Control of structured populations by harvest

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ABSTRACT

It has long been recognized that demographic structure within a population can significantly affect the likely outcomes of harvest. Many studies have focussed on equilibrium dynamics and maximization of the value of the harvest taken. However, in some cases the management objective is to maintain the population at a abundance that is significantly below the carrying capacity. Achieving such an objective by harvest can be complicated by the presence of significant structure (age or stage) in the target population. In such cases, optimal harvest strategies must account for differences among age- or stage-classes of individuals in their relative contribution to the demography of the population. In addition, structured populations are also characterized by transient non-linear dynamics following perturbation, such that even under an equilibrium harvest, the population may exhibit significant momentum, increasing or decreasing before cessation of growth. Using simple linear time-invariant models, we show that if harvest levels are set dynamically (e.g., annually) then transient effects can be as or more important than equilibrium outcomes. We show that appropriate harvest rates can be complicated by uncertainty about the demographic structure of the population, or limited control over the structure of the harvest taken.

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1. Introduction

Age- or stage-structure has long been included in the modelling of harvested populations, particularly fish and forests (Getz and Haight, 1989). Early models were linear and deterministic (Beddington and Taylor, 1973; Doubleday, 1975; Rorres and Fair, 1975), progressing later to models that included density dependence (Reed, 1980; Getz, 1980; Jensen, 1996, 2000), seasonal effects (Getz, 1980), environmental effects on vital rates (Milner-Gulland, 1994; Pascual et al., 1997; Xie et al., 1999), and spatial structure (Brooks and Lebreton, 2001). Optimization of harvest is usually carried out with the purpose of maximizing sustainable yield, and so equilibrium dynamics are a common focus.

As more complicated models have been developed, it has become common to simulate and observe dynamics under different scenarios as an alternative to formal optimization. Other characteristics of harvest strategies have been considered, such as variance in yield (Milner-Gulland, 1994; Sæther et al., 2001), harvest structure (Ginsberg and Milner-Gulland, 1994; Jensen, 1996), population structure (Milner-Gulland, 1994; Jensen, 1996, 2000; Xie et al., 1999), abundance (Ginsberg and Milner-Gulland, 1994; Milner-Gulland, 1994; Pascual et al., 1997; Xie et al., 1999; Sæther et al., 2001; Mayaka et al., 2004), and transient dynamics (Jensen, 1996).

Only a small number of studies have attempted to optimize harvest when the initial demographic structure of the population is markedly different from the equilibrium structure. In such cases, transient dynamics are of particular importance

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(Fox and Gurevitch, 2000). When sequential harvest decisions are made over time, transient dynamics may have a large influence on observed population change between decisions, and so must be accounted for during the decision-making process. Harley and Manson (1981) were the first to discuss how a structured population might be most efficiently brought to equilibrium in a finite number of steps. A small number of other studies (Stocker, 1983; Milner-Gulland, 1997; Hauser et al., 2005) have used stochastic dynamic programming to determine the optimal harvest decision for any possible initial population structure and abundance. However, these studies have divided the target population into only a small number of classes, and have generally assumed complete knowledge of the structure of the population at the time of the harvest. While modelling a small number of classes may have been adequate for these studies, incorporating more classes is likely to be limited by data constraints and the computational method.

Even in the absence of dynamic decision-making, population momentum can be used as a measure of the long-term effect of transient dynamics. It was first noted by Keyfitz (1971), but has only recently been discussed in the context of population management (Caswell, 2001; Koons et al., 2005a,b). While a management action such as harvest can reset the asymptotic growth rate of a population to replacement only, transient dynamics may cause the population to grow or decline before it reaches equilibrium.

In this paper, we will explore the harvest of a structured population with the purpose of control. Structured models have rarely been used to optimize harvest for control (but see Brooks and Lebreton, 2001). We assume that the desired level of control maintains the population at a steady abundance well below carrying capacity, so that a linear (density independent) matrix model is appropriate. This model has been considered frequently in the past (Beddington and Taylor, 1973; Doubleday, 1975; Rorres and Fair, 1975) but usually with the purpose of maximizing yield under equilibrium conditions. Instead we will consider the structure of the harvest taken, the structure and abundance of the population, and the possible effects of population momentum. We discuss our results in the context of uncertainty, outlining potential challenges in meeting the control objective (*sensu* Hunter and Runge, 2004).

2. The model

For the unharvested population, we use the matrix model

$$\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t,$$

where $\mathbf{N}_t$ is a vector giving the number of individuals in each stage at time t and $\mathbf{A}$ is the population projection matrix (Caswell, 2001). We will assume that $\mathbf{A}$ is primitive (aperiodic), so that it has a real positive eigenvalue λ which is greater in magnitude than all other eigenvalues. This eigenvalue gives the asymptotic growth rate and we will assume that the population is growing so that $\lambda > 1$.

The associated left and right eigenvalues $\mathbf{v}$ and $\mathbf{w}$ are strictly positive and give the stage-specific reproductive values and the stable stage distribution, respectively, such that

$$\mathbf{v}'\mathbf{A} = \lambda \mathbf{v}'. \tag{1}$$

$$\mathbf{A}\mathbf{w} = \lambda \mathbf{w}. \tag{2}$$

Note that for a given λ, the vectors $\mathbf{v}$ and $\mathbf{w}$ are uniquely defined only to a multiplicative constant. That is, for any solution $\mathbf{v}$, a scalar multiple $c\mathbf{v}$ of the vector is also a solution and likewise for $\mathbf{w}$.

The stable stage distribution $\mathbf{w}$ indicates the relative proportion of each stage-class in the population over the long term. The reproductive value of each stage-class (Fisher, 1958) indicates the relative contribution of that age-class to future population growth. It is customary to set $v_1 = 1$ so that the reproductive value of an individual in an advanced stage is measured relative to an individual in the first stage. Reproductive value has previously been shown to influence the optimal harvest of populations with demographic structure (MacArthur, 1960; Brooks and Lebreton, 2001).

We will introduce harvest to our structured matrix model in two ways: constant and proportional harvest. Under constant harvest, we remove a number of individuals from one or more stage-classes at each time t:

$$\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t - \mathbf{Y}_t, \tag{3}$$

where the vector $\mathbf{Y}_t$ gives the number of individuals removed from each stage-class.

Under proportional harvest, we remove a proportion of the individuals from stage-classes at each time t:

$$\mathbf{N}_{t+1} = (\mathbf{I} - \mathbf{H}_t)\mathbf{A}\mathbf{N}_t, \tag{4}$$

where $\mathbf{I}$ is the identity matrix of appropriate dimension, and $\mathbf{H}_t = \mathrm{diag}(h_{1,t}, h_{2,t}, \ldots)$ gives the proportion $h_{i,t}$ of individuals removed from stage i at time t.

3. Equilibrium condition: constant harvest

When the population is in equilibrium, it is neither growing nor declining. When our objective is to maintain the population at a particular abundance, the equilibrium condition indicates what this abundance can be. We find the equilibrium condition for the model with constant harvest by removing the time dependence in Eq. (3):

$$\mathbf{N}^{\mathrm{eq}} = \mathbf{A}\mathbf{N}^{\mathrm{eq}} - \mathbf{Y}^{\mathrm{eq}}. \tag{5}$$

Rearrangement of this equation gives the steady stage-structured population state

$$\mathbf{N}^{\mathrm{eq}} = (\mathbf{A} - \mathbf{I})^{-1}\mathbf{Y}^{\mathrm{eq}}. \tag{6}$$

Since $\lambda \neq 1$ then the inverse $(\mathbf{A} - \mathbf{I})^{-1}$ exists, but we must also ensure that all elements of $\mathbf{N}^{\mathrm{eq}}$ are nonnegative.

Now we examine the approach to this equilibrium when the same stage-specific harvest is removed at each time step. Subtracting (5) from (3) gives

$$\mathbf{N}_t - \mathbf{N}^{\mathrm{eq}} = \mathbf{A}(\mathbf{N}_{t-1} - \mathbf{N}^{\mathrm{eq}}),$$

and we can substitute this expression repeatedly into itself to see that

$$\mathbf{N}_t - \mathbf{N}^{\mathrm{eq}} = \mathbf{A}^k(\mathbf{N}_{t-k} - \mathbf{N}^{\mathrm{eq}}) \quad \text{for } k = 1, 2, \ldots, t.$$

Specifically when $k = t$,

$$\mathbf{N}_t - \mathbf{N}^{eq} = \mathbf{A}^t(\mathbf{N}_0 - \mathbf{N}^{eq}).$$

Since $\mathbf{A}$ is primitive, then we can approximate $\mathbf{A}^t$ by $\lambda^t \mathbf{w} \mathbf{v}'$ for large t (Seneta, 1980, p. 9). To do so we must choose eigenvectors $\mathbf{v}$ and $\mathbf{w}$ so that $\mathbf{v}' \mathbf{w} = 1$. Thus in the long-term

$$\mathbf{N}_t - \mathbf{N}^{eq} \approx [\mathbf{v}'(\mathbf{N}_0 - \mathbf{N}^{eq})]\lambda^t \mathbf{w}.$$

Since λ^t grows unbounded, then the population will approach a steady state over time only if

$$\mathbf{v}'(\mathbf{N}_0 - \mathbf{N}^{eq}) = 0 \quad \text{or} \quad \mathbf{v}'\mathbf{N}_0 = \mathbf{v}'\mathbf{N}^{eq}. \tag{7}$$

That is, the total reproductive value of the equilibrium population must be equal to the total reproductive value of the initial population. Note that the reproductive value v_i of an individual in stage i is fixed, but the total reproductive value of the population depends on the size and structure of the population.

The left eigenvector of $\mathbf{A}$ satisfies (1), from which we can see that

$$\frac{1}{\lambda - 1}\mathbf{v}'(\mathbf{A} - \mathbf{I}) = \mathbf{v}'. \tag{8}$$

Combining Eqs. (6)–(8) gives

$$\mathbf{v}'\mathbf{N}_0 = \mathbf{v}'\mathbf{N}^{eq} = \frac{1}{\lambda - 1}\mathbf{v}'(\mathbf{A} - \mathbf{I})\mathbf{N}^{eq} = \frac{1}{\lambda - 1}\mathbf{v}'(\mathbf{A} - \mathbf{I})(\mathbf{A} - \mathbf{I})^{-1}\mathbf{Y}^{eq}$$

$$= \frac{1}{\lambda - 1}\mathbf{v}'\mathbf{Y}^{eq}$$

$$\mathbf{v}'\mathbf{Y}^{eq} = \mathbf{v}'[\mathbf{N}_0(\lambda - 1)]. \tag{9}$$

Now $\lambda - 1$ is the asymptotic proportional increase in unharvested population size in one time step, e.g. if $\lambda = 1.1$ then the population will increase by 10% per time step in the long-term. The total reproductive value of these "surplus" individuals in the initial population $\mathbf{N}_0$ must be equal to the total reproductive value of the individuals to be harvested. This ensures that under a repeated harvest of $\mathbf{Y}^{eq}$ each time step, the population will approach steady state $\mathbf{N}^{eq}$.

It is worth noting that if we were to ignore stage-structure in the population and model only the total population abundance over time then

$$N_{t+1} = \lambda N_t - Y_t \tag{10}$$

approximates the structured model well when the stage-structure of the population is proportional to $\mathbf{w}$. For this scalar model, the equilibrium condition is

$$Y^{eq} = (\lambda - 1)N^{eq}. \tag{11}$$

Again the relationship is depends on the proportional surplus $\lambda - 1$ but in the absence of structure, reproductive value is meaningless. There is only one harvest rate at which the population can be maintained in equilibrium. When population structure is apparent, then different combinations of stage-classes can be removed that all achieve equilibrium in the long term. These combinations are determined by the reproductive value of each stage-class, and the initial population structure and abundance $\mathbf{N}_0$.
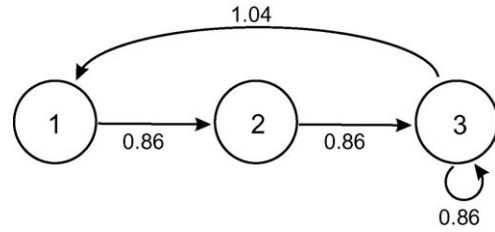

Fig. 1 – Life-cycle diagram of the 3-stage example population. Nodes represent 1-year-olds, 2-year-olds and adults (of at least 3 years of age); arrows pointing left-to-right give stage-specific survival rates; arrow pointing right-to-left gives stage-specific fertility.

Example. We will consider a simple model of a growing population with three stage-classes. Individuals are classified as 1-year-olds, 2-year-olds or adults (who are 3 or more years of age). Fig. 1 shows the life-cycle diagram for this population based on pre-breeding census (Caswell, 2001). The projection matrix $\mathbf{A}$ can be constructed directly from the life-cycle diagram:

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & 1.04 \\ 0.86 & 0 & 0 \\ 0 & 0.86 & 0.86 \end{bmatrix}. \tag{12}$$

Given $\mathbf{A}$, we can calculate the dominant eigenvalue and corresponding eigenvectors:

$$\lambda = 1.309, \quad \mathbf{v} = [1 \quad 1.522 \quad 2.317]', \quad \mathbf{w} = [0.203 \quad 0.134 \quad 0.256]'.$$

Note that the eigenvectors are not unique and that any scalar multiple of $\mathbf{v}$ and $\mathbf{w}$ above also satisfy the eigenvector Eqs. (1) and (2). We selected the combination above so that $v_1 = 1$ and $\mathbf{v}'\mathbf{w} = 1$.

The dominant eigenvalue indicates that in the long term, the unharvested population will grow by 31% each time step. Normalizing $\mathbf{w}$ shows that the projected population will eventually be composed of 34.3% 1-year-olds, 22.5% 2-year-olds and 43.2% adults. Reproductive value increases with age, so the removal of an adult by harvest could potentially have a greater impact on population growth than the removal of a 1-year-old by harvest (we note that the current value of an individual from a particular age-class is partially a function of whether or not the population is growing; Mertz, 1971) .

Assume first that the initial population is composed of 1000 individuals under the stable stage distribution of the unharvested population, i.e. $\mathbf{N}_0 = [343 \quad 225 \quad 432]'$. Then the equilibrium condition (9) becomes

$$[1 \quad 1.522 \quad 2.317]\begin{bmatrix} Y_1^{eq} \\ Y_2^{eq} \\ Y_3^{eq} \end{bmatrix} = [1 \quad 1.522 \quad 2.317]\begin{bmatrix} 343 \\ 225 \\ 432 \end{bmatrix}(1.309 - 1)$$

$$Y_1^{eq} + 1.522Y_2^{eq} + 2.317Y_3^{eq} = 520.863, \tag{13}$$

where Y_i^{eq} is the number of individuals in stage i harvested during each time step. That is, a particular linear combina-

tion of the harvest taken from each stage-class must be held at a constant. The constant (520.863) is a function of initial population size, and the harvest taken from each age-class is weighted by the reproductive value of individuals in that age-class. For biological realism we constrain $Y_i^{eq} \geq 0$ for all stage-classes i. We must also ensure that $N_i^{eq} \geq 0$ for all stage-classes. In this example all elements of $(\mathbf{A} - \mathbf{I})^{-1}$ are non-negative, so Eq. (6) indicates that $N_i^{eq} \geq 0$ holds whenever $Y_i^{eq} \geq 0$.

We plot the values of Y_1^{eq}, Y_2^{eq} and Y_3^{eq} that satisfy Eq. (13) in Fig. 2(i). They form a plane in three-dimensional space. A repeated structured harvest that falls above the plane will cause the population to decline over time, while a structured harvest that falls below the plane will allow the population to continue growing (at a rate slower than λ) over time. A structured harvest that falls on the plane, when taken repeatedly from the initial population $\mathbf{N}_0 = [343 \quad 225 \quad 432]'$, will cause the population to stabilize with some stage-structure and abundance, specified in Eq. (6).

For example if we take an equilibrium harvest and only 1-year-olds are removed from the population, then we choose

$$\mathbf{Y}^{eq} = [521 \quad 0 \quad 0]', \quad \text{so that} \quad \mathbf{N}^{eq} = [116 \quad 100 \quad 612]'.$$

Instead we might target 2-year-olds for harvest, but expect that we will incidentally remove 10% as many 1-year-olds and 10% as many adults as we do 2-year-olds. We substitute $(Y_1^{eq}, Y_2^{eq}, Y_3^{eq}) = (y, 10y, y)$ into Eq. (13) and solve to find that $y = 28.0989$ and so

$$\mathbf{Y}^{eq} = [28 \quad 281 \quad 28]', \quad \text{and} \quad \mathbf{N}^{eq} = [452 \quad 108 \quad 462]'.$$

Note that the harvest taken when removing only 1-year-olds is much larger than that of removing mostly 2-year-olds (with about 8% each of 1-year-old and adults in the harvest). The equilibrium population size is different under each approach (828 and 1022, respectively), and so is the stage-structure.

In Fig. 3(i) we plot population trajectories for the initial population $\mathbf{N}_0 = [343 \quad 225 \quad 432]'$, repeatedly subjected to different harvests that satisfy the equilibrium condition (13). The population does reach an equilibrium size over time in cases (c)–(e). However in cases (a) and (b) the population does not reach an equilibrium abundance and instead increases unbounded, even though the harvests taken in these cases satisfy condition (13). This is because in some time steps the number of individuals to be removed from some stage-class i at time t is larger than the number of individuals existing in that stage-class at that time. In our constant harvest model as given in Eq. (3), this causes the number of individuals in that class $N_{i,t+1}$ to be negative. Since this is not biologically feasible, we have assumed that $N_{i,t+1} = 0$ and that the full harvest $Y_{i,t}$ is not taken. As a consequence, the large reproductive value present in another stage-class is not counter-acted by negative individuals in stage i and so the population grows unbounded. Therefore, we require extra constraints to obtain biologically feasible equilibrium harvest. If we instead use proportional harvest (as in the next section), then this issue will not arise.

Now, let us consider a different initial population. We keep the same abundance of 1000, but change the structure by set-
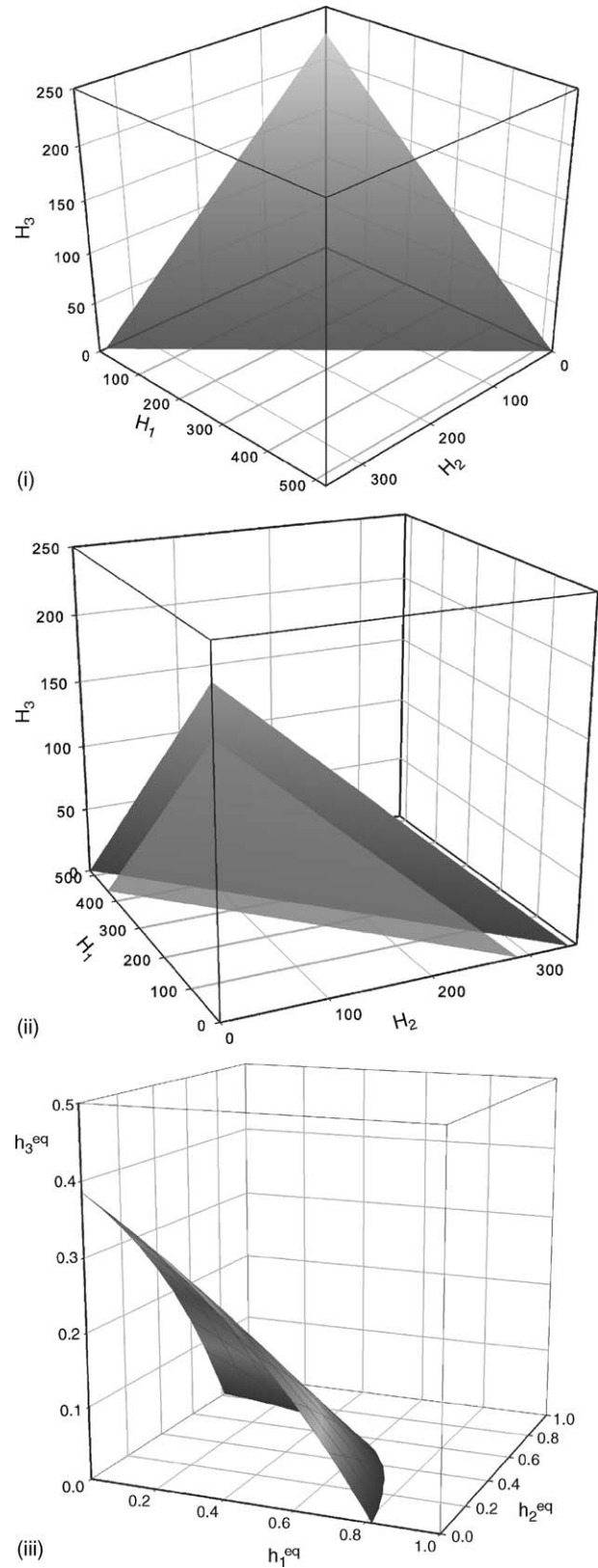

(i)

(ii)

(iii)

Fig. 2 – Stage-specific harvest combinations that satisfy the equilibrium condition for the example: (i) for constant harvest with $\mathbf{N}_0 = [343 \quad 225 \quad 432]'$ (see Eq. (13)), (ii) for constant harvest with $\mathbf{N}_0 = [500 \quad 300 \quad 200]'$ (see Eq. (14)) and (iii) for proportional harvest with any initial conditions (see Eq. (17)).
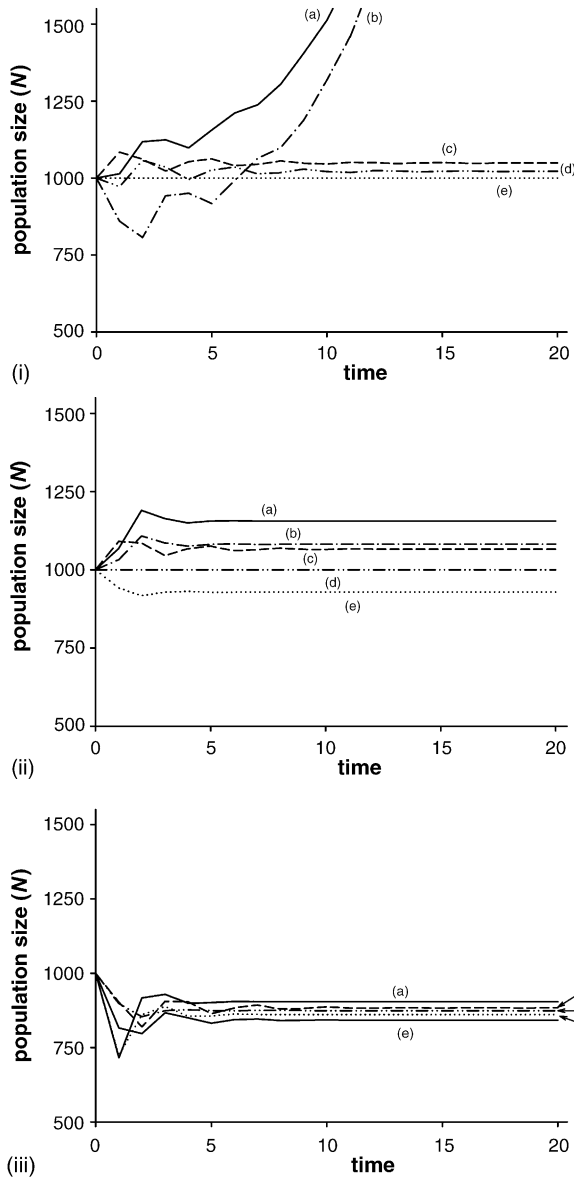
Fig. 3 – Total population size over time under a number of repeated harvest strategies. In plot (i) the initial population is $N_0 = [343 \quad 225 \quad 432]'$ with constant harvest levels: (a) $Y = [0 \quad 342 \quad 0]'$, (b) $Y = [521 \quad 0 \quad 0]'$, (c) $Y = [0 \quad 0 \quad 225]'$, (d) $Y = [28 \quad 281 \quad 28]'$, (e) $Y = [106 \quad 70 \quad 133]'$. In plot (ii) the initial population is $N_0 = [343 \quad 225 \quad 432]'$ with proportional harvest levels: (a) $(h_1, h_2, h_3) = (0, 0.8180, 0)$, (b) $(h_1, h_2, h_3) = (0.0699, 0.6992, 0.0699)$, (c) $(h_1, h_2, h_3) = (0, 0, 0.3862)$, (d) $(h_1, h_2, h_3) = (0.2360, 0.2360, 0.2360)$, (e) $(h_1, h_2, h_3) = (0.8180, 0, 0)$. In plot (iii) the initial population is $N_0 = [500 \quad 300 \quad 200]'$ with proportional harvest levels: (a) $(h_1, h_2, h_3) = (0, 0.8180, 0)$, (b) $(h_1, h_2, h_3) = (0, 0, 0.3862)$, (c) $(h_1, h_2, h_3) = (0.8180, 0, 0)$, (d) $(h_1, h_2, h_3) = (0.0699, 0.6992, 0.0699)$, (e) $(h_1, h_2, h_3) = (0.2360, 0.2360, 0.2360)$.

ting $N_0 = [500 \quad 300 \quad 200]'$. Then the equilibrium condition becomes

$$Y_1^{eq} + 1.522Y_2^{eq} + 2.317Y_3^{eq} = 438.672. \tag{14}$$

Again the harvest taken from each stage-class must satisfy a linear constraint, but the constant (438.672) is smaller than for the previous initial population. This is because the total reproductive value of the initial population is smaller, and so fewer individuals need to be harvested to reach equilibrium. If we plot the combinations of Y_1^{eq}, Y_2^{eq} and Y_3^{eq} that satisfy this equilibrium condition (14), we see that they form a plane that is parallel to the plane created by condition (13) for $N_0 = [343 \quad 225 \quad 432]'$ (Fig. 2(ii)). The smaller constant 438.672 means that the intercepts with the axes are also smaller.

4. Equilibrium condition: proportional harvest

We obtain the equilibrium condition under proportional harvest by removing the time dependence in Eq. (4):

$$\mathbf{N}^{eq} = (\mathbf{I} - \mathbf{H}^{eq})\mathbf{A}\mathbf{N}^{eq}. \tag{15}$$

Note that this is an eigenvalue equation in the form of (2). We wish to find harvest $\mathbf{H}^{eq}$ such that $(\mathbf{I} - \mathbf{H}^{eq})\mathbf{A}$ has a dominant eigenvalue of 1. That is, we set the long-term growth rate of the population to 1, replacement only. Then the steady population structure is given by the corresponding right eigenvector $\mathbf{N}^{eq}$.

If the initial population is given by vector $\mathbf{N}_0$, then we can find the equilibrium population size after repeated proportional harvests $\mathbf{H}^{eq}$ by using the result from Seneta (1980, p. 9):

$$\mathbf{N}^{eq} = (\mathbf{v}_H' \mathbf{N}_0)\mathbf{w}_H, \tag{16}$$

where $\mathbf{v}_H, \mathbf{w}_H$ are the left and right eigenvectors of $(\mathbf{I} - \mathbf{H}^{eq})\mathbf{A}$ corresponding to eigenvalue 1, normalized so that $\mathbf{v}_H' \mathbf{w}_H = 1$.

Example. Again, we consider the example age-structured population depicted in Fig. 1. We need to find $\mathbf{H}^{eq}$ such that the dominant eigenvalue of $(\mathbf{I} - \mathbf{H}^{eq})\mathbf{A}$ is 1. Then $\mathbf{H}^{eq}$ is the solution to

$$|(\mathbf{I} - \mathbf{H}^{eq})\mathbf{A} - \mathbf{I}| = 0.$$

Substituting the matrix $\mathbf{A}$ from the previous example gives

$$\begin{vmatrix} -1 & 0 & (1-h_1^{eq})1.04 \\ (1-h_2^{eq})0.86 & -1 & 0 \\ 0 & (1-h_3^{eq})0.86 & (1-h_3^{eq})0.86 - 1 \end{vmatrix} = 0,$$

which can be simplified to

$$h_3^{eq} = 1 - \frac{1}{0.86 + 1.04 \times 0.86^2 (1-h_1^{eq})(1-h_2^{eq})}. \tag{17}$$

The combinations of $h_1^{eq}, h_2^{eq}, h_3^{eq}$ that satisfy this equilibrium condition form a curved surface in three-dimensional space,

shown in Fig. 2(iii). Note that the equilibrium condition is not dependent on the initial population $\mathbf{N}_0$.

If we take an equilibrium proportional harvest and only 1-year-olds are removed from the population, then we choose $(h_1^{eq}, h_2^{eq}, h_3^{eq}) = (0.8180, 0, 0)$. That is, 82% of 1-year-olds must be removed each year to bring the population to equilibrium. Substituting this harvest strategy into (15) gives

$$\mathbf{N}^{eq} = \begin{bmatrix} 0 & 0 & 0.1893 \\ 0.86 & 0 & 0 \\ 0 & 0.86 & 0.86 \end{bmatrix} \mathbf{N}^{eq}.$$

We find that the left and right eigenvectors of this matrix $(\mathbf{I} - \mathbf{H}^{eq})\mathbf{A}$ are

$$\mathbf{v}_H = [1 \quad 1.1628 \quad 1.3521]' \quad \text{and}$$

$$\mathbf{w}_H = [0.1094 \quad 0.0941 \quad 0.5778]',$$

where we chose this specific eigenvector pair so that $v_1 = 1$ and $\mathbf{v}_H'\mathbf{w}_H = 1$.

Now the equilibrium population size and structure depends on the initial population. If the initial population is $\mathbf{N}_0 = [343 \quad 225 \quad 432]'$ then from (16)

$$\mathbf{N}^{eq} = [130 \quad 112 \quad 687]',$$

and if the initial population is $\mathbf{N}_0 = [500 \quad 300 \quad 200]'$ then

$$\mathbf{N}^{eq} = [122 \quad 105 \quad 647]'.$$

Fig. 3(ii and iii) show the approach to equilibrium for the above examples, and a number of other equilibrium proportional harvest strategies. When the initial population has the equilibrium structure of the unharvested population, then the eventual total population size may be larger or smaller than initial population size, depending on the stages targeted in the harvest. When the initial population is $\mathbf{N}_0 = [500 \quad 300 \quad 200]'$ then the equilibrium population size appears to be smaller than the initial population size under all harvest strategies.

5. Transient dynamics and population momentum

We have seen in our example that given an initial population of 1000 individuals, different harvest strategies can produce different short-term and long-term results even if all harvest strategies involve the repetition of a harvest that satisfies the equilibrium condition. Population momentum is one measure of the long-term outcome of managing using the equilibrium condition. It is defined as

$$M = \lim_{t \to \infty} \frac{|\mathbf{N}_t|}{|\mathbf{N}_0|},$$

where $|\mathbf{N}|$ denotes the total number of individuals in $\mathbf{N}$ (Caswell, 2001). This is the ratio of the long-term population size to the initial population size. For example if $M = 1.1$, then the long-term population size is 10% larger than the initial

population size. Momentum arises when the initial population structure is different from the long-term or equilibrium population structure. The "unbalanced" number of individuals in the reproductive stages mean that the short-term growth rate will be higher or lower than the long-term growth rate of 1, leading to population growth or decline before equilibrium is reached.

Population momentum M does not completely describe how the population is likely to respond in the short-term. In Fig. 3(i), we see that in case (c) (where 225 adults are harvested each time step) and case (d) (where 28 1-year-olds, 281 2-year-olds and 28 adults are harvested), the population reaches an equilibrium population that is larger in abundance than the initial population of 1000 individuals. However during the first time step, the population increases in case (c) and declines in case (d). In case (b), the population initially declines even more dramatically, only to grow unbounded in later time steps.

In case (d), the population eventually reaches steady state $\mathbf{N}^{eq} = [452 \quad 109 \quad 462]'$. The initial population has proportionally fewer adults than this equilibrium structure, and so in the first year the population decreases slightly due to a deficiency in reproduction. During the second year, the high proportion of 2-year-olds in the initial population have become adults, creating surplus reproduction and population increase. This year-to-year restructuring of the population creates a long-term population abundance that is larger than the initial 1000 individuals (momentum $M = 1.02$). In case (c), the population initially has a high proportion of breeding adults compared to the equilibrium population, causing an increase, and the same process of damped oscillations occur over time (momentum $M = 1.05$).

Specifying a target population momentum might be considered an appropriate objective in the context of population control (see the Appendix A for an outline of this problem). However, we have seen in the example above that transient dynamics can have large influence on population abundance when the stage-structure of the population is initially very different to the target stage-structure. In the first year, abundance may even change in the opposite direction to the long-term objective. If harvest decisions are made dynamically, then objectives relating to abundance may not be optimally met in the short-term when we manage for a target population momentum, or any other measure of long-term or equilibrium dynamics. Short-term strategies would be better developed using a method such as dynamic programming when the population structure is markedly different from the target equilibrium structure.

6. Partial control and observation

Let us briefly return to the unstructured model (10). To compare this model with our example involving three stage-classes, we set $N_0 = 1000$ and $\lambda = 1.309$. From the equilibrium condition (11) we might choose to remove 300 individuals from the population, with the intention of allowing the population to grow slightly over the next time step ($N_1 = 1009$). If the population actually has the life history characteristics given in (12), then we might observe the population to decline

over the next time step instead. This could arise if there is a large proportion of adults removed during the harvest, or a small proportion of adults in the initial population. Conversely the population could increase to an abundance much larger than expected if mostly 1-year-olds are removed, or there is a large proportion of adults in the initial population.

During dynamic decision-making it is possible to respond to these kinds of observations by resetting the harvest level in the following time step, instead of repeatedly removing the same number of individuals each time step. Optimization methods such as dynamic programming can take into account the effects of population momentum and transient dynamics if the full stage-structure of the population is included as a number of state variables. If the population has a large number of stages then this may become computationally intractable, and the results difficult to interpret. Furthermore, it is often difficult to observe the full stage-structure of a population at each time step. The monitoring required is likely to be more intensive than if only total abundance is estimated. In some cases distinguishing between stages visually may be impossible.

Similarly, it may be difficult to select individuals by stage for harvest. Managers may be unable to set regulations that target particular stages, or harvesters may be unable to visually distinguish between stages. In a dynamic optimization, the available management options can usually be constrained appropriately for these situations. For example, in many species, young inexperienced individuals are more susceptible (vulnerable) to harvest than are older individuals. In an optimization of harvest on a population of such species, the *realized* harvest rate on each stage-class is assumed to be proportional to the vulnerability of an individual in that stage-class, relative to adult individuals (e.g., Hauser et al., 2005). In some other studies, it is assumed that the harvest rate is applied evenly to all age-classes (Jensen, 1996, 2000; Pascual et al., 1997).

In commercial fisheries, it is common that the mesh size of the fishnets used will catch only or mostly individuals above a certain size class. An appropriate constraint may be that the harvest rate acts equally on all size classes above this level, while all individuals in smaller size classes escape harvest (Doubleday, 1975; Reed, 1980). We might imagine that the mesh size could be chosen as part of the optimization process, to increase the manager's ability to control the stage-structure of the harvest. In any case, such constraints are likely to limit the range of actions available to the manager. For example, there is only one stage-specific harvest that would satisfy both a vulnerability constraint and the equilibrium condition in this paper.

In other systems, some stage-selective harvesting may be possible using broad classes. Studies modelling impala (Ginsberg and Milner-Gulland, 1994), saiga antelope (Milner-Gulland, 1994), deer (Xie et al., 1999), moose (Sæther et al., 2001) and Buffon's kob (Mayaka et al., 2004) have used the assumption that there is some control over the number of adults and young, and/or males and females in the harvest taken, although there may be some incidental harvest of other classes (Xie et al., 1999) or poaching (Mayaka et al., 2004) beyond the control of managers.

7. Conclusions

Harvest management is never a simple task. The challenges of harvest management are compounded when structured populations are considered. We have shown that when populations are structured (based on age or some other demographic variable), the harvest required to achieve an equilibrium objective depends on initial population size, structure and reproductive value at the time of harvest.

Although derivation of the equilibrium harvest vector for simple structured models is straightforward, there are several potential difficulties in practice. First, uncertainty concerning the population structure at the time of harvest, and the ability to specify the structure of the harvest itself, are significant complications to population control. There will be substantial uncertainty about the system dynamics, the impacts of potential management and conservation decisions on those dynamics, and about how to optimize management decisions in the presence of such uncertainties (e.g. Hunter and Runge, 2004). These difficulties are compounded by the non-linear change in the dynamics of the population following harvest.

In practice, most systems are only partially specified (observable). Accommodating partial observability in an optimized adaptive framework (*sensu* Walters, 1986; Nichols et al., 1995; Williams, 1996, 1997) requires specifying the statistical association between the estimated current state of the system and the underlying distribution of possible system states. Derivation of the function relating current state given the distribution is difficult without simplifying assumptions. Further, accommodating partial observability in an adaptive optimization framework requires estimation of the transition probabilities for every state in the system, which is likely to be computationally intensive. Finally, in many cases, optimal strategy sets become stationary over a sufficiently long time horizon, such that the stationary strategy becomes the optimal strategy over the long-term. However, in some cases, especially involving structured populations, there may be no stationary solution, and the optimal strategy set may cycle among different management actions.

Appendix A. Finding the harvest that gives a target momentum

Here we determine the harvest strategies that will satisfy the equilibrium condition and achieve a target level of popula-

tion momentum in the long-term. We consider both the constant and proportional harvest models (Eqs. (3) and (4), respectively).

A.1. Constant harvest

Let the population have m stage-classes. Then the equilibrium condition (7) can be written as

$$v_1 N_1^{eq} + v_2 N_2^{eq} + \cdots + v_m N_m^{eq} = \mathbf{v}' \mathbf{N}_0,$$

where $\mathbf{v} = [v_1 \, v_2 \, \ldots \, v_m]'$ is the left eigenvector of $\mathbf{A}$ corresponding to the dominant eigenvalue λ, and $\mathbf{N}^{eq} = [N_1^{eq} \, N_2^{eq} \, \ldots \, N_m^{eq}]'$ is the long-term equilibrium population size and structure. We assume that we know the initial size and structure $\mathbf{N}_0$ of the population, so that the right hand side of the equation is a known constant.

Additionally, we must set the population momentum at the desired level M. We can rearrange

$$M = \frac{|\mathbf{N}^{eq}|}{|\mathbf{N}_0|}$$

so that

$$N_1^{eq} + N_2^{eq} + \cdots + N_m^{eq} = M \mathbf{e}' \mathbf{N}_0,$$

where $\mathbf{e}$ is an $m \times 1$ vector of ones. If we have set a required momentum M, then the right hand side of this equation is also constant.

Finally, we must ensure that both the harvest taken and the equilibrium population are non-negative. That is

$$Y_i \geq 0 \quad \text{and} \quad N_i^{eq} \geq 0 \quad \text{for } i = 1, 2, \ldots, m.$$

Using Eq. (6) we can rewrite $Y_i \geq 0$ as

$$a_{i1} N_1^{eq} + a_{i2} N_2^{eq} + \cdots + a_{im} N_m^{eq} \geq N_i^{eq} \quad \text{for } i = 1, 2, \ldots, m.$$

To summarize, we are seeking $\mathbf{N}^{eq} = [N_1^{eq} \, N_2^{eq} \, \ldots \, N_m^{eq}]'$ such that

$$v_1 N_1^{eq} + v_2 N_2^{eq} + \cdots + v_m N_m^{eq} = \mathbf{v}' \mathbf{N}_0$$
$$N_1^{eq} + N_2^{eq} + \cdots + N_m^{eq} = M \mathbf{e}' \mathbf{N}_0$$

subject to

$$a_{i1} N_1^{eq} + a_{i2} N_2^{eq} + \cdots + a_{im} N_m^{eq} \geq N_i^{eq}$$
$$N_i^{eq} \geq 0 \quad \text{for } i = 1, 2, \ldots, m.$$

We have two equations with m unknowns, subject to $2m$ constraints. When we have determined the solution $\mathbf{N}^{eq}$ then we can find the harvest $\mathbf{Y}$ required as

$$\mathbf{Y} = (\mathbf{A} - \mathbf{I}) \mathbf{N}^{eq}.$$

A.2. Proportional harvest

We can similarly state the problem for proportional harvest, using the equilibrium condition (15), the momentum equation and constraints that ensure the population and harvest are nonnegative. We must choose $\mathbf{N}^{eq} = [N_1^{eq} \, N_2^{eq} \, \ldots \, N_m^{eq}]'$ and $\mathbf{h} = [h_1 \, h_2 \, \ldots \, h_m]'$ such that

$$(1 - h_i)(a_{i1} N_1^{eq} + a_{i2} N_2^{eq} + \cdots + a_{im} N_m^{eq}) = N_i^{eq}$$
$$N_1^{eq} + N_2^{eq} + \cdots + N_m^{eq} = M \mathbf{e}' \mathbf{N}_0$$

subject to:

$$N_i^{eq} \geq 0$$
$$h_i \geq 0$$
$$h_i \leq 1$$

for $i = 1, 2, \ldots, m$.

Then we have $m + 1$ equations with $2m$ unknowns, subject to $3m$ constraints.

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