



Contribution to CR Special 35 'Sustainable management of renewable resources in northern ecosystems under climate change'



OPINION PIECE

Optimal harvesting in a changing climate

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ABSTRACT: Choosing the right harvesting strategy is crucial for sustainable utilization of biological resources but is challenging in real systems with fluctuating environments. This challenge is expected to become even greater with global warming, as environmental variability is predicted to increase. Additionally, harvesting strategies based on single-species models have been shown to carry a severe risk of species extinctions when species interactions are ignored, particularly in systems with more than one harvested species. As the climate continues to warm, we therefore need new reference points for harvesting in an ecosystem context with environmental fluctuations. In this paper, we discuss the development of harvesting strategies and suggest that a proportional threshold harvesting framework could be a useful starting point for developing such reference points and tackling the challenge of sustainable harvesting in the future.

KEY WORDS: Threshold harvesting · Proportional harvesting · Environmental stochasticity · Multi-species systems · Sustainable yield

1. INTRODUCTION

One of the most central topics in harvesting theory and resource management over the past decades has been how to choose the best harvesting strategies. The challenge is to find a strategy that maximizes some measure of yield without endangering the future growth of the harvested population. This is particularly challenging in fluctuating environments, as such fluctuations add an extra source of uncertainty and stochasticity to the fluctuations in population size. Climate predictions indicate that environmental variability is expected to increase in coming years as the climate warms (IPCC 2013). In addition, it has become apparent that harvesting strategies developed for single species separately, without accounting for interactions with other species, can have seriously detrimental consequences on communities (Legović et al. 2010). Thus, there is an urgent need for a re-evaluation of commonly used harvest-

ing strategies, and construction of general principles for choice of harvesting strategies for the future. In this paper, we discuss the development of harvesting strategies and identify some possible ideas for such general principles.

Choosing an appropriate strategy requires a thorough understanding of underlying stochastic population dynamics and potential population responses to harvesting. Projected climate changes are expected to cause altered population dynamics in many commercially important exploited species. This will affect not only mean population sizes but also patterns in the population fluctuations, which will be strongly influenced by changes in the temporal variability of the environment (Hansen et al. 2019). In addition, increasing evidence now indicates that harvesting in itself is likely to generate changes in the population dynamics (Hsieh et al. 2006, Anderson et al. 2008, Fryxell et al. 2010). A key challenge in the management of exploited species will therefore be to disen-

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tangle the effects on population dynamics of changes in the environment from those of harvest. A sustainable harvesting strategy must therefore be based on analyses of both environmental effects and impacts of harvesting in order to avoid over-exploitation and severe reduction in population sizes (Gamelon et al. 2019). In addition, several other factors such as demographic and spatial structure and interspecific interactions can alter the dynamics of harvested populations. Lee et al. (2022 in this Special) present recent research into some of the main factors that influence population responses to harvesting in fluctuating environments, providing a basis for harvesting models and identifying processes that must be considered when selecting a harvesting strategy for a particular system.

The theory and models that are used to predict consequences of different strategies generally assume that the strategies can be implemented accurately and without unintended bias. However, this is often difficult to ensure in natural populations. Peeters et al. (2022 in this Special) show how a quota system that is specifically developed to avoid changes in population structure in practice was found to affect the age, sex and spatial structure of the population due to hunter behavior and preferences. Once a strategy has been chosen, it is therefore essential to evaluate its implementation, both in terms of direct impacts (numbers and distribution of actual harvest offtake) and subsequent population responses. Ideally, this should be done within a framework of adaptive management and strategic foresight with stakeholder involvement (Hamel et al. 2022 in this Special).

2. OPTIMAL HARVESTING STRATEGIES

The idea of maximum sustainable yield (MSY) has been one of the most central and enduring concepts within harvesting theory. MSY assumes that there exists a certain size (Ricker 1954, Schaefer 1954) or composition (Beverton & Holt 1957) of the population at which the yield from harvesting can be maximized. Consequently, a major aim for the management of exploited species has been to direct the population towards some set reference points that are assumed to maximize the annual yield either in terms of population size, biomass or economy. MSY is a simple principle with an intuitive appeal based on transparent results from analyses of widely used population models (Clark 2010). It has therefore had an enormous impact on the development of management strategies of exploited species (Agnew 2019).

There are several challenges involved in the practical application of MSY (Larkin 1977). First, environmental stochasticity plays a major role in the realized dynamics of populations, e.g. affecting annual variation in recruitment. Second, uncertainties in population estimates may generate substantial potential for overharvesting that can seriously reduce future population sizes and hence dramatically decrease the future yield from the harvest. Third, harvested populations do not live in isolation but rather interact with other species, often changing population dynamics in relation to those predicted from the single-species models. Thus, calculations of harvesting pressures to obtain MSY are unlikely to be accurate when based on single-species deterministic harvest models, because these models fail to capture essential features affecting the dynamics of most exploited species, often leading to overharvesting (Mangel et al. 2002).

The development of harvesting theory that included stochastic fluctuations in the environment was pioneered by Beddington & May (1977) and May et al. (1978). An important general result to arise from these analyses was that in fluctuating environments, both a constant yield harvesting strategy (removing a fixed quota from the population each year) and a constant effort or proportional harvesting strategy (removing a fixed proportion of the population each year) destabilized the population dynamics by reducing the population growth rate and increasing the sensitivity to random variation in the environment. They also confirmed Larkin's (1977) assertion that MSY in a stochastically fluctuating environment was considerably lower than the deterministic MSY. Thus, it became clear that random variation in the environment has major implications for the best choice of harvesting strategy. These analyses also demonstrated that assumptions about underlying population dynamics (e.g. variation in the form of the stock-recruitment relationships) strongly affect the predicted population consequences of a given harvest strategy.

In deterministic systems, there will generally exist one optimal harvesting strategy that maximizes the annual yield, although finding this strategy can be challenging and requires knowledge of the underlying population growth model (Gilpin & Ayala 1973). However, due to the increased uncertainty and instability of harvested population dynamics in systems with fluctuating environments, choice of harvesting strategy becomes more of a trade-off between maximizing annual yield and minimizing extinction risk. There is a range of possible optimization criteria, limited by 2 extreme cases. The conservative criterion

proposed by Lande et al. (1995) maximizes the total cumulative yield from a harvested population before it ultimately goes extinct, and represents the upper limit for a sustainable harvest. In contrast, the classical goal as included in the concept of MSY formulated by Ricker (1954) is to maximize the mean annual yield, ignoring the risk of extinction or population collapse. Intermediate criteria can be selected by prescribing levels of risk related to the probability of reduction in population size to a given lower level (Lande et al. 1995). Small population sizes increase the risk of extinction and can be difficult to recover from even when exploitation is halted (Hutchings 2001).

Three of the most common simple harvesting strategies to be considered in the context of optimal harvesting are constant yield harvesting, proportional harvesting (in which the annual yield is proportional to the population size N) and threshold (or constant escapement) harvesting (in which all individuals above a critical population size are removed and no harvest takes place if the population is below the threshold) (Getz & Haight 1989, Lande et al. 1995). As long as the threshold is set high enough, threshold harvesting carries less risk of destabilizing population dynamics and driving populations to extinction, because exploitation does not continue at small population sizes (Fig. 1). In fact, a general outcome from analyses of these harvesting strategies is that for a wide class of population models, threshold harvesting is the strategy that maximizes the mean annual yield (Lande et al. 1997, Sæther et al. 2001). However, a major drawback of threshold harvesting is that it causes high annual variation in the yield, with frequent years of no harvest (Fig. 1e,k) (Lande et al. 1997). This variability causes problems for the people and industries relying on harvesting. An alternative proportional harvesting strategy, i.e. harvesting only a fraction of the excess individuals above a certain threshold population size and no harvesting otherwise, can reduce the variance in the annual yield but still give acceptable risks of population collapse (Fig. 1c,f,i,l) (Engen et al. 1997, Hilker & Liz 2019). This strategy has been applied in practice to calculate offtake of individuals to reduce the level of conflict with regard to large carnivores in Fennoscandia (Sæther et al. 2005, 2010).

When population estimates are uncertain, as is often the case, there is a risk of accidentally driving populations to extinction by setting harvest quotas based on overestimates of the actual population size (Walters & Maguire 1996, Wiedenmann & Jensen 2018). Greater uncertainty in population estimates

increases the optimal threshold for threshold harvesting (Engen et al. 1997, Tufto et al. 1999, Sæther et al. 2010). Because of this, when population estimates are highly uncertain, proportional threshold harvesting not only reduces the variance in annual yield, but also outperforms threshold harvesting in optimizing the expected cumulative yield before extinction (Engen et al. 1997). Thus, when uncertainty in population estimates is high, as is common in real systems, proportional threshold harvesting tends to be the optimal strategy (Engen et al. 1997).

During recent decades, the focus of management strategies for exploited species has started to shift from single species to a more ecosystem-based perspective, as several studies have demonstrated clearly that simultaneously extracting more or less independent single-species MSY from an assembly of interacting species will not produce an ecologically sustainable management strategy, but rather is likely to cause severe losses of biodiversity (Legović et al. 2010, Legović & Geček 2010, Fogarty 2014, Tromeur & Doyen 2019). This shift has been particularly pronounced within fisheries, where a number of complex models of multi-species systems have been suggested as tools to improve management decisions (Plagányi 2007). In practice, these ecosystem models are generally too complex to provide simple guidelines for harvesting in systems with more than a few species (Plagányi 2007, Curti et al. 2013), but they do show promise for identifying potential impacts of different harvest scenarios when enough data are available (Natugonza et al. 2019).

The shift towards more focus on ecosystem-based management has resulted in the development of new reference points that consider risk of stock depletion of several exploited species at once for use in the advice for the international management of commercially important fish stocks (Thorpe 2019), for example as provided by the International Council for the Exploration of the Sea (ICES 2017). However, in practice, the concept of MSY still provides an important benchmark in developing ecosystem-based harvest tactics, and these new reference points reflect that, attempting to balance the risk of stock depletion and yield across multiple species for a 'multispecies MSY' (Thorpe 2019). It is not clear how the complex interspecific interactions found in most ecosystems could be accommodated in such a framework. In addition, recent developments in general harvesting theory have provided strong evidence that in fluctuating environments, harvesting has a strong impact on the spatio-temporal abundance distribution and synchrony of interacting species (Jarillo et al. 2018,

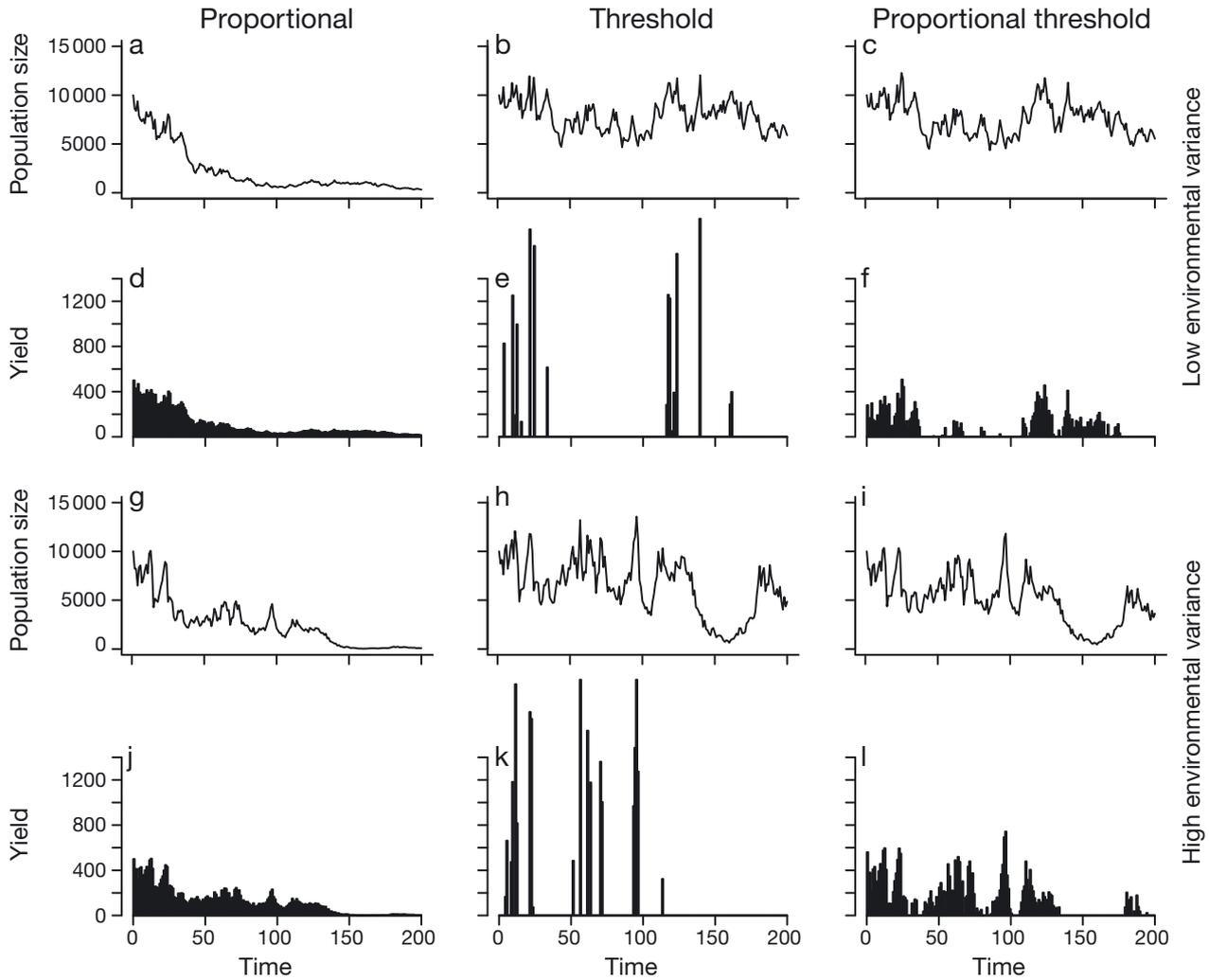


Fig. 1. Proportional threshold harvesting can give more stable annual yields than threshold harvesting without driving populations to extinction. Simulated (a–c, g–i) population trajectories and (d–f, j–l) annual yield under (a,d,g,j) proportional, (b,e,h,k) threshold and (c,f,i,l) proportional threshold harvesting for the population growth model $N_{t+1} = N_t + r_t N_t - \frac{r}{K} N^2 - y(N_t)$, where $\text{Var}(r_t) \sim N(r, \sigma_d^2 N + \sigma_e^2 N^2)$ (Engen et al. 1998), the third term on the right-hand side represents logistic density regulation, and $y(N_t)$ is harvesting yield. Population parameters were mean growth rate $r = 0.05$, carrying capacity $K = 10\,000$, demographic variance $\sigma_d^2 = 1$, and environmental variance $\sigma_e^2 = 0.01$ (a–f) and 0.04 (g–l). The harvest proportion was set equal to the mean growth rate (0.05) in a, d, g and j. The threshold above which harvesting took place was at K in b, e, h and k to maximize the expected cumulative yield before extinction (Lande et al. 1995). For proportional threshold harvesting (c,f,i,l), the proportion harvested above the threshold was set to $q = 0.1$ and the threshold was set to $K(1 - \sqrt{\pi\sigma_e^2/4q})$ to maximize the cumulative yield before extinction (Engen et al. 1997). We assumed no uncertainty in population estimates. Simulations were initiated at K using R version 4.0.1 (R Core Team 2020) and the seed was set to the same value for each harvesting strategy so that the stochastic fluctuations did not differ among strategies

2020). Thus, there is an urgent need for developing general principles for harvesting of interacting species in stochastic environments that provide reference points for an ecosystem-based management approach that preserves the structure and functioning of networks of interacting species and their spatial dynamics.

We suggest that application of a proportional threshold strategy can provide a useful approach. Within this framework, calculation of the necessary abundance, biomass or population growth to maintain interspecific interactions will provide the lower threshold below which no harvesting is allowed. This threshold can be set high for systems in which lack of data seri-

ously limits our ability to calculate sustainable population sizes. As data becomes available, allowing more accurate modeling of ecosystems, the threshold can be adjusted. In this way, complex ecosystem models (Plagányi 2007), knowledge of population dynamics and potential responses to harvesting (Lee et al. 2022) and simplified multi-species reference points for harvesting can be brought together to provide management guidance. Such a proportional threshold strategy generates less annual variation in the yield compared to the more conservative threshold strategy (Lande et al. 1995, 1997, 2003, Hilker & Liz 2019).

By combining a proportional threshold strategy with simple harvesting practices that are predicted to cause the least disruption to overall ecosystem structures, spatial patterns and interspecific interactions, this approach could generate reference points for management practices that are less likely to result in degradation of ecosystem processes. For example, balanced harvesting (Zhou et al. 2010, 2019, Garcia et al. 2012) might be a promising strategy. In balanced harvesting, different species are harvested in proportion to their natural productivity, causing less disruption to the relative abundance of species within an ecosystem than with more traditional harvesting strategies (Garcia et al. 2012). The definition and measure of productivity used can vary and has been the subject of some debate (Zhou et al. 2019), but the general idea is that more productive species with higher population growth or biomass production can sustain higher harvest mortality rates than less productive ones (Zhou et al. 2010, Garcia et al. 2012). Scaling harvest by species productivity in this way has the additional advantage of inherently accounting for differences in species' life history, which greatly influence their ability to recover from exploitation and their consequent extinction risk (Purvis et al. 2000).

Theoretical modeling has shown that adjusting harvesting of a single species by the productivity of different regions tends to reduce the spatial scale of population synchrony (Engen et al. 2018). If a similar result holds for multi-species harvesting, balanced harvesting could be a useful way to avoid forcing among-species population synchrony, which can cause multiple species in a system to simultaneously be in a population state vulnerable to stochastic extinction. By embedding new knowledge about ecosystem dynamics and responses to patterns of harvest within the proportional threshold harvest framework, the advantages of this strategy demonstrated for single-species systems in fluctuating environ-

ments (Lande et al. 1997, Sæther et al. 2001) can be harnessed for multi-species systems.

One important outcome of an approach implementing proportional threshold harvesting in an ecosystem setting is that it can provide the foundation for a long-term perspective on the implementation of harvest strategies. We are now experiencing a time in which the climate is rapidly changing and it is therefore important to apply harvest tactics that minimize interference with natural population dynamics (Gamelon et al. 2019). At the same time, we must consider the changes caused by global warming and other external factors. Many natural populations are assumed to be in a state of transient dynamics, away from stable equilibrium (Koons et al. 2005, Stott et al. 2011, Gamelon et al. 2014), and there is a possibility of harvested systems experiencing major regime shifts, reorganizing whole systems, and altering the dominance relationships among species (Scheffer et al. 2001, deYoung et al. 2004, Folke et al. 2004). In addition to developing harvesting strategies that prevent harvest-induced regime shifts, the dynamic state of natural systems requires flexible strategies that can be updated and adjusted as needed (Walters & Hilborn 1978), and suggests a need for a departure from the equilibrium theory that underlies classic harvesting theory to analysis of transient dynamics. We suggest that the advantages of proportional threshold harvesting can be extended to accommodate such changes. A proportional threshold strategy involves a threshold below which no harvest will occur. Periods without harvest will facilitate estimation of population parameters, thus improving our ability to detect trends in critical population parameters affected by climate changes and improving our foundation for modeling the population dynamics that determine responses to harvesting (Fieberg 2004). The underlying population models can be adjusted as needed to capture changes in population and community dynamics. In practice, the threshold and proportion of excess individuals removed can be kept constant for longer periods of time, making the yield a simple function of variation in population size. This will increase the potential for including climate projections in ecosystem-based harvest models because the management regimes will be simple and relatively stable over time, while at the same time improving sustainability.

3. CONCLUSIONS

Optimal harvesting requires thorough knowledge of population and community dynamics coupled with

a general harvesting strategy, followed by evaluation and adaptation of the outcome of harvesting. As the climate continues to warm and become more variable, we need new reference points for harvesting in an ecosystem context with a fluctuating environment. We suggest that a proportional threshold harvesting framework is a good starting point for developing such reference points, incorporating new knowledge of system dynamics as it becomes available.

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