(X)$ is stable for $r > 1$ which is an attractive quality.

Another key comparison is that made in Figure 3. The optimal escapement is remarkably consistent for the model $R(S)$, which would be ideal when the true proliferation is unknown or has some large uncertainty associated with it. You can safely harvest a more or less constant amount and achieve near-optimality without a highly constrained *a priori* proliferation. Compare that to the model $H(S)$, where if we overharvested in the event the true proliferation was low, the escapement would be critically low for the next time step's growth.

Question 2

We have the production model

$$\dot{x} = x(1 - x) + m - hx$$

where x is a proportion of some carrying capacity, while $m \in \mathbb{R}$.

(a) If $m > 0$, we could interpret this parameter as some population being added to the system; perhaps migration (if we're looking at a local area as opposed to a global population), humans releasing this 'species' (whatever it may be) into the wild/area, or maybe m could be the population added to the system as a byproduct of some other natural process (cells/molecules being broken down or decaying within a single biological system).

If $m < 0$, we could interpret this as a death rate or maybe even predation.

(b) We aim to find the equilibria in this production model. For a continuous model, we have an equilibrium when $\dot{x} = 0$. Hence,

$$0 = x(1 - x) + m - hx$$
$$= -x^2 + x(1 - h) + m$$
$$\Rightarrow x^*_{1,2} = \frac{-(1-h) \pm \sqrt{(1-h)^2 + 4m}}{-2}$$
$$= \frac{1}{2}(1 - h) \mp \frac{1}{2}\sqrt{1 - 2h + h^2 + 4m}$$

And so our equilibria are functions of the parameters h and m.

(c) We want biologically meaningful equilibria, meaning real solutions that are ≥ 0. As a first case, let's examine $x^* = 0 \Rightarrow (1 - h) = \pm\sqrt{1 - 2h + h^2 + 4m}$. Since $0 \leq h \leq 1$, we can take the positive root (since the LHS will be ≥ 0),

giving

$$1 - h = \sqrt{1 - 2h + h^2 + 4m}$$
$$1 - 2h + h^2 = 1 - 2h + h^2 + 4m$$
$$\Rightarrow m = 0$$

And so we expect $m = 0$ to give us an equilibrium at $x^* = 0$. By the same process as above, switching the equality to a greater than, we find that $m > 0$ gives us a positive equilibrium. Of course, we're interested in real solutions, meaning that we need

$$1 - 2h + h^2 + 4m \geq 0$$
$$\Rightarrow m \geq \tfrac{1}{2}h - \tfrac{1}{4}h^2 - \tfrac{1}{4}$$

for some harvest rate between 0 and 1. Hence, for a constant m, there will be some (high) harvest rates that present no equilibria. This condition above is actually a stronger condition on there being biologically meaningful equilibria, and we take this as the main bottleneck.

(d) Now to assess the stability of the criteria. For a continuous model, an equilibrium is stable if $f'(x^*) < 0$.

$$f'(x) = \frac{d}{dx}\dot{x}$$
$$= \frac{d}{dx}(x(1 - x) + m - hx)$$
$$= 1 - 2x - h$$

For the first root, $x_1^* = \tfrac{1}{2}[(1 - h) - \sqrt{1 - 2h + h^2 + 4m}]$, we find

$$f'(x_1^*) = 1 - 2\left(\tfrac{1}{2}(1 - h) - \tfrac{1}{2}\sqrt{1 - 2h + h^2 + 4m}\right) - h$$
$$= \sqrt{1 - 2h + h^2 + 4m} \geq 0$$

by the real conditions listed above. Hence the first root is never stable for any $m \geq \tfrac{1}{2}h - \tfrac{1}{4}h^2 - \tfrac{1}{4}$.
For the second root, $x_1^* = \tfrac{1}{2}[(1 - h) + \sqrt{1 - 2h + h^2 + 4m}]$,

$$f'(x_1^*) = 1 - 2\left(\tfrac{1}{2}(1 - h) + \tfrac{1}{2}\sqrt{1 - 2h + h^2 + 4m}\right) - h$$
$$= -\sqrt{1 - 2h + h^2 + 4m} \leq 0$$

by the same conditions above. Hence x_2^* is semi stable when $m \geq \tfrac{1}{2}h - \tfrac{1}{4}h^2 - \tfrac{1}{4}$ is an equality, and stable otherwise.

(e) A bifurcation diagram for varying values of m is shown in Figure 4.
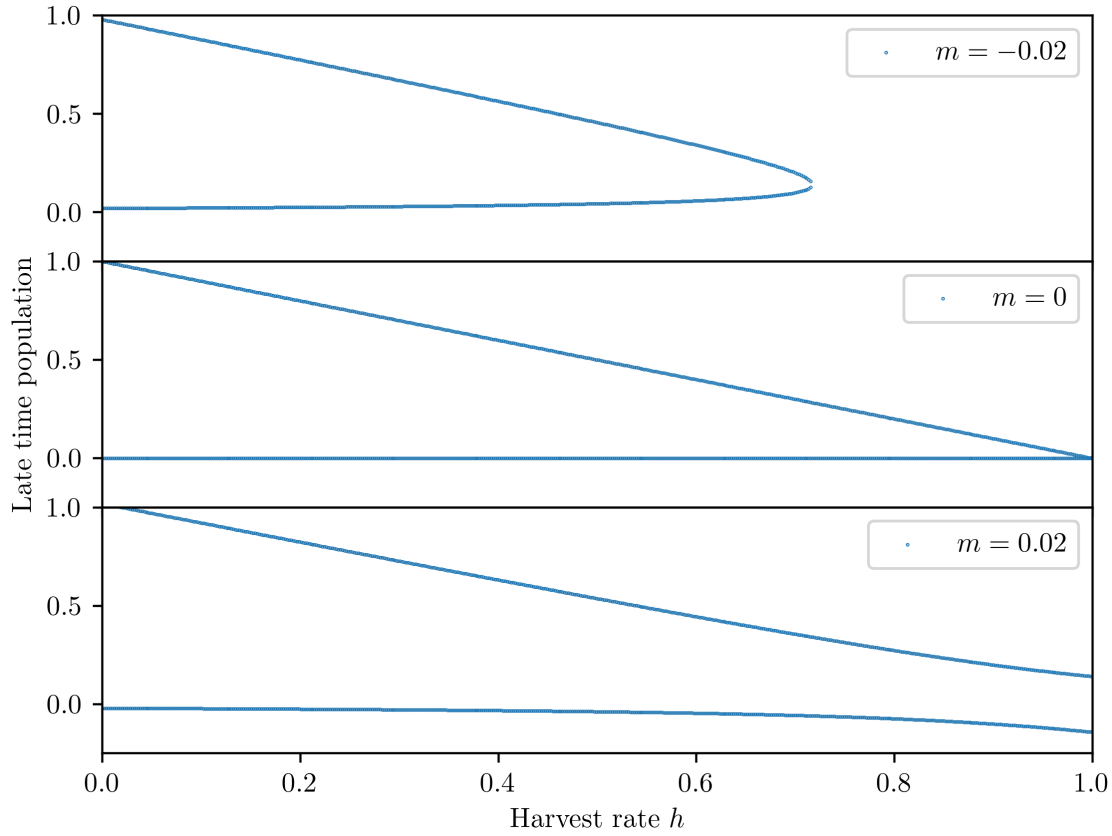
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Figure 4: *Top:* bifurcation diagram for $m = -0.02$. We see positive equilibria in the parameter space $0 \leq h \lesssim 0.7$. *Middle:* for $m = 0$, we see the aforementioned 0 equilibrium at all h, as well as an expected decreasing equilibrium with increasing harvest. *Bottom:* For positive m, we see that there is a family of equilibria that are always negative, and another that are always positive (which decreases non-linearly).

(f) We want an expression for the harvest that achieves the maximum sustainable yield. We expect the MSY should be an equilibrium, so we can define $Y = hx^*$ as the function to maximise. From before, we have the equilibria as

$$x^*_{1,2} = \tfrac{1}{2}(1 - h) \mp \tfrac{1}{2}\sqrt{1 - 2h + h^2 + 4m} \tag{3}$$

We'd previously shown that x^*_2 is the stable equilibrium, and so

$$
\begin{aligned}
Y &= hx^*_2 \\
&= h\left[\tfrac{1}{2}(1 - h) \mp \tfrac{1}{2}\sqrt{1 - 2h + h^2 + 4m}\right] \\
&= \frac{1}{2}\left[-h^2 + h + h\sqrt{1 - 2h + h^2 + 4m}\right]
\end{aligned}
$$

We want to maximise the value of Y with respect to h, and so we take the derivative giving

$$\frac{dY}{dh} = \frac{1}{2}\left[\frac{(h-1)h}{\sqrt{h^2 - 2h + 1 + 4m}} + \sqrt{h^2 - 2h + 1 + 4m} - 2h + 1\right]$$

Now we set this to 0 to find a stationary point (which will ideally be a maximum).

$$0 = \frac{(h-1)h}{\sqrt{h^2 - 2h + 1 + 4m}} + \sqrt{h^2 - 2h + 1 + 4m} - 2h + 1$$

$$= (h-1)h + h^2 - 2h + 1 + 4m - (2h-1)\sqrt{h^2 - 2h + 1 + 4m}$$

$$= 2h^2 - 3h + 1 + 4m - (2h-1)\sqrt{h^2 - 2h + 1 + 4m}$$

$$\Rightarrow \sqrt{h^2 - 2h + 1 + 4m} = \frac{2h^2 - 3h + 1 + 4m}{2h - 1}$$

$$= \frac{4m}{2h - 1} + h - 1$$

$$\Rightarrow h^2 - 2h + 1 + 4m = \frac{16m^2}{(2h-1)^2} + \frac{8mh}{2h-1} - \frac{8m}{2h-1} - 2h + h^2 + 1$$

$$\Rightarrow 4m(2h - 1) = \frac{16m^2}{2h - 1} + 8mh - 8m$$

$$8mh - 4m = \frac{16m^2}{2h - 1} + 8mh - 8m$$

$$\Rightarrow 4m(2h - 1) = 16m^2$$

$$2h - 1 = 4m$$

$$\Rightarrow h = 2m + \frac{1}{2}$$

To check if this is a maximum, we employ the first derivative test on the original (non-zero) derivative function dY/dh and note that as $h \to (2m + \frac{1}{2})^-$, $dY/dh \to 0^+$. Conversely, as $h \to (2m + \frac{1}{2})^+$, $dY/dh \to 0^-$. In both cases we came to this conclusion by plotting the solution for $m \geq 1/4$ (as in the non-complex conditions posed earlier) for sample values of h (e.g. $h = 2m + 1/3$, $h = 2m + 2/3$).

(g) Throughout this question, we've treated the parameter m as a constant, whereas the interpretations given in (a) lend themselves to being more realistic if m relies on the value of x. In the interpretation of death, we would expect $-x \leq m \leq 0$ rather than any negative number. Similarly (in the context of migration), we might expect $0 \leq m \leq 1$ such that mX represents the migration where X might be the global population. With that in mind, we can expect that this treatment of m might be a realistic model when $|m|$ is small compared to the value of x. For each of the respective scenarios listed above, we might consider changing the production model to

$$\dot{x} = x(1 - x + m) - hx, \qquad \text{or} \qquad \dot{x} = x(1 - x) + mX - hx$$