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Does harvesting amplify environmentally induced population fluctuations over time in marine and terrestrial species?

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Abstract

1. In marine and terrestrial ecosystems, organisms are affected by environmental variations that cause fluctuations in population size. The harvest-interaction hypothesis predicts that environmentally-induced fluctuations in population size are magnified by harvesting. Empirical evidence is urgently needed in the context of global change because greater fluctuations will increase extinction risk.
2. Here, we review theoretical and empirical work that has addressed the harvest-interaction hypothesis in fish, birds and mammals. We identify the mechanisms by which harvesting might make population size more variable over time and thereby increase the risk of extinction.
3. Theoretical models show that harvest can modify population structure in time and space, and that changes in the amplitude and synchrony of population dynamics both increase extinction risk. Empirical evidence indicates that fishing amplifies the effects of environmental changes on the population variability, but no empirical study of

terrestrial species has tested for amplified environmentally-induced fluctuations due to hunting.

4. *Synthesis and applications.* In terrestrial species, theoretical studies have evaluated how environmentally-induced fluctuations in population size are magnified by different harvest strategies, but there is now an urgent need for an empirical evaluation of this hypothesis. Future research is needed to explore how hunting and climate interact and to test whether hunting enhances environmentally induced fluctuations in population numbers of terrestrial species.

KEYWORDS

climate change, environmental factors, fishing, hunting, population dynamics, harvesting, population size, environmentally induced fluctuations

1 | INTRODUCTION

Free-ranging populations live in a global environment that is rapidly changing. All ecosystems, from marine to terrestrial, are impacted by global drivers of environmental change. Climate variation is one of the most important drivers of annual fluctuations in population size (Sæther 1997; Gaillard, Festa-Bianchet & Yoccoz 1998; Sæther *et al.* 2016). Variability in climate may influence population size through changes in phenotypic traits such as body condition or key demographic rates including fecundity or survival (Jenouvrier 2013; Jenouvrier *et al.* 2018). For instance, climate variation impacts age of maturity, recruitment rates and hence the overall population dynamics of large herbivores (Sæther 1997; Post *et al.* 1999). Climate effects can have strong consequences on population persistence, because greater environmentally-induced fluctuations in population size will lead to higher extinction risk (Lande, Engen & Saether 2003). Exploited natural populations are also affected by commercial, recreational or subsistence harvest, with removal of individuals through fishing or hunting. The magnitude of the fluctuations in population size can be large if declining populations are overharvested or populations that start to rebound have low harvest rates (Fryxell *et al.* 2010). To maintain sustainable harvest and to avoid extinction due to overexploitation in the current context of global change, it is crucial to include the effects of environmental trends and stochastic variation in the environment in the development of sustainable harvest strategies (May *et al.* 1978; Lande, Engen & Saether 1995; Brander 2007). The question of whether harvesting amplifies the effects of environmental changes on the variability in population size over time and increases extinction risk (hereafter called “*harvest-interaction hypothesis*”) or alternatively, stabilizes population dynamics has been an unsolved problem for some years. During the last fifteen years, the question of potential interactions between climate and harvest has received growing interest in marine ecology, mainly due to the collapse of commercially important fisheries (Hutchings & Myers 1994;

Myers, Hutchings & Barrowman 1997). Here, we assess whether harvesting can amplify environmentally-induced population fluctuations and affect dynamics of exploited populations in the changing environments in both marine and terrestrial ecosystems.

Our objective was to assess the ecological consequences of harvesting in a variable environment by identifying the mechanisms causing fishing/hunting to increase environmentally-induced population fluctuations in terms of changes in population size over time. Here, we review theoretical and empirical studies based on observational or experimental approaches that have evaluated the harvest-interaction hypothesis of higher variability in exploited population sizes over time. Based on our findings, we propose new avenues of research for understanding the effects of harvest on exploited populations of marine and terrestrial organisms.

2 | HARVEST EFFECTS ON AGE/SIZE STRUCTURE

Harvesting can be proportional (or balanced) on all age/size classes in a population. However, removal of individuals through harvesting is rarely random with respect to size or demographic classes (Kuparinen & Festa-Bianchet 2017). If the oldest and largest individuals are preferentially removed, or if harvesting pressure is high, the proportion of old individuals in the populations decreases. In exploited populations of northern cod *Gadus morhua*, the age structure contained 18 age classes in the 1960s, but the older fish disappeared and the age structure was truncated to 9 age classes more recently (Drinkwater 2002). The northern cod is not an exception: age truncation is pervasive in exploited populations where the proportion of individuals in the oldest age classes drastically decreases at a severe rate (reviewed by Barnett *et al.* 2017 for 63 exploited populations of fish). A growing body of empirical evidence shows that fishing plays a key role in changes in size structure, and that climate changes such as increasing water temperature contribute to a less extent to the observed changes in size

distribution (Tu, Chen & Hsieh 2018). Size-selective harvest is problematic because the oldest individuals may have different fecundity and survival rates that buffer the population against environmental changes. In fish, large/old females are generally more fertile than small/young ones and spawn during different temporal and spatial windows (Berkeley, Chapman & Sogard 2004), hence spreading the risk of losing all the offspring when conditions are unfavorable. In ungulates, selective harvest can also lead to age truncation with a larger proportion of individuals in younger age-classes than populations not subject to hunting. Many studies have documented that in long-lived species, young individuals exhibit more variable survival rates over years than adults, adult survival being canalized and thus buffered against environmental variation (Gaillard & Yoccoz 2003), a process called “demographic buffering” (Morris & Doak 2004). Consequently, harvest-induced changes in age structure might increase sensitivity of the population dynamics to climate variation if the remaining age classes are more sensitive to climate variation. Conversely, one can expect dampened environmentally-induced population fluctuations if harvest targets young individuals that are the most sensitive to climate variation. Harvest strategies are often designed to target specific demographic classes. In many European ungulates, harvest quotas are designed to take more calves and yearlings with low reproductive value (Apollonio, Andersen & Putman 2010). In fisheries management, evidence is also accumulating that regulations stipulating a maximum size of fish that can be harvested and thus favoring the removal of the youngest/smallest individuals can reduce the negative effects of harvest (Birkeland & Dayton 2005). Selective harvest directed towards some specific age classes implies that hunters can identify the age of the individuals. Group composition, phenotypic traits or coat color can be used to identify age classes. For example, in wild boar (*Sus scrofa*), a social group is led by an old female, followed by juveniles striped until 4 months of age and wearing a reddish coat until 6 months

of age (Gamelon *et al.* 2012), making age determination straightforward. In fish, gill nets are commonly used tools to select and remove individuals of specific size-classes.

A growing body of empirical evidence shows that age truncation might enhance climate sensitivity and generate fluctuations in population size over years (Anderson *et al.* 2008). In 2012, from long-term data of 6 fish species, Rouyer *et al.* (2012) showed that high mortality due to fishing is associated with a change in age structure that enhances the population susceptibility to extrinsic environmental forcing (table 1). Five years later, Shelton and Mangel (2011) confirmed through modeling and demographic data collected from the literature including 45 fish species (table 1) that age-selective fishing increases the relative contribution of recruits and thus amplifies the destabilizing effect of climate variation. This finding has been further discussed by Sugihara *et al.* (2011). Recently, Cameron *et al.* (2016) experimentally tested the hypothesis of enhanced fluctuations in population size when adult/old individuals were removed using a terrestrial species, the soil mite (*Sancassania berlese*). The experiment consisted of different harvesting treatments under different regimes of environmental fluctuations. The authors showed that harvesting adults increased population variability but only in variable environments. In a constant environment, harvest had no effect on the coefficient of variation (CV) of population sizes over time. The laboratory study provided experimental evidence that harvesting directed towards adults can increase climatic sensitivity of exploited populations (table 1). Harvest may also select for accelerated life histories with higher fecundity, early maturity and short lifespan (Anderson *et al.* 2008; Allendorf & Hard 2009; Kuparinen & Festa-Bianchet 2017). When the rate of turnover of individuals is accelerated, a population is moved towards the fast end of the continuum of life history variation (see Gaillard *et al.* 2016) and becomes more prone to greater fluctuations in population sizes in response to variation in environmental conditions (Gamelon *et al.* 2014). In particular, environmental fluctuations generate temporal autocorrelations among fecundity,

survival and other demographic rates that in turn influence both the mean and the variance of population size (Engen et al. 2013). The effects of temporal autocorrelation on the demography depend on life history variation: species with fast life histories are more sensitive to autocorrelation than slow species with opposite characteristics (Paniw, Ozgul & Salguero-Gómez 2018). A shift towards younger age classes due to harvest that accelerates the pace of life may thus also favour autocorrelation in population dynamics. Thus, it may be difficult to disentangle whether changes in population size are caused by harvest or changes in climate conditions, which in turn may increase the risk for overexploitation and population collapse.

3 | HARVEST EFFECTS ON SPATIAL DISTRIBUTION

The distributional range of some exploited species may shift in response to climate change (Mysterud & Sæther 2010). For example, cod and pollock (*Gadus chalcogrammus*) distributions have changed over the last years in the northern oceans (Hollowed & Sundby 2014). Northbound shifts in spatial distribution allow individuals to better cope with changing environmental conditions. Harvesting per se may affect the spatial distribution of exploited species (Takashina & Mougi 2015). For instance, in a network of patches with and without harvest, individuals can move from patches without harvest to harvested patches, a process called compensatory immigration (see Gervasi *et al.* 2015 for an example on wolverines *Gulo Gulo*). Alternatively, when exposed to harvest, individuals might move to new habitats and exploit any available niche to avoid mortality risk (see Lefebvre *et al.* 2017 for an example on greater snow goose *Anser caerulescens*). Displacement can result in high spatial aggregation, or enhanced spatial heterogeneity of animal distribution (see Ciannelli *et al.* 2013 for a review on fish). Similarly, different age classes can inhabit contrasting habitats according to their age-specific needs, mobile abilities and competitive advantages (Rijnsdorp & Pastoors 1995; Nøttestad *et al.* 1999; Fauchald, Mauritzen & Gjøsæter 2006; Breau, Cunjak & Bremset

2007), resulting in homogeneous populations in terms of spatial structure capable of occupying various habitats. Harvest-induced changes in (st)age structure can also alter spatial structure and favour heterogeneity (Kuo *et al.* 2016). Empirical work has shown that such a constriction of geographic distributions associated with harvest pressure can weaken the populations' ability to buffer the effects of unfavorable environmental conditions (Planque *et al.* 2010). Populations become more vulnerable to climate variability, and fluctuations in population numbers and risk of local extinction increase (Hsieh *et al.* 2008; Kuo *et al.* 2016). If the goal of managers is to decrease population sizes, for instance to control overabundant populations of geese, increasing vulnerability to climate variability and local extinction risks might be a desirable outcome. Similarly, migration is a simple way to buffer climate-driven variations in terrestrial and marine ecosystems. Seasonal migration is a widespread phenomenon in vertebrates, being observed in fish, birds and mammals (Milner-Gulland, Fryxell & Sinclair 2011). Migration patterns can be culturally transmitted through social learning in both marine (Corten 2002) and terrestrial environments (Jesmer *et al.* 2018). Harvest of mature individuals may lead to a loss of transmission of migration knowledge to younger individuals, alter migration patterns and lead to greater sensitivity to climate change (Fryxell *et al.* 2010). Hence, harvesting can affect the spatial distribution of exploited species and shifts in distribution can be unfavourable when facing a changing climate (see Hsieh *et al.* 2010 for a review in fisheries).

Moving from the effects of harvesting on the spatial structure of a single population to populations structured in space, populations separated in space that exhibit correlated fluctuations in population size over years are theoretically more prone to extinction because local patches can go extinct without being rescued by immigration from other populations (Heino *et al.* 1997; Earn, Levin & Rohani 2000; Engen 2007). One of the key insights that has been derived from spatial population models is that increased synchrony in population

fluctuations over larger areas tends to reduce population size and increase the risk of extinction (Foley 1994; Engen, Lande & Saether 2002). Recent theoretical analyses have shown that proportional harvest itself, where the annual yield is proportional to the population size, tends to induce spatial synchrony (Engen 2017; Engen, Cao & Sæther 2018). Greater synchrony implies that spatially variation in harvest strategies including protected areas could be a way of avoiding this effect. In fact, theoretical results have shown that adjusting the harvesting rate according to local population fluctuations can result in reduced spatial scaling of the population synchrony. Spatio-temporal changes in the covariation of key environmental variables are expected due to changes in climate, which may provide a mechanism to counteract climate-induced changes in the dynamics of exploited species. For example, if the spatial scaling of the environmental noise is altered because of alteration of the climate regime, the proportion of juveniles included in the harvest will influence the spatial scaling of the distribution of abundance (Engen, Lee & Sæther 2018). Growing empirical evidence in fisheries indicates that synchronized harvest at a large spatial scale plays a key role in affecting the degree of spatial synchrony in population fluctuations, providing support for theoretical expectations. For instance, Frank et al. (2016) showed that the size of 22 populations of cod fluctuate synchronously in North Atlantic not solely due to climate but also due to harvesting.

4 | HARVEST EFFECTS ON DENSITY REGULATION

Fluctuations in size of natural populations are driven by climate effects (Sæther *et al.* 2000; Coulson *et al.* 2001; Stenseth *et al.* 2003; Berryman & Lima 2006) and also by density dependence, involving a negative feedback of the population density on the population growth rate (Royama 1992; Turchin 1995). Mechanisms can vary but include intraspecific competition, social behavior and other factors. Importantly, climate effects can interact with

density-dependent regulation of population dynamics (Turchin 1995; Stenseth *et al.* 2003; Barbraud & Weimerskirch 2003; Gamelon *et al.* 2017; Hansen *et al.* 2019). For example, effects of climate on demographic rates and population size can be stronger at high density than at low density because when climate conditions are bad, food resources are more limiting if the population is at or above carrying capacity (see Gamelon *et al.* 2017 for a case study on dippers *Cinclus cinclus*; see Hansen *et al.* 2019 for a case study on Svalbard reindeer *Rangifer tarandus*). If the population is above carrying capacity, the remaining individuals in the population after harvest might exhibit improved fecundity and survival via *compensatory density dependence* (Bonenfant *et al.* 2009), being for instance more likely to colonize habitats of better quality instead of occupying less optimal places (MacCall 1990; Marshall & Frank 1995). In contrast, reduced population sizes can be associated with lower demographic performance for the remaining individuals via Allee effects such as higher risk of starvation due to stress (reviewed by Courchamp, Berec & Gascoigne 2008; Péron 2013). The interplay between climate and density dependence (Gamelon *et al.* 2017; Hansen *et al.* 2019), and between harvest and density dependence (Boyce, Sinclair & White 1999; Sandercock *et al.* 2011) have been well studied, but an integrative approach to the combined effects of harvesting and climate on density-regulated populations remains lacking. An integrated approach is strongly needed because complex interactions between harvest, density dependence and climate variation might arise. For instance, harvest might influence the way in which a population responds to density dependence, make it more or less vulnerable to climate variation, and thus might ultimately amplify or dampen fluctuations in population sizes over time.

5 | EVIDENCE FOR HARVEST EFFECTS ON POPULATION DYNAMICS

Empirical evidence is accumulating in marine species of fish that harvesting might magnify environmentally-induced fluctuations in population sizes. In a pioneering study, Hsieh et al. (2006) compared the temporal variability of 13 exploited vs. 16 unexploited fish populations living in a common environment and subject to the same environmental fluctuations. From long-term data, they found that the CV of annual larval abundance was lower in unexploited than in exploited populations and concluded that the addition of mortality from fishing resulted in increased temporal variability of all species subject to variable environments (table 1). In terrestrial species, some studies have shown that specific harvesting strategies may increase fluctuations in population size and favor cyclicity, accentuating the risk of population collapse when environmental conditions are harsh (Fryxell et al. 2010). In a case study of black grouse (*Tetrao tetrix*), Jonzen et al. (2003) demonstrated that harvesting can cause quasi-cyclic fluctuations when the harvest fraction was time-dependent, thus reducing the ability of the population to recover when environmental conditions are unsuitable. Similarly, Bunnefeld et al. (2011) used simulations to explore the effects of selective harvest by sex and age on population cycles in red grouse (*Lagopus lagopus*). In general, a *threshold harvest strategy* that involves immediate removal of all individuals above a critical population size generates a large variance in annual yield (Sæther, Engen & Solberg 2001; Sæther et al. 2005) and large fluctuations in age distributions. Engen et al. (1997) therefore proposed a *proportional threshold strategy*, in which only a fraction of the excess individuals above a lower critical threshold is removed. Proportional threshold involves a reduction of the threshold when harvest is allowed compared to a pure threshold strategy. The modified strategy allows for an increase in the number of years harvesting is permitted, which in turn generates less variability in the annual yield (Sæther, Engen & Solberg 2001; Aanes et al. 2002; Sæther et al. 2005). Thus, the strategy should make it easier

to separate out climate-induced influences on the population dynamics and hence adjust the harvest tactics accordingly.

6 | EVIDENCE FOR HARVEST EFFECTS ON COMMUNITY DYNAMICS IN SPACE

Species live in communities with other species and can compete for limiting resources. The harvest of one species may induce cascading effects on other species because it may affect interspecific interactions and hence ecosystem processes leading to alternative stable states (Barkai & McQuaid 1988; Kirby, Beaugrand & Lindley 2009; Selkoe *et al.* 2015; Gårdmark *et al.* 2015). Surprisingly, a topic that to a large extent has been ignored is how harvesting affects the fluctuations of population size of interacting species. Jarillo *et al.* (2018) showed that proportional harvesting, in which the catches at each location are proportional to the population size, tends to synchronize fluctuations in population size of competing harvested species in space, and thus ultimately increases the probability of extinction. However, if other harvesting strategies are applied, such as *fixed quota* strategy for catches more concentrated in areas with high population sizes, the outcome can be opposite: harvesting can reduce the synchrony of the species (Engen, Cao & Sæther 2018) and thus the risk of local extinction. However, fixed quota harvest strategies are generally not sustainable on the long-run (Lande, Engen & Saether 1995; Lande, Sæther & Engen 1997). Thus, different harvesting strategies can have contrasting effects on vulnerability of interacting species over large geographical areas to changes in climate and cause spatial decoupling of ecosystem structures. Interactions imply that harvest of a given species may affect the dynamics of entire food webs, also affecting non-harvested species. The removal of species at low-trophic levels affects the dynamics of upper-trophic levels and thus the entire community (Smith *et al.* 2011). Similarly, when apex predators are removed from the ecosystem or when

their dynamics are modified by trophic down-grading, the entire ecosystem can be destabilized through trophic cascades, involving changes in the abundance of multiple interacting species subsequently to the change in abundance of a single species (McCann 2012; Terborgh 2015). Cascades can modify the response of the entire community to changing climate conditions (Estes *et al.* 2011). For instance, the removal of carnivores might lead to high abundance in herbivores as ungulates, higher herbivory and lower frequency and intensity of wildfires (Estes *et al.* 2011). In marine systems, overfishing of large-bodied fish might reduce herbivory, increase levels of disease and prevent the recovery of corals after cyclones (Hughes *et al.* 2003). In this later example, interactions among species are essential to the resilience of the community (Loreau 2010), and when some species decline or are removed from the system, interactions are broken and the ability of the entire community to recover from disturbances such as changing climate conditions decreases. Understanding such interactions has received an increasing interest in the recent years and multi-species interactions are now included in models for sustainable harvest of exploited populations (Leslie & McLeod 2007; Persson, Van Leeuwen & De Roos 2014). Ecosystem-based approaches are crucial to gain a comprehensive understanding of harvest-induced effects at the community level.

7 | CONCLUSIONS

Does harvesting increase environmentally-induced fluctuations in population size? Among empiricists, this question has mainly been addressed by marine ecologists and evidence for the “harvest-interaction hypothesis” is accumulating (table 1). The combined effect of fishing and climate on population fluctuations in fish stocks has received increasing interest in the recent years (Lindegren *et al.* 2013; Frank *et al.* 2016) and both theoretical and empirical works have provided evidence that specific types of harvesting strategies might

increase environmentally-induced fluctuations in population size and thus extinction risk. In terrestrial environments, studies evaluating the “harvest-interaction hypothesis” have mainly developed theoretical approaches to evaluate how contrasting harvesting strategies might enhance or reduce environmentally-induced fluctuations in population size. Surprisingly, empirical evidence is lacking. Few field experiments have been conducted and little is known on the combined effect of hunting and climate on population fluctuations in terrestrial species. Available studies have measured the relative contributions of climate, density dependence and harvesting on the population growth rate fluctuations (Koons *et al.* 2015 for a study on American bison *Bison bison*; López-Montoya, Moro & Azorit 2017 for a study on red *Cervus elaphus hispanicus* and fallow deer *Dama dama*) whereas other studies have evaluated the effect of different harvesting strategies on population dynamics (McGowan 1975; Mentis & Bigalke 1985; Connelly *et al.* 2003; Gervasi *et al.* 2015). Other studies have compared the dynamics of harvested vs. natural populations in similar environments (Palmer & Bennett Jr 1963; Pedersen *et al.* 2004). Tests of how harvesting enhances or dampens environmentally-induced fluctuations in population sizes by comparing the dynamics of harvested vs. natural populations in similar environments have not yet been conducted. We strongly encourage analyses of this question on a large range of species with contrasting life histories (slow versus fast species), with contrasting abilities to face environmental fluctuations (mobile versus resident species, ectotherms versus endotherms), at different trophic levels (carnivores versus herbivores) by using some of the existing long-term field studies of exploited populations. Long-term individual-based studies with capture-mark-recapture data and population counts are available for many exploited bird and mammalian populations. Analyses of time series of classified counts and harvest data can be complicated by hunting regulations and hunter preferences and also by covariation between abundance and regulations. As stated by Festa-Bianchet *et al.* (2017) “*It remains unclear, therefore, whether*

the response of heavily hunted populations to changes in density, weather, and resource availability differs from that documented by long-term studies of un hunted populations.” A promising avenue of research is to explore how hunting and climate interact and evaluate whether, like observed in marine species, hunting enhances environmentally-induced fluctuations in population sizes for terrestrial exploited species. Both the theory and the data are now available to address this question of major importance in ecology, management and conservation in exploited avian and mammalian populations.

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AUTHORS’ CONTRIBUTIONS

M.G. led the writing of the manuscript. B.K.S. and B.-E.S contributed to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data have not been archived because this article does not contain data.

356 Table 1 – Case studies with evidence that harvesting enhances environmentally-induced fluctuations in population sizes.

Species	Environment	Approach	Evidence for effects of harvest on greater environmentally-induced fluctuations in population sizes	Source
29 species	Marine	Observational	“This well-documented mechanism [age truncation] suggests how fishing can make populations more susceptible to extrinsic environmental forcing.”	Hsieh et al. 2006
6 species	Marine	Observational	“Our results demonstrate that populations exhibiting a truncation of their age structure were associated with shorter-term fluctuations in time series, which suggests an increased sensitivity to the short-term changes in the environment.”	Rouyer et al. 2012
45 species	Marine	Observational	“In a variable environment, the addition of mortality from fishing leads to increased temporal variability for all species examined.”	Shelton and Mangel 2011
1 species of acarid mite	Terrestrial	Experimental	“Only when environmental variation and harvesting were combined did we see strong evidence of magnified fluctuations in abundance.”	Cameron et al. 2016

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