Theor Ecol (2017) 10:235–244
DOI 10.1007/s12080-016-0325-9

ORIGINAL PAPER

Effects of strength and timing of harvest on seasonal population models: stability switches and catastrophic shifts

Eduardo Liz[1]

Received: 27 June 2016 / Accepted: 7 December 2016 / Published online: 15 December 2016

Abstract Population abundance of many species is controlled by a combination of density-dependent processes during different periods of the annual cycle. In the context of population exploitation or conservation programs, sequential density dependence has the potential to dramatically change population responses to harvesting. Looking for a better understanding of the potential effects of harvesting on the dynamics of seasonal populations, we carry out a theoretical analysis of a discrete model for a semelparous population with an annual cycle involving three discrete density-dependent events: breeding, natural mortality, and harvesting. Our study reveals how the interplay between the model parameters determines the importance of harvest timing on stability and population abundance, especially when two nontrivial stable equilibria coexist. We address the possibility for compensatory mortality and report different forms of the hydra effect, including non-smooth ones due to catastrophic shifts. These drastic switches may include hysteresis, which has important implications for conservation goals. Regarding variability, we show that increasing the harvesting effort may either stabilize or destabilize the population, and these effects strongly depend on harvest timing and natural mortality rates. Our results also emphasize the importance of sampling populations after every discrete event occurs during one cycle. Indeed, though the dynamics are not affected by census timing, the model shows that changes in population abundance in response to changes in harvesting pressure are substantially different depending on when population is sampled. Thus, a manager would receive different (and sometimes contradictory) messages depending on census time, which could lead to managing mistakes.

Keywords Seasonal population · Discrete dynamical system · Stability · Sequential density dependence · Harvest timing · Hydra effect · Catastrophic shift

Introduction

Population abundance of many species is influenced by density-dependent events that operate at different periods of the annual cycle. For example, migratory waterfowl have life cycles consisting of breeding and non-breeding seasons, and they are subject to commercial and sport hunting. It is known that both the intensity and timing of hunting have a strong influence on population abundance. In most countries, the legal hunting season of migratory birds is autumn, which is sometimes argued as preferable because density-dependent processes will compensate for hunting losses (McCulloch et al. 1992). In Canada and USA, pre-breeding hunting of greater snow geese was prohibited by the Migratory Bird Convention, and the population of these birds experienced a rapid growth during the late twentieth century, becoming overabundant. Thus, managers introduced control actions, including a special spring hunt season (Calvert and Gauthier 2005; Juillet et al. 2012). Anadromous salmonids constitute another migratory species subject to density-dependent processes of reproduction and mortality and substantial human exploitation. For some populations, commercial and recreational fishing for anadromous salmon kills over 80–90 % of individuals (Hilborn and Walters 1992; Hard et al. 2008). Apart

---

✉ Eduardo Liz
eliz@dma.uvigo.es

[1] Departamento de Matemática Aplicada II, Universidade de Vigo, 36310, Vigo, Spain

from migratory animals, annual plants experience seasonal density-dependent events (Watkinson 1980) and can be subject to human and herbivory harvest. For example, fennel pondweed is a submerged macrophyte that survives the winter in the form of tubers, which are harvested by Bewick's swans in the Netherlands every autumn. Jonzén et al. (2002) analyzed the potential effects of this seasonal harvest on mean densities and variability of tubers using a discrete model of sequential density dependence.

The mathematical modeling approach used by Jonzén et al. (2002) consists of a discrete-time model involving a breeding and a non-breeding season. This approach goes back at least to Fretwell (1972) and has been recently used for migratory birds (Ebbinge et al. 2002; Norris 2005). From a theoretical perspective, it has been shown that the dynamics of discrete models with density regulation in two seasons within the same annual cycle can be more involved that the dynamics of simple models without temporal separation between events, and one important difference is the possibility of multiple positive equilibria (Kot and Schaffer 1984; Rodriguez 1988). Multistability opens the door for boundary collisions, catastrophic shifts between attractors, and hysteresis, which are responsible for dramatic changes in the dynamics in response to smooth changes in the model (May 1977; Scheffer et al. 2001; Vandermeer and Yodzis 1999).

In the context of population harvesting or conservation programs, a seasonal model incorporates a harvesting event during each life cycle. Jonzén and Lundberg (1999) considered a discrete model with three different seasons (corresponding to three discrete events: breeding, survival to the non-breeding season, and constant effort harvesting). They showed that population stability is strongly affected by the temporal structure of density dependence, and yield varies depending on when harvesting occurs in the annual cycle. The importance of the order of events in these types of models had already been highlighted by Åström et al. (1996). The population model proposed by Jonzén and Lundberg (1999) has also been used to show how seasonality can result in compensation, that is, increasing harvesting effort can increase annual survival (Boyce et al. 1999), and how these compensatory effects depend on harvest timing (Ratikainen et al. 2008).

The ecological questions that drive our work are related to the management of seasonal populations and, in particular, the relevance of harvest timing. A biological example of the different times of harvest is autumn hunting versus spring hunting; Kokko (2001) concludes that a simple mistiming of harvesting may cause drastic declines in population abundance. Autumn harvest is typically argued as preferable, as it removes individuals who might have died anyway (Ratikainen et al. 2008). However, some examples using the population model proposed by Jonzén and Lundberg (1999) suggest that spring harvest may result in a higher mean population density. In regard to stability, the results in (Jonzén and Lundberg 1999) suggest that increasing harvesting is stabilizing, and the stabilizing effect also depends on harvest timing.

This repertoire of complicated dynamics in discrete seasonal models stresses the need for a deeper analysis of population responses to harvesting, accounting for changes in population abundance, stability properties, and resilience (Holling 1973). In this paper, we follow the approach in Jonzén and Lundberg (1999) and consider a discrete model of an annual cycle that includes three seasons: mortality, harvesting, and reproduction. We make a thorough examination of the dynamics, putting special emphasis on the possibility for compensatory effects, for which we use the term hydra effect coined by Abrams (2009), that is, an increase in mean population density in response to an increase in its per-capita mortality rate. Our numerical simulations show typical hydra effects for parameter regions where the model has a global attractor, conditional hydra effects (a hydra effect for one attractor in regions of bistability), and non-smooth hydra effects, that is, the average population size undergoes a sudden jump leading to a hydra effect of large magnitude (Sieber and Hilker 2012). Non-smooth hydra effects sometimes lead to hysteresis, which may have important implications for conservation goals.

Our results help to understand how harvest timing determines the responses of population size to increasing harvesting not only for the possibility of hydra effects but also for population variability. Although previous work (e.g., Jonzén and Lundberg (1999)) suggests that increasing harvesting is stabilizing, we report the possibility for bubbling effects (which means that a stable equilibrium can be destabilized and then stabilized again by increasing harvesting effort), and these effects may occur both when harvesting precedes or follows reproduction. Actually, an important novelty of our study is that we analyze how the influence of harvest timing—both on stability and population abundance—depends in a subtle way on other parameters of the model.

Finally, census time is another important factor. Although census time does not influence the dynamics, the message that a manager receives from the mathematical model strongly depends on when the population is censused.

Mathematical model and dynamical analysis

We consider a single-species discrete-time population model involving an annual cycle divided into a breeding and a non-breeding season. In each of these seasons, a discrete event occurs, which in general is assumed to be density-dependent: reproduction (R) during the breeding season, and mortality (M) during the non-breeding season. In addition, we assume a third discrete event, harvesting (H), that can occur before or after breeding.

The annual cycle begins during the non-breeding season. Denoting by $N_b(n)$, $N_{nb}(n)$, and $N_h(n)$, the population sizes at the end of the breeding, the non-breeding, and the harvesting seasons after n generations, respectively, we arrive at two systems of difference equations that govern the population dynamics, depending on the relative order of events (see Fig. 1). If harvesting occurs before reproduction, the order of events is mortality → harvesting → reproduction (we refer to it as MHR), and the model is defined by

$$\begin{aligned} N_b(n+1) &= R(N_h(n+1)), & (1)\\ N_h(n+1) &= H(N_{nb}(n+1)), & (2)\\ N_{nb}(n+1) &= M(N_b(n)). & (3) \end{aligned}$$

Thus, if we census the population at the end of the breeding season, the difference equation for the MHR model comes from the composition of the three maps involved in system (1)–(3), that is

$$N_b(n+1) = R(H(M(N_b(n)))). \tag{4}$$

Using the same simple argument, the difference equation for the HMR model (harvesting → mortality → reproduction) is

$$N_b(n+1) = R(M(H(N_b(n)))). \tag{5}$$

Next, we define the maps H, M, R involved in models (4) and (5).

- For the recruitment function R we use the classical Ricker map $R : [0,\infty) \to [0,\infty)$ defined by $R(x) = xe^{r(1-x)}$ (Ricker 1954; May and Oster 1976). Note that, for simplicity, the map is normalized so that the positive equilibrium is $K = 1$; this is not a restriction for the qualitative study of the model. The parameter r is related to the birth rate, and it is assumed to be positive.
- For the density-dependent mortality, we also use an exponential function $M(x) = xe^{-ax}$, where $a > 0$ is a mortality rate during the non-breeding season.
- Finally, we assume a constant effort (proportional) harvesting defined by $H(x) = (1-h)x$, where $h \in [0,1)$ is a measure of the harvesting strength (for simplicity, we will refer to h as to the harvesting rate).

Using these functions, the explicit equation for the MHR model is

$$\begin{aligned} N_b(n+1) = (1-h)N_b(n)\exp\Big(&-aN_b(n) + r(1-(1-h)\\ &\times N_b(n)e^{-aN_b(n)})\Big) := f(N_b(n)), \end{aligned} \tag{6}$$

with $a > 0$, $r > 0$, $0 \le h < 1$.

Analogously, the explicit equation for the HMR model is

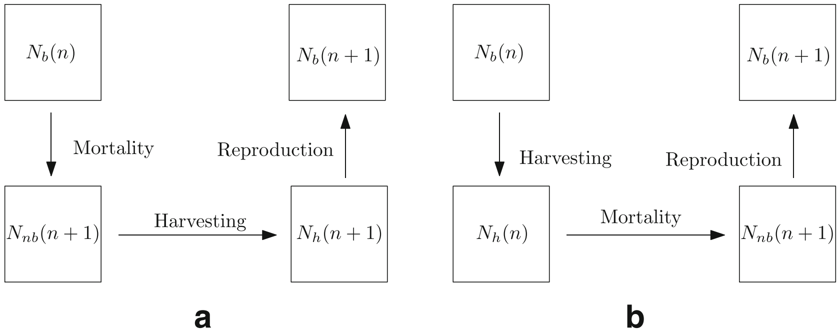
$$\begin{aligned} N_b(n+1) &= (1-h)N_b(n)\exp\Big(-a(1-h)N_b(n)\\ &\quad + r(1-(1-h)N_b(n)e^{-a(1-h)N_b(n)})\Big)\\ &:= g(N_b(n)). \end{aligned} \tag{7}$$

We emphasize that models (6) and (7) assume that population is measured after reproduction. With this convention, HMR and MHR are the only possible relative positions for the three involved discrete events, but allowing census at the end of each discrete event, there are six possible combinations. We only pay attention to this aspect in our discussion about the importance of census timing.

Next, we discuss some basic properties of functions f and g defined in Eqs. 6 and 7, respectively. An interesting observation is that the only difference between maps f and g is that parameter a in the expression of g is multiplied by $(1-h)$. This simple fact allows us to easily translate the properties of one map to the other and also to analyze the difference between them. This difference becomes crucial, because it explains (theoretically) the different dynamical consequences between harvesting after or before breeding.

It is easy to check that maps f and g do not have any positive fixed point if $R_0 := r + \ln(1-h) \le 0$, so populations are doomed to extinction if h exceeds the critical value $h^* := 1 - e^{-r}$. Next, we assume that $h < h^*$ (equivalently, $R_0 > 0$). An elementary analysis (see, e.g., (Rodriguez 1988) for a related study) shows that f can have either one or three critical points. Indeed, if $r(1-h) \le ae$ then f is

Fig. 1 Schematic representations of the MHR model (*left*) and the HMR model (*right*)



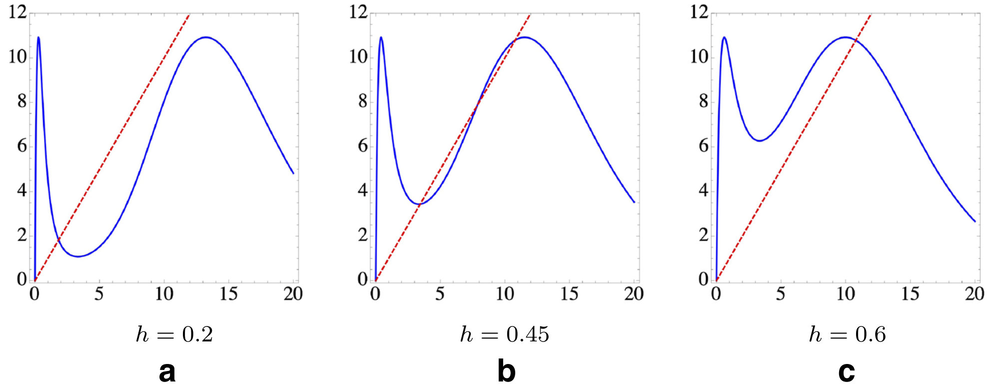


Fig. 2 Representation of the curve $y = f(x)$ defined by the right-hand side of the MHR model (6) (*solid line*) and the line $y = x$ (*dashed line*) for $r = 5, a = 0.3$, and three different values of the harvesting rate h

unimodal, with a unique critical point (a local maximum) at $c_2 = 1/a$. If $r(1 - h) > ae$ then the point c_2 becomes a local minimum, and f has two local maxima at c_1, c_3, with $0 < c_1 < c_2 < c_3$ and $f(c_1) = f(c_3) = e^{r-1}/r$.

If f is unimodal, then it has a unique positive equilibrium K, which is a global attractor if it is locally asymptotically stable. Otherwise, there is a nontrivial attractor that can be a periodic orbit or a chaotic attractor, but bistability is not possible. However, if f has three critical points, the possibility for coexistence of two nontrivial attractors appears if r is large enough (see, e.g., Fig. 4). Analytic conditions for the existence of more than one positive equilibrium are available (using the Appendix by Rodriguez (1988)). A necessary condition is $R_0 \geq 4$, and therefore, r cannot be small.

An interesting outcome of the existence of three positive equilibria is that increasing harvesting can either promote or prevent bistability and also lead to an abrupt change of the attracting equilibrium. For an illustration, see Fig. 2, where the map f is represented for $r = 5, a = 0.3$, and three different values of h. For $h = 0.2$, there is only one positive equilibrium; for $h = 0.45$, f has three positive fixed points; and, for $h = 0.6$, there is again only one positive equilibrium, but it is much larger than the one for $h = 0.2$. We notice that when f has only one positive equilibrium, it attracts all solutions of Eq. 6 with positive initial conditions (the same arguments from Liz (2016) are valid). Thus, an increasing mortality due to harvesting leads to a non-smooth hydra effect. This effect was formally defined by Sieber and Hilker (2012), and it means that the average population size undergoes a sudden jump leading to a hydra effect of large magnitude (see also Schreiber and Rudolf (2008), Abrams (2009)).

In order to understand the influence of the involved parameters on the dynamics of model (6), we fix $r = 5$ and plot the stability diagram in the plane of parameters (h, a); see Fig. 3. The solid lines correspond to the border of the region where there are three positive equilibria; these curves can be determined analytically by a procedure similar to the one reported in the Appendix by Rodriguez (1988). The dashed lines determine the regions where one of the equilibria loses its asymptotic stability; if we denote the equilibria by K_1, K_2, K_3, with $0 < K_1 < K_2 < K_3$, then K_2 is always unstable. The stability boundaries for K_1 and K_3 are plotted numerically.

Figure 3 is especially useful to understand the changes in the dynamics of Eq. 6 as the harvesting rate h is increased. To further illustrate this item, we plot the bifurcation diagrams for the values $a = 0.3$ and $a = 0.37$. See Fig. 4.

From Fig. 4, we can report some interesting phenomena in the population responses to increasing harvesting.

1. First, increasing harvesting can either promote or prevent coexistence of two nontrivial attractors. For $a = 0.3$ (Fig. 4a), two stable positive equilibria coexist for $h \in (0.405, 0.495)$, while for $h > 0.495$ there is a globally attracting equilibrium. For $a = 0.37$ (Fig. 4b), coexistence of two nontrivial attractors occur for $h \in$

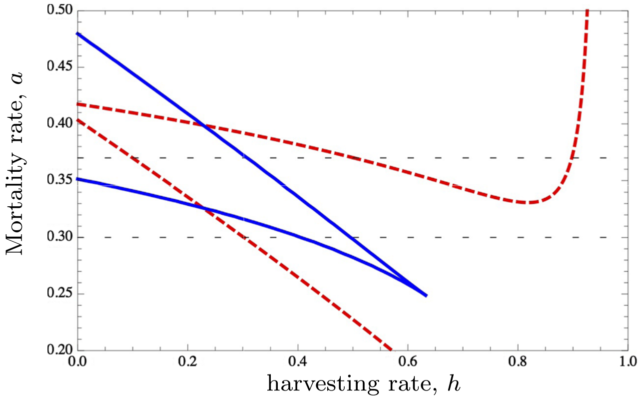


Fig. 3 Stability diagram for the MHR model defined by Eq. 6, with $r = 5$. In the region enclosed by the two *solid lines*, the equation has three equilibria. The *red dashed lines* are the stability boundaries where the lower equilibrium K_1 or the higher equilibrium K_3 undergo stability switches. The *horizontal black dashed lines* correspond to the values of parameter a for which a bifurcation diagram is plotted in Fig. 4; namely, $a = 0.3$ in Fig. 4a, and $a = 0.37$ in Fig. 4b

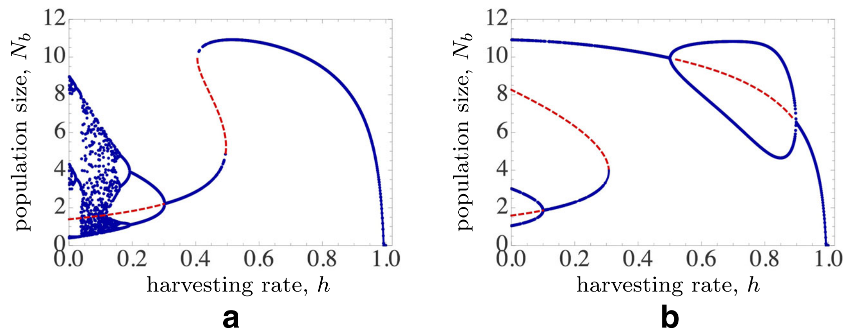


Fig. 4 Two bifurcation diagrams for the MHR model defined by Eq. 6, using the harvesting rate h as the bifurcation parameter (*red dashed lines* correspond to unstable equilibria). **a** For $a = 0.3$ and $h = 0$, there is an unstable equilibrium K_1, and Eq. 6 exhibits chaotic behavior; as h increases, the equilibrium becomes stable at $h \approx 0.302$ and remains stable until it disappears after a tangent bifurcation at $h \approx 0.495$. At $h \approx 0.405$, two new equilibria $K_2 < K_3$ arise; while K_2 is unstable, K_3 is asymptotically stable until it disappears at $h^* = 1-e^{-5} \approx 0.993$. **b** For $a = 0.37$ and $h = 0$, there are three positive equilibria $K_1 < K_2 < K_3$, but only K_3 is stable. K_1 becomes stable at $h \approx 0.1$, and remains stable until it disappears at $h \approx 0.307$. K_3 undergoes two stability switches, being unstable between $h \approx 0.501$ and $h \approx 0.897$

$(0, 0.307)$; on the interval $(0, 0.1)$, the equilibrium K_3 coexists with a two-periodic cycle, while for $h \in (0.1, 0.307)$, two attracting positive equilibria coexist. Thus, the long-term behavior of population size depends on the initial size, being the unstable equilibrium K_2 the boundary between the two basins of attraction.

2. The second phenomenon is a *conditional hydra effect.* This means that a population increase in response to increasing mortality is observed depending on population size. For $a = 0.3$, the equilibrium K_1 is attracting and exhibits a hydra effect for harvesting rate values in the interval $(0.302, 0.495)$. However, the upper attractor K_3 only exhibits a hydra effect in a small range of values. For $a = 0.37$, we observe a similar phenomenon, and in this case no hydra effect is observed for large values of the population size. As far as we know, conditional hydra effects do not seem to have been reported in the literature, although they are observed in other models; for example, in a structured consumer resource model studied by Schreiber and Rudolf (2008).
3. The third phenomenon is a *non-smooth hydra effect.* Non-smooth hydra effects occur in the two examples showed in Fig. 4, and they are due to tangent bifurcations where the lower equilibria K_1 and K_2 disappear. Moreover, for $a = 0.3$, the model exhibits hysteresis (Scheffer et al. 2001; Schreiber and Rudolf 2008). A dramatic consequence of the hysteresis is that if the harvesting strength is reduced, there is a dramatic drop in population size at some critical value ($h \approx 0.405$ in Fig. 4a).
4. Other phenomena that are not due to the existence of more than one positive equilibrium are a period-halving route from chaos to stability in Fig. 4a, and a *bubbling* phenomenon in Fig. 4b, that is, increasing harvesting is able to destabilize the positive equilibrium K_3, although higher values of the harvesting rate stabilize it again (see Liz and Ruiz-Herrera (2012)).

The influence of harvest timing

A biological example of the different times of harvest is autumn hunting versus spring hunting (Kokko 2001; Ratikainen et al. 2008). Thus, assuming that the breeding season corresponds to summer and the non-breeding season to winter, it can be illustrative to identify spring hunting (more generally, spring harvest) with harvesting before reproduction and after mortality (MHR model (6)), and autumn hunting with harvesting after reproduction and before mortality (HMR model (7)).

Assuming that population size is measured after recruitment, to analyze the differences between both harvesting strategies, we have to look at the relationship between maps f and g defined in Eqs. 6 and 7, respectively.

In regard to the existence of more than one positive equilibrium, the qualitative study is similar, but there are important differences. Figure 5a shows the regions where the maps f and g have more than one positive fixed point for $r = 5$. The symmetry of these regions has two consequences: first, the HMR model is more likely to exhibit bistability for larger mortality rates; second, the shift between alternative attractors that produces a non-smooth hydra effect in model MHR has the opposite effect in model HMR, that is, increasing harvesting can produce an abrupt decline of population abundance (see Fig. 5b, where the bifurcation diagram is shown for HMR with $r = 5$ and $a = 0.5$). Analogously, the sudden drop in population abundance observed in Fig. 4a due to hysteresis has the contrary effect for the MHR model. Indeed, there is a sudden increase in population size if h is reduced below a critical value $h \approx 0.137$.

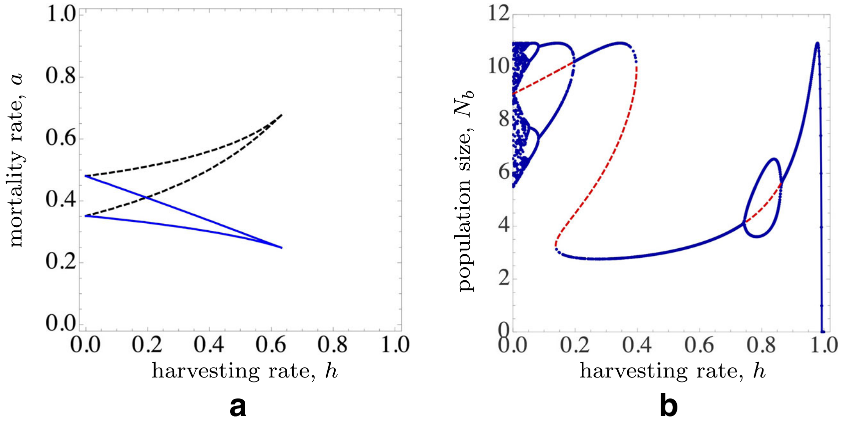


Fig. 5 **a** Regions where the MHR model defined by Eq. 6 and the HMR model defined by Eq. 7 have more than one positive equilibria for $r = 5$. The MHR model corresponds to the region enclosed by the *solid lines*, and the HMR model to the region enclosed by the *dashed lines*. Notice that the ranges of values for the parameter a where harvesting induces bistability in the two models are disjoint. Namely, increasing harvesting in the MHR model leads to bistability for $a \in [0.25, 0.35]$, while for the HMR model bistability due to harvesting occurs for $a \in [0.48, 0.68]$. For $a \in (0.35, 0.48)$ and $h = 0$, the system exhibits bistability, and increasing harvesting leads the dynamics towards a unique attractor, regardless of harvest timing (see, e.g., Fig. 4b). **b** Bifurcation diagram for the HMR model (7) with $r = 5$ and $a = 0.5$ (*red dashed lines* correspond to unstable equilibria). Increasing harvesting promotes coexistence of two nontrivial attractors. A dramatic consequence of this fact is observed at $h \approx 0.397$, where a tangent bifurcation produces a sudden population decrease from the upper stable equilibrium $K_3 \approx 9.927$ to the lower stable equilibrium $K_1 \approx 2.842$. Hydra effects, hysteresis, and a bubbling effect are also observed

Next, we use models (6) and (7) to make a theoretical interpretation of the differences between autumn and spring harvest both in regard to population abundance and stability. We notice that our model is very similar to the one proposed by Jonzén and Lundberg (1999); although we use Ricker-type functions for reproduction and mortality instead of the quadratic ones used in that reference, this fact is not crucial for the general result. According to their numerical simulations, Jonzén and Lundberg (1999) suggest that increasing harvesting is stabilizing, and the stabilizing effect is stronger for the HMR model (autumn harvest). This means that harvesting may stabilize a population that cycles in the absence of harvesting, and the necessary harvesting strength to achieve stabilization is lower if harvest occurs after reproduction but before the density-dependent mortality (HMR model). However, there is a lack of analysis of the influence of other model parameters (such as the strength of the density dependence in birth and mortality rates) in Jonzén and Lundberg (1999). This is one of the main contributions of our study, because we will show that the influence of harvest timing is parameter-dependent both for the occurrence of hydra effects and for the stabilizing role of harvesting.

As we have already observed, the difference between maps f and g defined as the right-hand sides of Eqs. 6 and 7, respectively, is that the parameter a in g is multiplied by $(1 - h)$, which makes it smaller. Hence, for stable populations, we can estimate the influence of harvest timing on population size by looking at the rate of change of the equilibrium K for Eq. 6 with respect to the mortality parameter a. This rate of change is formally represented by the partial derivative of K with respect to a and can be calculated using implicit differentiation. A negative value of $\partial K/\partial a$ means that smaller values of a make K larger, and therefore, HMR is more favorable. Analogously, a positive value of $\partial K/\partial a$ means that MHR is better if we look for higher population abundance. Our results show that $\partial K/\partial a$ is negative if either a is large enough, r is small, or h is close to 1. But for small values of a and h, $\partial K/\partial a$ is positive if r is not very small. See Fig. 6.

Roughly speaking, we can conclude that spring harvest MHR benefits population abundance for small values of the mortality parameter a and small to moderate values of the harvesting rate h. Curiously enough, we obtain similar results for stability: the stabilizing effect of harvesting is stronger for the MHR model if a is sufficiently small, and vice versa. In Fig. 7, we represent the stability boundaries for $r = 4$ (obtained numerically); notice that, for small values of a, harvesting stabilizes the MHR model first, and a bubbling effect is only possible for HMR; the opposite situation is observed for larger values of a. This observation follows from the fact that a bubbling effect is only possible if the corresponding stability boundary is not monotone. Other values of r lead to similar results.

To better visualize the influence of a in the dynamics of Eqs. 6 and 7 as harvesting rate is increased, we show the bifurcation diagrams for $r = 4$ and different values of a in Fig. 8. For $a = 0.4$, harvesting can destabilize the equilibrium (via a bubbling phenomenon) if it occurs after reproduction and before mortality (HMR), and the average

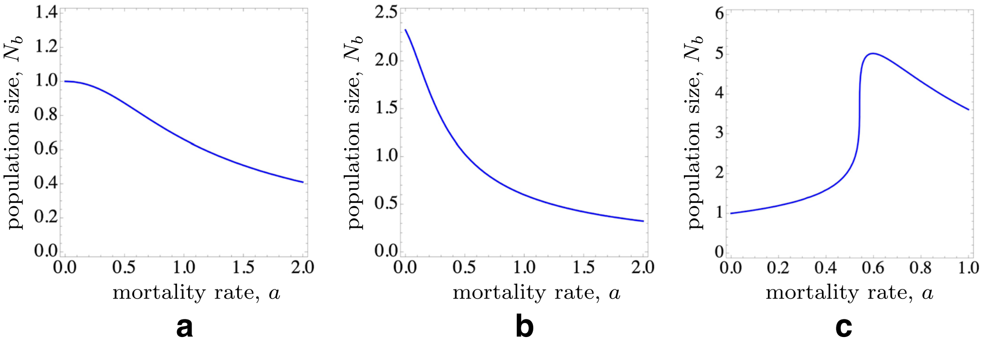


Fig. 6 Variation of the positive equilibrium K with respect to the mortality rate a in Eq. 6. **a**, **b** K is decreasing for $r = 1,\ h = 0$, and $r = 3,\ h = 0.9$, respectively. **b**, **c** For $r = 4,\ h = 0$, the profile of the equilibrium points is increasing for small values of a, and decreasing for larger values

population size is higher in the MHR model (spring harvest), except for large values of h. For $a = 0.55$, the equilibrium is stable for all values of h, and the response of the population size to increasing harvesting is dramatically different for both models when h is small, in agreement with Fig. 6c. Finally, for $a = 0.75$, the bubbling effect occurs for the MHR model, and average population size is larger in the HMR model (autumn harvest).

We also notice that the profile of the equilibrium size as harvesting rate increases may exhibit several turning points (e.g., see Fig. 8c), making hydra effects more subtle; this behavior is a direct consequence of the fact that map g can have several critical points (the profile of g with $h = 0$ determines the shape of the equilibrium curve, as explained in Liz (2010)).

The importance of census timing

Many of the bifurcation diagrams showed in the previous sections exhibit a hydra effect in different ways (smooth, non-smooth, conditional). For it to exist, the fact that population density is measured after reproduction is crucial, because in this way harvesting precedes density-dependent compensatory natality (Abrams 2009; Boyce et al. 1999). Clearly, a hydra effect due to harvesting cannot be apparent in a stable population if the population is censused just after the harvest season; in this case, hydra effects occur, but they are "hidden" if only spawners are measured (Hilker and Liz 2013).

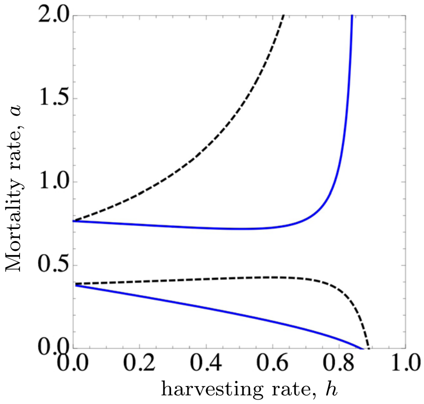


Fig. 7 Stability boundaries for the MHR model (6) (*solid lines*), and the HMR model (7) (*dashed lines*), with $r = 4$. For a given value of a, the positive equilibrium becomes stable at the corresponding stability boundary. Successive stability switches as h increases are possible for some values of a

In models of sequential density dependence, census timing is crucial, and populations should be measured as many times as a discrete event occurs during one year (Åström et al. 1996). The MHR and HMR models studied in this paper provide good examples of the different messages for management depending on census time. Recall that each of the two possible relative orders produces three different models depending on census time, although so far we have only considered one of them.

In Fig. 9, we consider the M→H→R model, corresponding to spring harvest, with $r = 4$ and $a = 0.75$. The bifurcation diagram exhibits a bubbling phenomenon regardless of census time because the dynamics do not change if the relative order of events is the same (Åström et al. 1996). However, regarding population abundance, there are important differences. Census after reproduction (MHR) shows a population decline due to an increasing harvesting rate, but population size does not reach too low values due to the compensatory natality, unless harvest pressure is too high. Thus, a manager would find acceptable moderate harvesting rates. If census takes place at the end of the non-breeding period and prior to harvest (HRM), we observe a hydra effect for low to moderate values of h, so that the manager can decide that increasing harvest is beneficial to increase population abundance. However, if we census after harvesting and before reproduction, the bifurcation diagram for the RMH model shows a population decline with very low population abundance, so that a manager would probably conclude that spring harvest is not a good strategy for this population because even low harvest rates can lead the population to extinction due to stochastic perturbations.

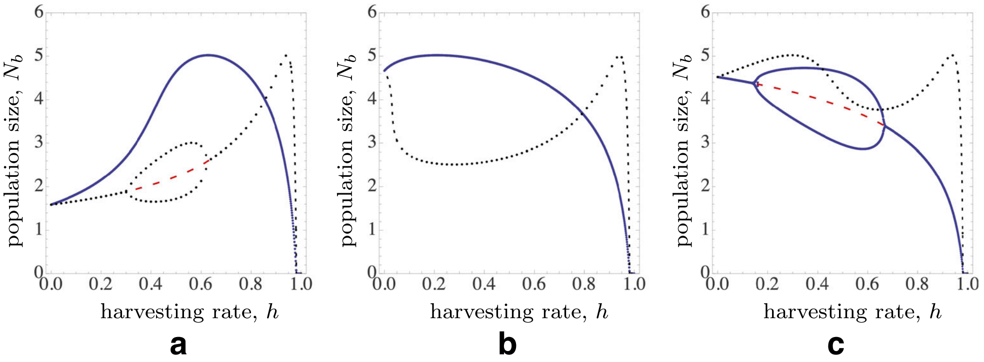


Fig. 8 Bifurcation diagrams for Eqs. 6 (*blue solid lines*) and 7 (*black dotted lines*), with $r = 4$. *Red dashed lines* correspond to unstable equilibria. **a** $a = 0.4$, **b** $a = 0.55$, **c** $a = 0.75$. See the text for more comments

Discussion

A big challenge in harvesting and management theory is predicting population responses to the removal of individuals (Ratikainen et al. 2008). Here, we aimed to address this challenge by using mathematical models to understand population responses to harvesting. Our motivation comes from seasonal populations, which are regulated by several density-dependent mechanisms operating at different seasons within the annual cycle.

We have used a time-structured discrete-time model, which is a common approach to model seasonality (Åström et al. 1996; Boyce et al. 1999; Jonzén and Lundberg 1999; Jonzén et al. 2002), and has been argued to be more intuitive than other approaches, such as the use of differential equations with periodic coefficients (Xu et al. 2005). The consideration of seasonality in discrete models not only leads to a larger repertoire of complicated dynamics (Kot and Schaffer 1984; Rodriguez 1988; Vandermeer and Yodzis 1999) but also helps to understand the influence of harvest timing, a relevant issue that has been highlighted in previous papers using other models (e.g., Kokko and Lindström (1998), Kokko (2001), Seno (2008), Cid et al. (2014)). In our approach, the consequences of different harvest timing can be easily explored by changing the relative order in which we choose to model the discrete events that operate within an annual cycle (following Åström et al. (1996), Jonzén and Lundberg (1999)). Not only harvest timing, but also the moment at which populations are censused is very relevant because some important effects might remain hidden if population abundance is only measured one time during each annual cycle (Hilker and Liz 2013); in a discrete model of sequential density dependence, the dynamics do not change if the relative order of events in the model is the same (Åström et al. 1996), but we have shown that it is crucial to look at the predictions given by the model considering all possible cyclic permutations for a given order, which corresponds to sampling the population after every process within the annual cycle.

Density-dependent processes of breeding and mortality may produce different forms of compensation if they occur after harvesting (Boyce et al. 1999), which leads populations to exhibit the so-called hydra effect (Abrams 2009). The possibility of hydra effects is one important question when managing populations, which include fishing, hunting, or control of plagues, among others. One of the more interesting outcomes of our study is to show that seasonal populations may exhibit different forms of the hydra

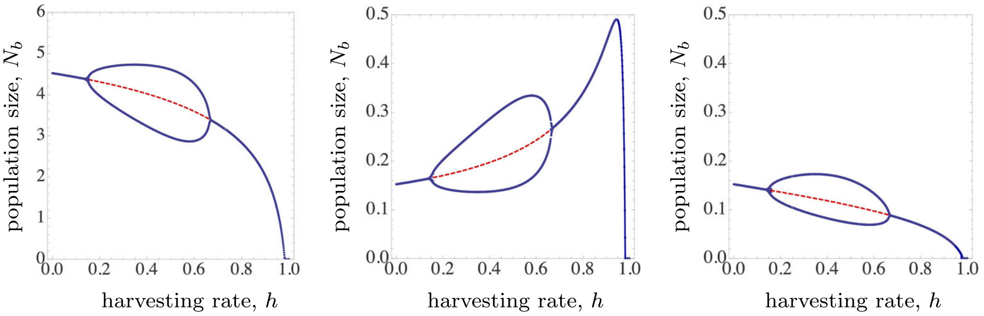


Fig. 9 Bifurcation diagrams for harvest after mortality and prior to reproduction, depending on census time. We fix $r = 4$, $a = 0, 75$, and use h as the bifurcation parameter. **a** Census after reproduction(MHR). **b** Census after mortality (HRM). **c** Census after harvesting (RMH). Notice the difference in the vertical scale; while HRM and RMH coincide when there is no harvest ($h = 0$), MHR is not comparable in magnitude. Moreover, it is worth mentioning that the only difference between panels **b** and **c** is that census occurs after harvesting in panel **c**, so that the values for population size in **b** are multiplied by $(1 - h)$ in **c**

effect. In particular, the possibility of non-smooth hydra effects reveals that there might be some critical values of the harvesting effort that induce dramatic changes in population abundance. We would like to add some cautionary words here: as it has been stressed by Abrams (2009), mathematical models usually predict that the harvest rate that maximizes population stock is slightly less than that which lead to a fast decrease in population abundance. This fact is illustrated by Fig. 5b for values of h close to one. But it is worth noticing that even for lower harvest rates (h less than 0.4), a smooth hydra effect maximizing population stock is very close to a sudden and large decline.

The phenomenon of hysteresis is also very relevant from a management point of view. For a manager who were to reduce harvest in an attempt to increase population size, the possibility of hydra effects coupled with hysteresis reveals to be crucial. For example, Fig. 4a shows that, when harvest occurs before reproduction and after natural mortality (MHR), for moderate values of h we observe that a decrease in the harvest strength would initially result in an increase in population size, but a further reduction of h leads to a dramatic drop due to hysteresis. In the opposite case, Fig. 5b shows that if harvest occurs after reproduction, then a decrease in h would result in a decrease in population abundance due to the hydra effect, but hysteresis could lead to an unexpected and dramatic increase for lower values of h.

Thus, hydra effects together with hysteresis and harvest timing must be taken into account for the management of populations that are affected by sequential density dependence. Our results emphasize that an important question in a seasonal population with a breeding (say summer) and a non-breeding season (say winter) is whether autumn harvest (HMR) is preferable to spring harvest (MHR). Our simulations (see Figs. 6, 7 and 8) reveal that the strength of density dependence in the mortality rate during winter plays an important role. Spring harvest seems to be better for increasing population abundance and decreasing variability if mortality rates are low. However, for larger values of the mortality rate a, autumn harvest is preferable (as argued in previous works). This fact may be explained because a moderate value of a together with high population abundance lead to a greater mortality due to the exponential term e^{-ax} in the equation; thus, reducing the population individuals who enter the non-breeding season will increase the number of individuals surviving it Kokko (2001).

We notice that the effects we have described are stage-specific, because we have considered a semelparous population model without age- or stage-structure. Of course, age structure can further complicate the study; for example, even if seasonality does not play a role, in a population with two age classes (juveniles and adults), it may happen that hydra or bubbling effects occur when adults are targeted, but not in a strategy of juvenile-only harvest (Zipkin et al. 2009; Liz and Pilarczyk 2012). The importance of harvest timing in structured populations has been discussed by Ratikainen et al. (2008) using the control of European rabbits as an example (e.g., see Angulo and Villafuerte (2004)).

Finally, we would like to stress that the interplay between sequential density dependence and other effects affecting population fitness can further complicate the dynamics. On the one hand, the introduction of carry-over effects in a seasonal model (Norris 2005; Ratikainen et al. 2008) influence population abundance and stability, and carry-over effects can interact with seasonal harvesting (Juillet et al. 2012); moreover, it has been recently shown that changes induced by carry-over effects in harvesting models may strongly depend on harvest timing (Liz and Ruiz-Herrera 2016). On the other hand, the consideration of Allee effects due to mate limitation in simple discrete single-species models can lead to chaotic transients and sudden collapses (Schreiber 2003). Our simulations with models (6) and (7) using—for the breeding season—a modified Ricker model with mate limitation introduced by Schreiber (2003) show that the possibility of boundary collisions producing catastrophic shifts is even higher than for the models without Allee effect considered here. We also expect a very complicated dynamics if constant quota harvesting is used instead of proportional harvesting. These issues require further study, and they will be considered in future work.

Acknowledgments The author is very much indebted to the Associate Editor and three anonymous referees, whose useful comments and insightful critique on previous versions of this manuscript led to greatly improve it. This research has been supported by the Spanish Government and FEDER, under grant MTM2013–43404–P.

References

Abrams PA (2009) When does greater mortality increase population size? The long history and diverse mechanisms underlying the hydra effect. Ecol Lett 12:462–474

Angulo E, Villafuerte R (2004) Modelling hunting strategies for the conservation of wild rabbit populations. Biol Conserv 115(2):291–301

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

Boyce MS, Sinclair ARE, White GC (1999) Seasonal compensation of predation and harvesting. Oikos 87:419–426

Calvert AM, Gauthier G (2005) Effects of exceptional conservation measures on survival and seasonal hunting mortality in greater snow geese. J Appl Ecol 42(3):442–452

Cid B, Hilker FM, Liz E (2014) Harvest timing and its population dynamic consequences in a discrete single-species model. Math. Biosci. 248:78–87

Ebbinge BS, Heesterbeek H, Ens BJ, Goedhart PW (2002) Density dependent population limitation in dark-bellied brent geese Branta b. bernicla. Avian Science 2(2):63–75

Fretwell SD (1972) Populations in a seasonal environment. Princeton University Press, Princeton

Hard J, Gross MR, Heino M, Hilborn R, Kope RG, Law R, Reynolds JD (2008) Evolutionary consequences of fishing and their implications for salmon. Evol Appl 1(2):388–408

Hilborn R, Walters CJ (1992) Quantitative Fisheries Stock Assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York

Hilker FM, Liz E (2013) Harvesting, census timing and "hidden" hydra effects. Ecol Complex 14:95–107

Holling CS (1973) Resilience and stability of ecological systems. Annu Rev Ecol Syst 4:1–23

Jonzén N, Lundberg P (1999) Temporally structured density dependence and population management. Ann Zool Fenn 36:39–44

Jonzén N, Nolet BA, Santamaría L, Svensson MG (2002) Seasonal herbivory and mortality compensation in a swan–pondweed system. Ecol Model 147(3):209–219

Juillet C, Choquet R, Gauthier G, Lefebvre J, Pradel R (2012) Carry-over effects of spring hunt and climate on recruitment to the natal colony in a migratory species. J Appl Ecol 49(6):1237–1246

Kokko H (2001) Optimal and suboptimal use of compensatory responses to harvesting: timing of hunting as an example. Wildl Biol 7:141–150

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

Kot M, Schaffer WM (1984) The effects of seasonality on discrete models of population growth. Theor Popul Biol 26:340–360

Liz E (2010) How to control chaotic behaviour and population size with proportional feedback. Phys Lett A 374(5):725–728

Liz E (2016) On the global stability of periodic Ricker maps. Electron J Qual Theory Differ Equ 76:1–8

Liz E, Pilarczyk P (2012) Global dynamics in a stage-structured discrete-time population model with harvesting. J Theor Biol 297:148–165

Liz E, Ruiz-Herrera A (2012) The hydra effect, bubbles, and chaos in a simple discrete population model with constant effort harvesting. J Math Biol 65:997–1016

Liz E, Ruiz-Herrera A (2016) Potential impact of carry-over effects in the dynamics and management of seasonal populations. PLoS ONE 11(5)

May RM (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269(5628):471–477

May RM, Oster GF (1976) Bifurcations and dynamic complexity in simple ecological models. Am Nat 110(974):573–599

McCulloch MN, Tucker GM, Baillie SR (1992) The hunting of migratory birds in Europe: a ringing recovery analysis. Ibis 134(Suppl 1):55–65

Norris DR (2005) Carry-over effects and habitat quality in migratory populations. Oikos 109(1):178–186

Ratikainen II, Gill JA, Gunnarsson TG, Sutherland WJ, Kokko H (2008) When density dependence is not instantaneous: theoretical developments and management implications. Ecol Lett 11:184–198

Ricker WE (1954) Stock and recruitment. Journal of the Fisheries Board of Canada 11(5):559–623

Rodriguez DJ (1988) Models of growth with density regulation in more than one life stage. Theor Popul Biol 34(2):93–117

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413(6856):591–596

Schreiber SJ (2003) Allee effects, extinctions, and chaotic transients in simple population models. Theor Popul Biol 64:201–209

Schreiber S, Rudolf VH (2008) Crossing habitat boundaries: coupling dynamics of ecosystems through complex life cycles. Ecol Lett 11(6):576–587

Seno H (2008) A paradox in discrete single species population dynamics with harvesting/thinning. Math Biosci 214:63–69

Sieber M, Hilker FM (2012) The hydra effect in predator-prey models. J Math Biol 64:341–360

Vandermeer J, Yodzis P (1999) Basin boundary collision as a model of discontinuous change in ecosystems. Ecology 80:1817–1827

Watkinson A (1980) Density-dependence in single-species populations of plants. J Theor Biol 83(2):345–357

Xu C, Boyce MS, Daley DJ (2005) Harvesting in seasonal environments. J Math Biol 50(6):663–682

Zipkin EF, Kraft CE, Cooch EG, Sullivan PJ (2009) When can efforts to control nuisance and invasive species backfire Ecol Appl 19:1585–1595