Temporally structured density-dependence and population management

Niclas Jonzén & Per Lundberg

Jonzén, N. & Lundberg, P., Department of Theoretical Ecology, Ecology Building, Lund University, SE-223 62, Lund, Sweden

Jonzén, N. & Lundberg, P. 1999: Temporally structured density-dependence and population management. — *Ann. Zool. Fennici* 36: 39–44.

We used a simple discrete-time population model to investigate how temporally structured density-dependence influences a population's response to loss due to harvesting. We assumed that reproduction is a relative discrete event in time, followed by density-dependent mortality and then harvesting, or followed by harvesting and then density-dependent mortality. Such an ordering of events in time may have profound influences on the dynamics of the population. The extra mortality due to harvesting may either be additive or compensatory depending on the strength of the density-dependence and the ordering of events. Population stability is also strongly affected by the temporal structure of density-dependence. Moreover, the yield and the (unconstrained) optimal harvest rate will vary depending on when harvesting occurs in the annual cycle. We argue that a correct identification of the temporal structure of density-dependence may be of great importance for understanding population dynamics in general and population management in particular.

1. Introduction

Many populations live in temporally varying environments (Fretwell 1972). The seasonality can vary in strength and on which scale it occurs (Pimm 1991). Mild seasonality may have a stabilising effect on populations but large seasonality is inevitably destabilising (Kot & Schaffer 1984). Often, seasonality has been included in population models by periodically changing the value of a demographic parameter, e.g., the carrying capacity (Boyce & Daley 1980, Kot & Schaffer 1984). However, this implies that reproduction occurs all year around, which may be true for some tropical organisms, but is not a suitable representation of the majority of species living in more temperate areas. An alternative approach would be to identify the different temporal sequences a population goes through in a seasonal environment. For instance, an important factor is the possible occurrence of sequential density-dependence.

The necessity to keep track of the temporal ordering of mortality factors to express correctly the survivorship pattern of a population was pointed out already by Walters (1986). He also concluded that the resulting model becomes more

complex and less general. The importance of sequential density dependence was more recently brought up again by Åström *et al.* (1996). They also concluded that populations demonstrating sequential density-dependence may give rise to $N_{t+1}(N_t)$ maps (recruitment functions, N_{t+1} plotted against N_t, where N_t and N_{t+1} are the population density at time t and $t + 1$, respectively) with more than one hump and multiple equilibria. This suggests that we can expect a larger and more complex variety of dynamics compared to non-sequential models. Hence, to be able to understand population fluctuations or how to manage populations, the identification of the temporal sequence of density-dependent mortality and reproduction should be important.

In spite of this, very few studies have explicitly incorporated temporal structure in population models (but *see* Ruxton 1996) and even fewer have focused on practical applications, for example in population harvesting (Kokko & Lindström 1998) or conservation programmes. The importance of seasonality has been noticed by insect ecologists (e.g., Sota 1988, Iwasa *et al.* 1992). Allen *et al.* (1991) provide an interesting example of how to control a pest (the apple twig borer on grapes) under such conditions. Sutherland (1996), who investigated the consequences of habitat loss in a migrating bird, the oystercatcher (*Haematopus ostralegus*), studied a related problem. He asked whether or not the effect on equilibrium population density is different if breeding or wintering habitat is destroyed. Because the oystercatcher is migratory, the question of where habitat loss occurs coincides with the question of when it occurs.

In this paper, we develop a simple model of a population in a seasonal environment. We assume no stage-structure, and we let the seasons be distinct and unambiguously defined. We also introduce into this model temporally distinct and density-independent mortality events that can be interpreted as constant effort harvesting. Harvesting can take place before or after reproduction, and we were interested in the potential effects of the timing of harvesting on mean population density, the variation in mean population density, and the maximum sustainable yield. This does not mean that the resulting dynamics and yield consequences of the harvesting necessary should be

indicative of optimal harvesting strategies in the direct applied sense. Such recommendations naturally require a much more detailed knowledge about the organisms in question. Here, we are focussing on the principal consequences of temporally structured density-dependence on populations' ability to respond to losses distinct in time.

2. The model

Let us assume three unique and temporally well-separated events occurring during a year: birth (B), mortality (M), and harvesting (H). Each of these events is (or is not) a density-dependent process. Density-independent mortality may occur at all times. A sequence of n processes can be ordered in $n!$ different ways. However, the relative position of the events is different only in $(n - 1)!$ of these, and that is one of the requirements for changing the stability properties of the model and the equilibrium density after a given process (Åström *et al.* 1996). Hence, H, B and M can be ordered during a year, say, in two different ways — HBM and BHM — resulting in two different discrete-time population models, which map the population density at year t to the population density one year later ($t + 1$):

$$t \xrightarrow{\hspace{4cm}} t + 1$$
$$\underbrace{\underbrace{N_t + B(N_t)N_t - H(\varphi)\varphi}_{\varphi} - M(\delta)\delta}_{\delta} = N_{t+1} \quad (1)$$

$$t \xrightarrow{\hspace{4cm}} t + 1$$
$$\underbrace{\underbrace{N_t - H(N_t)N_t + B(\gamma)\gamma}_{\gamma} - M(\phi)\phi}_{\phi} = N_{t+1} \quad (2)$$

$H(\cdot_t)$, $B(\cdot)$ and $M(\cdot)$ indicate that the processes are functions of the population density resulting from the preceding processes. Now, let us assume that both per capita birth rate and death rate are linearly related to population density such that

$$B(N) = \beta - bN \quad (3)$$

and

$$M(N) = \alpha + aN \quad (4)$$

where β is the maximum per capita birth rate, α is

the minimum per capita death rate, and b and a determine the strength of the density-dependence in the birth and mortality rate, respectively. For simplicity, we have assumed linear density-dependence, but this is not crucial for the general result. The per capita risk of being harvested is assumed to be independent on population density, i.e., a certain fraction, h, of the population is removed every year. Inserting Eqs. 3 and 4 in Eqs. 1 and 2, respectively, gives the following two models:

$$\text{HBM}: \quad (1-h)N_t\left[1+\beta-bN_t(1-h)\right]\times \\ \times(1-\alpha-a\Gamma)=N_{t+1} \tag{5}$$

$$\text{BHM}: \quad N_t\left(1+\beta-bN_t\right)(1-h)\times \\ \times(1-\alpha-a\Psi)=N_{t+1} \tag{6}$$

where:

$$\Gamma=(1-h)N_t\left[1+\beta-bN_t(1-h)\right]$$

and

$$\Psi=(1-h)N_t\left(1+\beta-bN_t\right).$$

The population density is calculated after all processes, i.e., N_{t+1} is the evaluated population density. In the following section we present how the timing of harvesting influences the mean population density, the variation in mean population density, and finally, the effect on the maximum sustainable yield.

3. Results

Removing individuals from the population immediately decreases the population density. However, as clearly demonstrated in Fig. 1, harvesting may not only be compensated for, but also overcompensated. The maximum per capita birth rate has to exceed a certain value and the harvest rate must be low enough for this overcompensation to occur. In Fig. 1, we present two examples (for each sequence of events) of how compensation is related to per capita birth rate and harvest rate. Interestingly, harvesting before reproduction may result in a higher mean equilibrium population density compared to harvesting after reproduction or no harvesting at all.

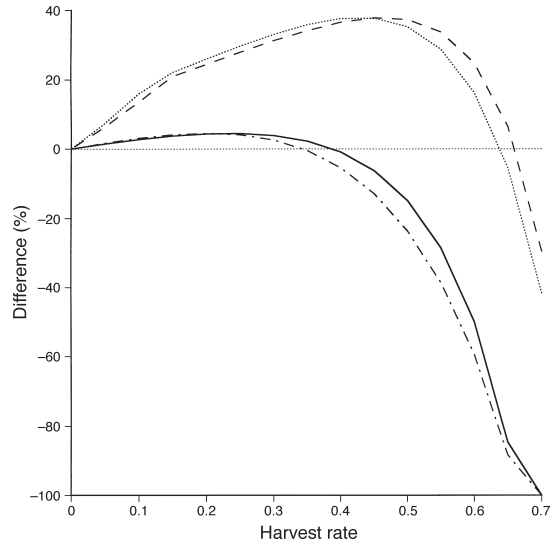Another important aspect with consequences for population conservation and management is

Fig. 1. The difference in mean population density (%) between a harvested and an unharvested population for different values of the harvest rate, maximum per capita birth rate (β), and for the two different sequences of events (HBM and BHM). H = Harvest, B = Birth, M = Mortality. Solid curve (HBM and β = 2), dashed-dot curve (BHM, β = 2), dashed curve (HBM, β = 3), dotted curve (BHM, β = 3). The other parameter values are α = 0, b = 0.0005 and a = 0.00025.

the relative variation in mean equilibrium population density over time. We calculated the coefficient of variation (CV) by simulating the time dynamics for the two models for 200 time steps, discarding the first 100 to avoid the influence of transients. The coefficient of variation increases with increasing maximum per capita birth rate, because the dynamics changes from stable to cyclic, and finally, multi-point cycles or chaos (Fig. 2). Harvesting, no matter when, stabilises the dynamics. The effect is stronger when the population is subject to harvesting after reproduction but before the density-dependent mortality (Fig. 2, dotted line).

The harvest rate resulting in the maximum sustainable yield is dependent not only on the maximum per capita birth rate, but also on the timing of harvesting (Fig. 3). Notice that for a wide range of harvest rates below the optimum level, the yield is higher if the maximum per capita birth rate β is 2 instead of 3. That actually reflects a higher equilibrium size for lower per capita birth rate, which is possible only if density-dependent
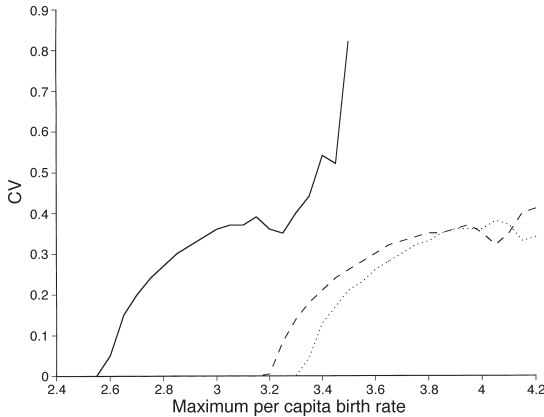
Fig. 2. Coefficient of variation (CV) of mean population density for different values of the maximum per capita birth rate (β). HBM (dashed curve) and BHM (dotted curve) refer to the two different sequences of events when the population is harvested. H = Harvest, B = Birth, M = Mortality. In this figure, the harvest rate is either zero (solid curve) or 0.2 (dashed and dotted curves). The other parameter values are $\alpha = 0$, $b = 0.0005$ and $a = 0.00025$. Positive mean population density is not possible without harvesting for $\beta >$ 3.5 and, hence, the coefficient of variation is not defined.

reproduction and mortality are separated in time. This effect of sequential density-dependence on the relationship between maximum per capita birth rate and mean population density is presented in Fig. 4 for a wider range of β-values.

4. Discussion

In population models where density-dependent reproduction and mortality occur simultaneously (and there is no stage-structure), an increase in the per capita birth rate inevitably results in increased equilibrium size. Temporally structured density-dependence makes it less obvious how changes in demographic parameters translate into equilibrium population density. This has far-reaching consequences for how, e.g., habitat loss or harvesting affect populations. For example, let us assume that we study a population described by Eq. 1. In order to manage this population we have to carry out a population survey before reproduction to estimate N_t. Often, this is the only piece of information we have at hand. Second, we must know $B(N_t)$, i.e., how per capita birth rate relates
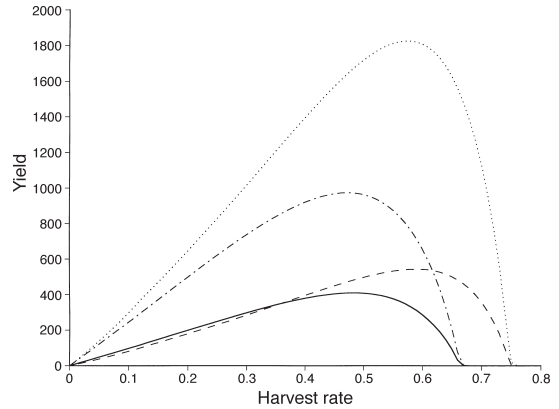

Fig. 3. Yield (the mean number of individuals harvested) for different harvest rates, maximum per capita birth rates (β) and sequences of events (HBM vs. BHM). H = Harvest, B = Birth, M = Mortality. Solid curve (HBM and $\beta = 2$), dashed-dot curve (BHM, $\beta = 2$), dashed curve (HBM, $\beta = 3$), dotted curve (BHM, $\beta = 3$). The other parameter values are $\alpha = 0$, $b = 0.0005$ and $a = 0.00025$.

to population density. Now, we can calculate the population density before harvesting (φ) and if harvests are reported, we can easily get an estimate of how per capita mortality rate due to harvesting is related to population density ($H(\varphi)$). The next step is the straightforward calculation of population density before the density-dependent mortality event (δ). The per capita mortality rate $M(\delta)$ can now be calculated as $\dfrac{\delta - N_{t+1}}{\delta}$. After several years of careful data collection we will have an estimate of how $M(\delta)$ varies with population density and the population processes have been identified. Although this protocol is simple in theory, we fully realise the practical problems of obtaining the adequate data. If experimentation is not possible, it will be even more difficult. Without this indispensable information, however, it will be extremely difficult to gain any real understanding of the population we are manipulating.

Our results also have implications for the never-ending debate on additive and compensatory harvesting mortality (e.g., Anderson & Burnham 1976, Burnham & Anderson 1984, Burnham *et al.* 1984, Hudson & Rands 1988, Barker *et al.* 1991, Smith & Reynolds 1992, Smith & Reynolds 1994, Sedinger & Rexstad 1994). The solution of

this problem hinges on the recognition of the temporal structure of density-dependent processes. It is thus obvious that we have to know how the per capita birth and death rates vary with population density for different seasonal processes. So far, few attempts have been made in this direction. Sinclair and Pech (1996) addressed the problem with a model without explicit seasonality and consequently failed to resolve it. Harvesting mortality can only be compensated (or overcompensated) for if there is one or more density-dependent processes following it. Kokko and Lindström (1998), who used a modelling approach different from ours, recently pointed out the importance of the timing of harvesting in relation to density-dependent events. They used a continuous-time model with periodic forcing, whereas we have explicitly included seasons as discrete events in the life cycle. Biologists with no training in mathematics may perhaps find our approach more easily digested.

The mean population density does not have to be the only critical factor for the persistence of a population. In fact, large population density does little to extend the final phase of extinction, and high growth rate may actually lead to a faster decline (e.g., Lande *et al.* 1995). In our model, increasing maximum per capita birth rate (β) leads to higher population variability. Harvesting may stabilise variation between years relative to the mean population density. This is only true if β is low or the harvest rate is large. If β is large enough for a harvest-related compensation to occur, the harvest rate must be high in order to dampen the increased population variability. But if the harvest rate exceeds a certain value, harvesting tends to be additive to the density-dependent mortality, not compensatory. Hence, there may exist a trade-off between high population density and stability between years.

In conclusion, sequential density-dependence calls for collection of data on per capita birth and death rates in relation to population density. If this information is lacking, the underlying causes of population fluctuations can never be understood and population management faces another source of uncertainty, adding to the inevitable variance in parameter estimates caused by environmental, demographic, and observation uncertainty. Only by understanding the basic mechanisms of population dynamics is it possible to improve man-
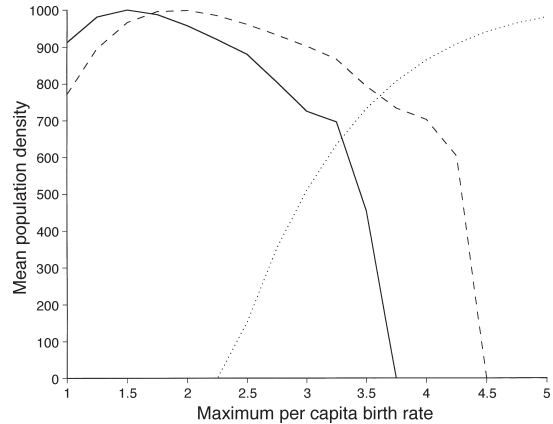

Fig. 4. Mean population density for different values of the maximum per capita birth rate and harvest rate (h), when the sequence of events is HBM (H = Harvest, B = Birth, M = Mortality). The harvest rate is either zero (solid curve) 0.2 (dashed curve) or 0.7 (dotted curve). Parameter values are α = 0, *b* = 0.0005 and *a* = 0.00025.

agement and, in an acceptable way, decide about population harvesting in space and time.

References

Allen, L. J. S., Strauss, M. J., Thorvilson, H. G. & Lipe, W. N. 1991: A preliminary mathematical model of the apple twig borer (Coleoptera: Bostrichidae) and grapes on the Texas High Plains. — *Ecol. Model.* 58: 369–382.

Anderson, D. R. & Burnham, K. P. 1976: Population ecology of the mallard VI. The effect of exploitation on survival. — *U.S. Fish and Wildlife Service Resource Publication* 128: 1–66.

Åström, M., Lundberg, P. & Lundberg, S. 1996: Population dynamics with sequential density-dependencies. — *Oikos* 75: 174–181.

Barker, R. J., Hines, J. E. & Nichols, J. D. 1991: Effect of hunting on annual survival of grey ducks in New Zealand. — *J. Wildl. Manage.* 55: 260–265.

Boyce, M. S. & Daley, D. J. 1980: Population tracking of fluctuating environments and natural selection for tracking ability. — *Am. Nat.* 115: 480–491.

Burnham, K. P. & Anderson, D. R. 1984: Tests of compensatory vs. additive hypothesis of mortality in mallards. — *Ecology* 65: 105–112.

Burnham, K. P., White, G. C. & Anderson, D. R 1984: Esti-

mating the effect of hunting on annual survival rates of adult mallards. — *J. Wildl. Manage*. 48: 350–361.

Fretwell, F. D. 1972: *Populations in a seasonal environment*. — Princeton Univ. Press, New Jersey. 217 pp.

Hudson, P. J. & Rands, M. R. W. (eds) 1988: *Ecology and management of gamebirds*. — BSP. Professional Books, Oxford. 263 pp.

Iwasa, Y., Yamauchi, A. & Nozoe, S. 1992: Optimal seasonal timing of univoltine and bivoltine insects. — *Ecol. Res*. 7: 55–62.

Kokko, H. & Lindström, J. 1998: Seasonal density dependence, timing of mortality, and sustainable harvesting. — *Ecol. Model*. 110: 293–304.

Kot, M. & Schaffer, W. M. 1984: The effects of seasonality on discrete models of population growth. — *Theor. Popul. Biol*. 26: 340–360.

Lande, R., Engen, S. & Saether, B.-E. 1995: Optimal harvesting of fluctuating populations with a risk of extinction. — Am. Nat. 145: 728–745.

Pimm, S. L. 1991: *The balance of nature?* — The Univ. of Chicago Press, Chicago. 434 pp.

Ruxton, G. D. 1996: Effects of the spatial and temporal ordering of events on the behaviour of a simple cellular automaton. — *Ecol. Model*. 84: 311–314.

Sedinger, J. S. & Rexstad, E. A. 1994: Do restrictive harvest regulations result in higher survival rates in the mallard? A comment. — *J. Wildl. Manage*. 58: 571–577.

Sinclair, A. R. E. & Pech, R. P. 1996: Density dependence, stochasticity, compensation and predator regulation. — *Oikos* 75: 164–173.

Smith, G. W. & Reynolds, R. E. 1992: Hunting and mallard survival, 1979–88. — *J. Wildl. Manage*. 56: 306–316.

Smith, G. W. & Reynolds, R. E. 1994: Hunting and mallard survival: A reply. — *J. Wildl. Manage*. 58: 578–581.

Sota, T. 1988: Univoltine and bivoltine life cycles in insects: a model with density-dependent selection. — *Res. Popul. Ecol*. 30: 135–144.

Sutherland, W. J. 1996: Predicting the consequences of habitat loss for migratory populations. — *Proc. R. Soc. Lond*. B. 263: 1325–1327.

Walters, C. 1986: *Adaptive management of renewable resources*. — Macmillan Publishing Company, New York. 374 pp.