Question 1

Consider a fish population, experiencing proportional harvest at rate h:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - hN$$

(a) If managers keep the harvest rate consistent for a long period of time, what will be the equilibrium population N^*?

(b) What level of harvest is "unsustainable"? That is, what values of h will drive the population to extinction?

(c) If the yield of the fishery is $Y = hN$, use either calculus or simulations to calculate h_{MSY}: the harvest rate that maximises the sustainable yield.

(d) In a programming language of your choice, simulate the evolution of a population with the following parameter values:

$$r = 1.1; N(0) = 10;\ K = 100;\ h = 0.5$$

Produce a labelled plot of $N(t)$ for $0 \leq t \leq 100$.

Question 2

Consider two sessile marine species (i.e., species that do not move as adults, such as barnacles) competing for limited space along a coastline (Figure 1).

***Figure 1**: Smaller barnacles* (Chthamalus stellatus) *and larger limpets* (Patella vulgata) *competing for habitat space in the intertidal zone near Newquay, Cornwall, England. (Source: Mark A. Wilson; Wikimedia)*

Species 1 is a dominant competitor, which means it can supplant species 2 from any space it occupies. Let p_1 be the fraction of the sites occupied by this species, and let the two species have equal per-capita mortality rate m and birth rate b_1. The dynamics of species 1's abundance are:

$$\frac{dp_1}{dt} = b_1 p_1 (1 - p_1) - m p_1.$$

The first term on the RHS reflects the fact that a recently born individual can only survive if it is fortunate enough to find space that is unoccupied by conspecifics $(1 - p_1)$. The second species is competitively subordinate, and therefore cannot occupy space that is taken up by either its own conspecifics, or by the dominant competitor:

$$\frac{dp_2}{dt} = b_2 p_2 (1 - p_1 - p_2) - m p_2 - b_1 p_1 p_2.$$

The final term on the RHS in this equation reflects additional mortality of species 2, when new offspring from the dominant competitor displace existing individuals. Note that in these equations, the abundance of species 1 is unaffected by species 2.

(a) Solve for the equilibrium of the two species, p_1^* and p_2^*, in sequence. How much of the available space in the ecosystem is unoccupied by either species at equilibrium? That is, what is $1 - p_1^* - p_2^*$?

(b) Under what conditions on m and b_i will both species persist (i.e., will $p_1 > 0$ and $p_2 > 0$)? There should be two conditions. Try to give a one-sentence ecological interpretation of each condition.

Answers: Question 1

Consider a fish population, experiencing proportional harvest at rate h:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - hN$$

(e) If managers keep the harvest rate consistent for a long period of time, what will be the equilibrium population N^*?

Assume $N \neq 0$ and solve for N^* when $\frac{dN}{dt} = 0$:

$$0 = r\left(1 - \frac{N^*}{K}\right) - h$$

$$1 - \frac{N^*}{K} = \frac{h}{r}$$

$$\boldsymbol{N^* = K\left(1 - \frac{h}{r}\right)}$$

(f) What level of harvest is "unsustainable"? That is, what values of h will drive the population to extinction?

Solve for h where $N^* = 0$:

$$N^* = K\left(1 - \frac{h}{r}\right) = 0$$

$$1 - \frac{h}{r} = 0$$

$$h = r$$

This makes intuitive sense, since r is the most rapid per-capita growth rate. When the per-capita harvest rate h exceeds this value, the population can never grow.

(g) If the yield of the fishery is $Y = hN$, use either calculus or simulations to calculate h_{MSY}: the harvest rate that maximises the sustainable yield.

The sustainable yield for a given harvest rate is $Y = hN^*$. By differentiating yield with respect to the harvest rate, we can determine the point at which yield is maximised:

$$\frac{dY}{dh} = \frac{d}{dh}\left[hK\left(1 - \frac{h}{r}\right)\right] = 0$$

$$K - \frac{2h}{r} = 0$$

$$h_{\mathrm{MSY}} = \frac{rK}{2}$$

(h) In a programming language of your choice, simulate the evolution of a population with the following parameter values:

$$r = 1.1; N(0) = 10;\ K = 100;\ h = 0.5$$

Produce a labelled plot of $N(t)$ for $0 \leq t \leq 100$.

In Matlab, the code is:

```
function PreQuiz_Q1h()

global r N0 K h

r = 1.1; % The per-capita growth rate
N0 = 10; % Initial population abundance
K = 100; % Carrying capacity
h = 0.5; % Per-capita harvest rate

[T,N] = ode45(@logistic_ode,[0 100],N0);

figure(1), clf, hold on, box on
FS = 22;

plot(T,N,'linewidth',2)
ylim([0 max(N)*1.1])
ylabel('Abundance','fontsize',FS,'interpreter','latex')
xlabel('Time','fontsize',FS,'interpreter','latex')

function dndt = logistic_ode(t,n)
global r N0 K h

dndt = r.*n.*(1-n/K)-h.*n;
```

Question 2

Consider two sessile marine species (i.e., species that do not move as adults, such as barnacles) competing for limited space along a coastline (Figure 1).

Species 1 is a dominant competitor, which means it can supplant species 2 from any space it occupies. Let p_1 be the fraction of the sites occupied by this species, and let the two species have equal per-capita mortality rate m and birth rate b_1. The dynamics of species 1's abundance are:

$$\frac{dp_1}{dt} = b_1 p_1 (1 - p_1) - m p_1.$$

The first term on the RHS reflects the fact that a recently born individual can only survive if it is fortunate enough to find space that is unoccupied by conspecifics $(1 - p_1)$. The second species is competitively subordinate, and therefore cannot occupy space that is taken up by either its own conspecifics, or by the dominant competitor:

$$\frac{dp_2}{dt} = b_2 p_2 (1 - p_1 - p_2) - m p_2 - b_1 p_1 p_2.$$

The final term on the RHS in this equation reflects additional mortality of species 2, when new offspring from the dominant competitor displace existing individuals. Note that in these equations, the abundance of species 1 is unaffected by species 2.

(c) Solve for the equilibrium of the two species, p_1^* and p_2^*, in sequence. How much of the available space in the ecosystem is unoccupied by either species at equilibrium? That is, what is $1 - p_1^* - p_2^*$?

The abundance of species 1 is unaffected by species 2, and its equilibrium can therefore be solved by itself. We assume that $p_1^* \neq 0$:

$$\frac{dp_1}{dt} = 0 = b_1 p_1 (1 - p_1) - m p_1$$

$$m = b_1 (1 - p_1)$$

$$p1^* = 1 - \frac{m}{b_1}$$

Given this abundance for species 1, the equilibrium for species 2 is (assuming $p_2^* \neq 0$):

$$\frac{dp_2}{dt} = 0 = b_2 (1 - p_1^* - p_2) - m - b_1 p_1^*$$

$$m + b_1 \left(1 - \frac{m}{b_1}\right) = b_2 \left(\frac{m}{b_1} - p_2\right)$$

$$p_2^* = \frac{m}{b_1} - \frac{b_1}{b_2}$$

The amount of unoccupied space at equilibrium is:

$$s = 1 - p_1^* - p_2^*$$

$$s = 1 - \left(1 - \frac{m}{b_1}\right) - \left(\frac{m}{b_1} - \frac{b_1}{b_2}\right)$$

$$s = \frac{b_1}{b_2}$$

(d) Under what conditions on m and b_i will both species persist (i.e., will $p_1 > 0$ and $p_2 > 0$)? There should be two conditions. Try to give a one-sentence ecological interpretation of each condition.

The first species will persist where:

$$1 - \frac{m}{b_1} > 0$$

$$b_1 > m$$

Which follows the same logic as Q1(f).

The second species will persist where:

$$\frac{m}{b_1} - \frac{b_1}{b_2} > 0$$

$$b_2 > b_1 \left(\frac{b_1}{m}\right)$$

If the first species is persisting, then we already know that $b_1 > m$, and hence that $\frac{b_1}{m} > 1$. Thus the condition above demands that $b_2 > b_1$ at the very least.

Our simple ecological interpretation could therefore be that (1) the dominant species must have a per-capita birth rate larger than its per-capita mortality rate, and that (2) the subordinate species must be better at reproducing than the dominant species. This is a common finding in multispecies ecological theory: for two species to coexist, they must each be better at doing something. In this case, one is better at competing, the other is better at reproducing.