

SHORT COMMUNICATION

HARVESTING MODELS FOR RESOURCE-LIMITED POPULATIONS

Summary: 'Extensive' herbivore/vegetation models and 'intensive' grazing models yield two conclusions for sustained-yield harvesting of populations regulated by an interaction with their resources. First, the growth curve for the population, relating growth rate to current density, and the equilibrium yield/effort curve under harvesting, are likely to be asymmetric, with peaks displaced to the right and maximum growth rate and harvest greater than predicted by the symmetrical, single-species logistic model. In general, the growth curve for a consumer has its peak displaced to the right relative to that of its resource. Second, stability of the population and harvest is greater at moderately high harvesting intensities than at low ones, and is greater the more leftward-peaked the resource growth curve.

Keywords: Sustained-yield harvesting; maximum sustainable yield; population models; grazing models.

Introduction

Conventional models for estimating maximum sustainable yields from populations are generally single-species ones, like the logistic or its variants. Such variants embody depensation, in which population growth is reduced or becomes negative at low densities (Clark, 1976), and asymmetric growth, in which the curve relating population growth rate to current density has its peak displaced to the left or right (Schoener, 1973; Fowler, 1981; Barlow and Clout, 1983). They also include stochastic versions of the basic model, in which randomly-varying parameters provide insights into the relationship between the size and variability of the harvest. However, these models take no explicit account of population regulation through an interaction with other species, notably a resource upon which the harvested population depends.

Such a system was briefly analysed by May *et al.* (1979) and Barlow and Clout (1983), using predator/prey-type models with harvesting imposed on the predator. May *et al.* (1979) used an 'interferential' model (Caughley, 1976), in which predators are regulated by intra-specific competition as well as by prey density, while Barlow and Clout (1983) employed a 'laissez-faire' (Caughley, 1976) herbivore/vegetation one, with herbivores regulated solely by vegetation density. Both models suggested that resource limitation leads to asymmetric growth curves and yield/effort curves for the harvested population, with peaks displaced to the right and maximum sustainable yields greater than predicted by the single-species logistic.

However, a separate body of theory dealing with 'intensive' grazing systems (Noy-Meir, 1975, 1978;

Barlow, 1987), in which herbivore numbers are fixed (c.f. the above 'extensive' systems), suggests that these conclusions may be open to question; specifically, they may depend on the assumption by both the above models that the resource grows logistically. Models of intensive grazing systems (Barlow, 1987) show that the shape of the animal productivity/stocking rate curve depends on that of the vegetation growth curve, and can be almost symmetrical if the latter is leftward-peaked (Fig. 3d in Barlow (1987)). These models appear equally applicable to extensive systems in which herbivore numbers are held constant by harvesting, so similar conclusions should apply to the population growth rate (= sustained harvest)/ density curve, growth rate being simply another measure of animal productivity.

Intensive grazing models also suggest that the stability of resource-limited populations under harvesting may differ substantially from that predicted by the single-species harvesting models. In particular, the system is most stable when the herbivore is scarce and the vegetation abundant, that is, under a lightly-stocked intensive system or a heavily, not lightly harvested extensive one.

This note, therefore, returns to Caughley's (1976) laissez-faire model to address two questions relating to sustained-yield harvesting of resource-limited populations. Firstly, is the population growth curve necessarily rightward-peaked, as suggested by May *et al.* (1979) and Barlow and Clout (1983)? Secondly, what is the effect of environmental stochasticity when it acts through variations in resource growth and availability, rather than directly on the harvested population as assumed in the single species models?

Model

The model used is:

$$\dot{V} = rV(1 - V/K)/(1 + qV/K) - c(1 - \exp(-dV)) \tag{1}$$

$$\dot{H} = H(-a + b(1 - \exp(-dV)) - E) \tag{2}$$

- where \dot{V} = growth rate of vegetation at a density V
- \dot{H} = growth rate of the herbivore population at a density H
- q = parameter determining the shape of the vegetation growth curve ($= (1 - 2p)/p^2$ where p is the fraction of the maximum vegetation density at which vegetation growth peaks)
- E = harvest rate or effort (proportion removed per unit time)
- r = maximum specific vegetation growth rate ($= \dot{V}/V$ as $V \rightarrow 0$)
- K = maximum ungrazed vegetation density
- c = maximum rate of food intake per herbivore
- d = grazing efficiency of herbivore when vegetation is sparse
- a = rate of decline of herbivores when the vegetation is fully depleted
- b = maximum effect of abundant vegetation on herbivore growth rate (intrinsic rate of increase $= b - a$).

This is essentially Caughley's (1976) model, with vegetation growing logistically ($rV(1 - V/K)$) and being consumed at a rate per herbivore which levels off asymptotically as vegetation density increases ($c(1 - \exp(-dV))$). The herbivore rate of increase is linearly related to per capita intake; if intake is zero, herbivores die at a specific rate of a per unit time. The model is only modified here by the introduction of the term $-EH$ for harvesting, and $1/(1 + qV/K)$ which allows the vegetation growth curve to be asymmetric; this vegetation model is discussed further in Barlow (1987). Note that maximum vegetation growth occurs when $V/K = p$, so the maximum growth rate in the absence of grazing is rp^2/K , from equation 1.

For the sake of example, parameter values are used as in Caughley (1976), namely $r=0.8$, $K=3000$, $c= 1.2$, $d= 0.001$, $a= 1.1$, $b= 1.5$. These values are strictly hypothetical but not inconsistent with a population of white-tailed deer in a grassland/forest mosaic (Caughley, 1976). Three different vegetation growth curves are considered, with $p = 0.25$ (leftward-peaked), $p = 0.5$ (symmetrical logistic), and $p = 0.7$ (rightward-peaked), and the equation standardised to give the same maximum growth rate as in Caughley's

logistic model ($p = 0.5$). This is achieved by varying r such that the maximum vegetation growth rate ($rp^2/3000$) equals 600 ($= 0.18 \times 0.5^2 / 3000$ in Caughley's model). Results were obtained by running the model as a simple simulation until equilibrium was established at each imposed level of effort (E) from zero to 0.35.

Results and Discussion

Fig. 1 shows the effects of different shaped resource growth curves on that of the harvested consumer population, and on the yield/effort relationship. The basic model with a logistic resource growth equation is given by Fig. 1d, and, as demonstrated analytically by Barlow and Clout (1983), it yields a rightward-peaked curve for the harvested population (Fig. 1e). The yield/effort curve is also rightward-peaked (Fig. 1f). The leftward-peaked resource growth curve with $p = 0.25$ (Fig. 1a) gives an almost symmetrical consumer one (Fig. 1b), though the yield/effort curve (Fig. 1c) is still rightward-peaked and maximum sustainable yield is reached at the same level of harvesting effort (0.2) as in Fig. 1f. In the case of the rightward-peaked resource growth curve (Fig. 1g), that of the consumer is displaced still further to the right

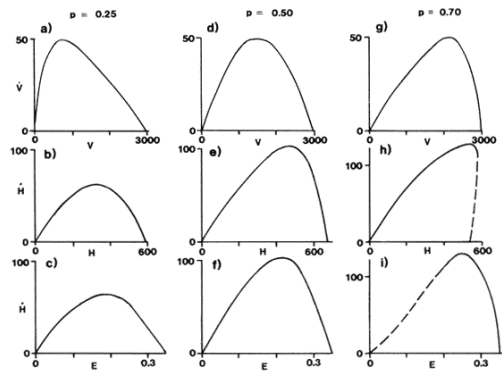


Figure 1: Herbivore growth rate (second row) and yield/effort curves (third row), given different shaped vegetation growth curves (first row). a), b), c) leftward-peaked vegetation growth ($p = 0.25$); d), e), f) symmetrical vegetation growth ($p = 0.5$); g), h), i) rightward-peaked vegetation growth ($p = 0.7$). V = vegetation growth rate, \dot{H} = herbivore growth rate and sustained yield, H = herbivore density, E = harvesting 'effort' (proportion removed per unit time), ----- denotes unstable equilibrium points (see text).

and also exhibits two growth rates corresponding to each density when the latter is high (Fig. 1h). The lower (dashed) line corresponds to a low equilibrium resource level and the upper line to a higher equilibrium resource level at the same herbivore density. The second equilibrium is stable but the first is unstable, since any disturbance initiates diverging oscillations in population density and yield. The sustained yield/effort curve is also rightward-peaked, the dashed line in Fig. 1i again denoting an unstable equilibrium.

To assess the stability of the harvested populations, the isoclines for zero resource change and zero consumer change are plotted in Fig. 2 for the three vegetation growth curves ($p=0.25, 0.5$ and 0.7) and two levels of harvesting effort ($E = 0.05$ and $E = 0.25$). The isoclines are the relationships between H and V when $\dot{V} = 0$ in equation 1 and $\dot{H} = 0$ in equation 2 thus:

when $\dot{V}=0$ in 1):

$$H = rV(1 - V/K)/c((1 + qV/K)(1 - \exp(-dV)))$$

when $\dot{H}=0$ in 2):

$$V = -d \frac{1}{a} \ln \left(\frac{E+a}{1-b} \right)$$

and they allow the directions of change in V and H to be predicted from any starting point in the V/H plane, depending on which side of the $\dot{V} = 0$ and $\dot{H} = 0$ lines the point lies (see Caughley (1976) for a fuller discussion). These directions are indicated by the arrows in Fig. 2a, and two examples given in Fig. 2c.

The overall equilibrium point for the system is given by the intersection of the V and H isoclines, and the further this intersection is to the right the more stable the system (Caughley, 1976). In particular, if it lies to the left of the peak in the V isocline, the system is unstable and any disturbance will result in divergent oscillations (Fig. 2c). Thus, rightward displacement of the resource growth curve (Fig. 2c compared with Fig. 2a) tends to reduce stability, moving the peak of the V isocline to the right. This is the same effect as an increase in the maximum vegetation density, K (Caughley 1976, Fig. 6.4), which gives rise to Rosenzweig's (1971) paradox of enrichment. The paradox lies in the fact that increasing the maximum resource abundance renders the consumer population less stable. Interestingly, increasing harvesting effort tends to stabilise the population because it moves the H isocline to the right (i.e. V increases as E increases in equation 4). Caughley (1976) showed that increasing the maximum specific mortality rate of the consumer

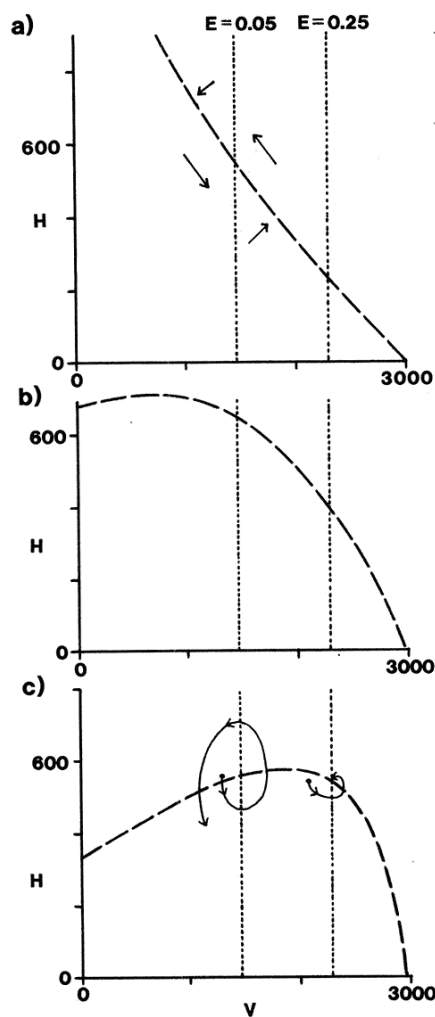


Figure 2: Isoclines relating herbivore density (H) to vegetation density (V) when $\dot{V}=0$ (—), and $\dot{H}=0$ (- - -) for two levels of harvesting effort indicated on the Figure. a) leftward-peaked vegetation growth ($p=0.25$), b) symmetrical vegetation growth ($p=0.5$), c) rightward-peaked vegetation growth ($p=0.7$). Arrows in a) indicate directions of change in V and H , and initial sample trajectories are shown in c) resulting from 10% reductions in V from the equilibrium points corresponding to the two levels of effort.

(a) increased stability, and this is precisely the effect of harvesting.

Increased stability implies reduced variability in the face of perturbations and environmental stochasticity. Fig. 3 shows the effect of a single perturbation on yields, with V instantaneously reduced by 20%, given the basic vegetation model ($p = 0.5$) and low ($E = 0.05$) and high ($E = 0.25$) levels of harvesting effort. Under intensive harvesting the yield returns to its original value more quickly, and asymptotically rather than through converging oscillations, compared with a population exploited at a lower rate.

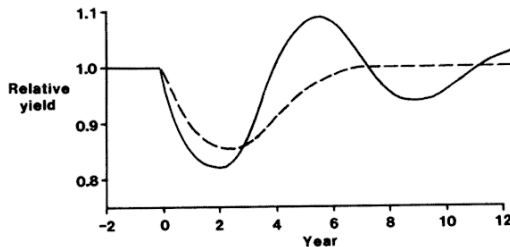


Figure 3: Trend in relative yield (actual/equilibrium yield) with time, following a single 20% reduction in vegetation density in year 0. — effort level = 0.05/year, - - - effort level = 0.3/year.

When the specific growth rate of the vegetation is varied continuously, by multiplying by uniform random numbers between 0.6 and 1.4, the coefficient of variation of the yield declines as effort is increased. The absolute standard deviation of the yield first increases to a maximum at an effort level of 0.15, then declines as effort increases up to and beyond the level giving maximum sustainable yield (0.2; Fig. 4).

This contrasts with conclusions from single-species models with stochastic density-independent variation. These suggest that absolute fluctuations in yield increase as effort increases, markedly so if exploitation exceeds the MSY (maximum sustainable yield) level, and that the coefficient of variation of the yield can increase or decrease as effort approaches the MSY level but thereafter always increases (May *et al.*, 1978). May *et al.* (1978) acknowledge that the conclusions may differ if stochastic variation affects the density-dependent term in the model rather than the density-independent one, and if the population is prone to overcompensatory oscillations in its virgin state, as in the present model. However, these alternatives appear to have received little subsequent

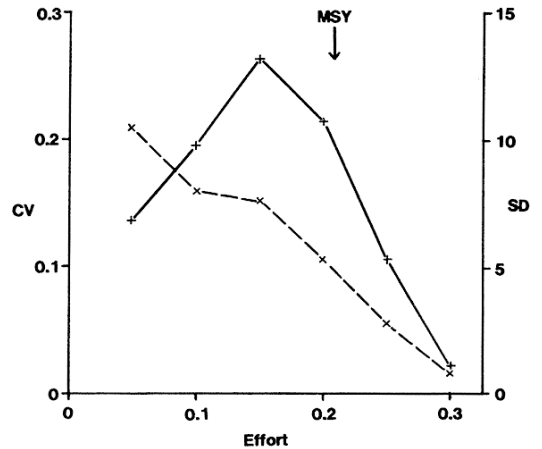


Figure 4: Effect of effort level (proportion harvested per year) on the standard deviation of the yield (SD, —) and the coefficient of variation (= standard deviation/mean; CV, - - -), given the logistic vegetation growth model ($p = 0.5$) and random variation in the maximum specific vegetation growth rate (see text). MSY indicates the effort level giving maximum sustainable yield of the herbivore.

attention given the likelihood of their occurrence in nature.

Conclusions

An interactive herbivore/vegetation model suggests that the growth curve for a consumer has its peak displaced to the right relative to the growth curve of its resource. Where the resource curve is leftward-peaked, as appears to be the case for continuously-grazed grassland for instance (Barlow, 1987), the population growth curve may then approach the symmetric logistic. However, the resource curve must be extremely asymmetric for this to be true and if, as seems more likely, it lies somewhere within the range given in Fig. 1, then the original conclusion of May *et al.* (1979) and Barlow and Clout (1983) appears to hold: the growth curve of a population limited by an interaction with a renewing food supply is never leftward-peaked, and is more likely to be rightward-peaked than symmetric. That is, the θ -logistic (see Barlow and Clout, 1983):

$$H = r'H(1 - (H/K')^\theta)$$

where r' = intrinsic rate of increase, K' = maximum density or carrying capacity and $\theta = 2$, may be a more

appropriate single-species model that the ordinary logistic ($\theta = 1$) for a resource-limited population. The yield/effort curve for such a population under sustained yield harvesting is also likely to be rightward-peaked.

The model further suggests that closely coupled predator/prey or herbivore/vegetation systems, in which growth of the consumer is entirely dependent on the abundance of its resource, can be stabilised by cropping the consumer. Intensive harvesting, therefore, even at or above maximum sustainable yield, may not necessarily threaten a population's stability or persistence in the face of fluctuations in resource availability.

Classical, symmetric yield/effort curves (Schaefer, 1968), and the conclusion from single-species models that variability increases and stability decreases with harvesting intensity, appear to apply well to fisheries. However, this may simply indicate that their populations are regulated by factors other than an interaction with the food supply, or that the interaction is of a different form to the above. For instance, they may be regulated during their larval stages by food abundance but themselves have little effect on the food supply (May *et al.*, 1979). For other harvested populations Caughley's (1976) model described here, and the considerable body of theory developed for intensive grazing systems by Noy-Meir (1975, 1978), suggest feasible alternative conclusions which may well be more appropriate. However, the models require at least a quantitative knowledge of the mechanism of population regulation or empirical estimates of the shape of the population growth curve. In the case of New Zealand's terrestrial harvested populations, such as possums and deer, such data are still sparse.

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