



**HAL**  
open science

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

Marlène Gamelon, Brett K Sandercock, Bernt-erik Sæther

► **To cite this version:**

Marlène Gamelon, Brett K Sandercock, Bernt-erik Sæther. Does harvesting amplify environmentally induced population fluctuations over time in marine and terrestrial species?. *Journal of Applied Ecology*, 2019, 56 (9), pp.2186 - 2194. 10.1111/1365-2664.13466 . hal-03282120

**HAL Id: hal-03282120**

**<https://hal.science/hal-03282120v1>**

Submitted on 8 Jul 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3

4 Marlène Gamelon<sup>1,\*</sup>, Brett K. Sandercock<sup>2</sup> and Bernt-Erik Sæther<sup>1</sup>

5 <sup>1</sup>Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science  
6 and Technology, 7491 Trondheim, Norway.

7 <sup>2</sup>Department of Terrestrial Ecology, Norwegian Institute for Nature Research, 7485  
8 Trondheim, Norway.

9

10 \*Correspondence: [marlene.gamelon@ntnu.no](mailto:marlene.gamelon@ntnu.no)

11

12 **Abstract**

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

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

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

34

35 **KEYWORDS**

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

38

## 39 1 | INTRODUCTION

40 Free-ranging populations live in a global environment that is rapidly changing. All  
41 ecosystems, from marine to terrestrial, are impacted by global drivers of environmental  
42 change. Climate variation is one of the most important drivers of annual fluctuations in  
43 population size (Sæther 1997; Gaillard, Festa-Bianchet & Yoccoz 1998; Sæther *et al.* 2016).  
44 Variability in climate may influence population size through changes in phenotypic traits such  
45 as body condition or key demographic rates including fecundity or survival (Jenouvrier 2013;  
46 Jenouvrier *et al.* 2018). For instance, climate variation impacts age of maturity, recruitment  
47 rates and hence the overall population dynamics of large herbivores (Sæther 1997; Post *et al.*  
48 1999). Climate effects can have strong consequences on population persistence, because  
49 greater environmentally-induced fluctuations in population size will lead to higher extinction  
50 risk (Lande, Engen & Saether 2003). Exploited natural populations are also affected by  
51 commercial, recreational or subsistence harvest, with removal of individuals through fishing  
52 or hunting. The magnitude of the fluctuations in population size can be large if declining  
53 populations are overharvested or populations that start to rebound have low harvest rates  
54 (Fryxell *et al.* 2010). To maintain sustainable harvest and to avoid extinction due to  
55 overexploitation in the current context of global change, it is crucial to include the effects of  
56 environmental trends and stochastic variation in the environment in the development of  
57 sustainable harvest strategies (May *et al.* 1978; Lande, Engen & Saether 1995; Brander 2007).  
58 The question of whether harvesting amplifies the effects of environmental changes on the  
59 variability in population size over time and increases extinction risk (hereafter called  
60 “*harvest-interaction hypothesis*”) or alternatively, stabilizes population dynamics has been an  
61 unsolved problem for some years. During the last fifteen years, the question of potential  
62 interactions between climate and harvest has received growing interest in marine ecology,  
63 mainly due to the collapse of commercially important fisheries (Hutchings & Myers 1994;

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

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

75

## 76 **2 | HARVEST EFFECTS ON AGE/SIZE STRUCTURE**

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

89 distribution (Tu, Chen & Hsieh 2018). Size-selective harvest is problematic because the oldest  
90 individuals may have different fecundity and survival rates that buffer the population against  
91 environmental changes. In fish, large/old females are generally more fertile than small/young  
92 ones and spawn during different temporal and spatial windows (Berkeley, Chapman & Sogard  
93 2004), hence spreading the risk of losing all the offspring when conditions are unfavorable. In  
94 ungulates, selective harvest can also lead to age truncation with a larger proportion of  
95 individuals in younger age-classes than populations not subject to hunting. Many studies have  
96 documented that in long-lived species, young individuals exhibit more variable survival rates  
97 over years than adults, adult survival being canalized and thus buffered against environmental  
98 variation (Gaillard & Yoccoz 2003), a process called “demographic buffering” (Morris &  
99 Doak 2004). Consequently, harvest-induced changes in age structure might increase  
100 sensitivity of the population dynamics to climate variation if the remaining age classes are  
101 more sensitive to climate variation. Conversely, one can expect dampened environmentally-  
102 induced population fluctuations if harvest targets young individuals that are the most sensitive  
103 to climate variation. Harvest strategies are often designed to target specific demographic  
104 classes. In many European ungulates, harvest quotas are designed to take more calves and  
105 yearlings with low reproductive value (Apollonio, Andersen & Putman 2010). In fisheries  
106 management, evidence is also accumulating that regulations stipulating a maximum size of  
107 fish that can be harvested and thus favoring the removal of the youngest/smallest individuals  
108 can reduce the negative effects of harvest (Birkeland & Dayton 2005). Selective harvest  
109 directed towards some specific age classes implies that hunters can identify the age of the  
110 individuals. Group composition, phenotypic traits or coat color can be used to identify age  
111 classes. For example, in wild boar (*Sus scrofa*), a social group is led by an old female,  
112 followed by juveniles striped until 4 months of age and wearing a reddish coat until 6 months

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

115 A growing body of empirical evidence shows that age truncation might enhance climate  
116 sensitivity and generate fluctuations in population size over years (Anderson *et al.* 2008). In  
117 2012, from long-term data of 6 fish species, Rouyer *et al.* (2012) showed that high mortality  
118 due to fishing is associated with a change in age structure that enhances the population  
119 susceptibility to extrinsic environmental forcing (table 1). Five years later, Shelton and  
120 Mangel (2011) confirmed through modeling and demographic data collected from the  
121 literature including 45 fish species (table 1) that age-selective fishing increases the relative  
122 contribution of recruits and thus amplifies the destabilizing effect of climate variation. This  
123 finding has been further discussed by Sugihara *et al.* (2011). Recently, Cameron *et al.* (2016)  
124 experimentally tested the hypothesis of enhanced fluctuations in population size when  
125 adult/old individuals were removed using a terrestrial species, the soil mite (*Sancassania*  
126 *berlese*). The experiment consisted of different harvesting treatments under different regimes  
127 of environmental fluctuations. The authors showed that harvesting adults increased population  
128 variability but only in variable environments. In a constant environment, harvest had no effect  
129 on the coefficient of variation (CV) of population sizes over time. The laboratory study  
130 provided experimental evidence that harvesting directed towards adults can increase climatic  
131 sensitivity of exploited populations (table 1). Harvest may also select for accelerated life  
132 histories with higher fecundity, early maturity and short lifespan (Anderson *et al.* 2008;  
133 Allendorf & Hard 2009; Kuparinen & Festa-Bianchet 2017). When the rate of turnover of  
134 individuals is accelerated, a population is moved towards the fast end of the continuum of life  
135 history variation (see Gaillard *et al.* 2016) and becomes more prone to greater fluctuations in  
136 population sizes in response to variation in environmental conditions (Gamelon *et al.* 2014).  
137 In particular, environmental fluctuations generate temporal autocorrelations among fecundity,

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

146

### 147 **3 | HARVEST EFFECTS ON SPATIAL DISTRIBUTION**

148 The distributional range of some exploited species may shift in response to climate  
149 change (Mysterud & Sæther 2010). For example, cod and pollock (*Gadus chalcogrammus*)  
150 distributions have changed over the last years in the northern oceans (Hollowed & Sundby  
151 2014). Northbound shifts in spatial distribution allow individuals to better cope with changing  
152 environmental conditions. Harvesting per se may affect the spatial distribution of exploited  
153 species (Takashina & Mougi 2015). For instance, in a network of patches with and without  
154 harvest, individuals can move from patches without harvest to harvested patches, a process  
155 called compensatory immigration (see Gervasi *et al.* 2015 for an example on wolverines *Gulo*  
156 *Gulo*). Alternatively, when exposed to harvest, individuals might move to new habitats and  
157 exploit any available niche to avoid mortality risk (see Lefebvre *et al.* 2017 for an example on  
158 greater snow goose *Anser caerulescens*). Displacement can result in high spatial aggregation,  
159 or enhanced spatial heterogeneity of animal distribution (see Ciannelli *et al.* 2013 for a review  
160 on fish). Similarly, different age classes can inhabit contrasting habitats according to their  
161 age-specific needs, mobile abilities and competitive advantages (Rijnsdorp & Pastoors 1995;  
162 Nøttestad *et al.* 1999; Fauchald, Mauritzen & Gjøsaeter 2006; Breau, Cunjak & Bremset



163 2007), resulting in homogeneous populations in terms of spatial structure capable of  
164 occupying various habitats. Harvest-induced changes in (st)age structure can also alter spatial  
165 structure and favour heterogeneity (Kuo *et al.* 2016). Empirical work has shown that such a  
166 constriction of geographic distributions associated with harvest pressure can weaken the  
167 populations' ability to buffer the effects of unfavorable environmental conditions (Planque *et*  
168 *al.* 2010). Populations become more vulnerable to climate variability, and fluctuations in  
169 population numbers and risk of local extinction increase (Hsieh *et al.* 2008; Kuo *et al.* 2016).  
170 If the goal of managers is to decrease population sizes, for instance to control overabundant  
171 populations of geese, increasing vulnerability to climate variability and local extinction risks  
172 might be a desirable outcome. Similarly, migration is a simple way to buffer climate-driven  
173 variations in terrestrial and marine ecosystems. Seasonal migration is a widespread  
174 phenomenon in vertebrates, being observed in fish, birds and mammals (Milner-Gulland,  
175 Fryxell & Sinclair 2011). Migration patterns can be culturally transmitted through social  
176 learning in both marine (Corten 2002) and terrestrial environments (Jesmer *et al.* 2018).  
177 Harvest of mature individuals may lead to a loss of transmission of migration knowledge to  
178 younger individuals, alter migration patterns and lead to greater sensitivity to climate change  
179 (Fryxell *et al.* 2010). Hence, harvesting can affect the spatial distribution of exploited species  
180 and shifts in distribution can be unfavourable when facing a changing climate (see Hsieh *et al.*  
181 2010 for a review in fisheries).

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

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

206

#### 207 **4 | HARVEST EFFECTS ON DENSITY REGULATION**

208 Fluctuations in size of natural populations are driven by climate effects (Sæther *et al.*  
209 2000; Coulson *et al.* 2001; Stenseth *et al.* 2003; Berryman & Lima 2006) and also by density  
210 dependence, involving a negative feedback of the population density on the population  
211 growth rate (Royama 1992; Turchin 1995). Mechanisms can vary but include intraspecific  
212 competition, social behavior and other factors. Importantly, climate effects can interact with

213 density-dependent regulation of population dynamics (Turchin 1995; Stenseth *et al.* 2003;  
214 Barbraud & Weimerskirch 2003; Gamelon *et al.* 2017; Hansen *et al.* 2019). For example,  
215 effects of climate on demographic rates and population size can be stronger at high density  
216 than at low density because when climate conditions are bad, food resources are more limiting  
217 if the population is at or above carrying capacity (see Gamelon *et al.* 2017 for a case study on  
218 dippers *Cinclus cinclus*; see Hansen *et al.* 2019 for a case study on Svalbard reindeer *Rangifer*  
219 *tarandus*). If the population is above carrying capacity, the remaining individuals in the  
220 population after harvest might exhibit improved fecundity and survival via *compensatory*  
221 *density dependence* (Bonenfant *et al.* 2009), being for instance more likely to colonize  
222 habitats of better quality instead of occupying less optimal places (MacCall 1990; Marshall &  
223 Frank 1995). In contrast, reduced population sizes can be associated with lower demographic  
224 performance for the remaining individuals via Allee effects such as higher risk of starvation  
225 due to stress (reviewed by Courchamp, Berec & Gascoigne 2008; Péron 2013). The interplay  
226 between climate and density dependence (Gamelon *et al.* 2017; Hansen *et al.* 2019), and  
227 between harvest and density dependence (Boyce, Sinclair & White 1999; Sandercock *et al.*  
228 2011) have been well studied, but an integrative approach to the combined effects of  
229 harvesting and climate on density-regulated populations remains lacking. An integrated  
230 approach is strongly needed because complex interactions between harvest, density  
231 dependence and climate variation might arise. For instance, harvest might influence the way  
232 in which a population responds to density dependence, make it more or less vulnerable to  
233 climate variation, and thus might ultimately amplify or dampen fluctuations in population  
234 sizes over time.

235

236 **5 | EVIDENCE FOR HARVEST EFFECTS ON POPULATION DYNAMICS**

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

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

263

## 264 **6 | EVIDENCE FOR HARVEST EFFECTS ON COMMUNITY DYNAMICS IN** 265 **SPACE**

266 Species live in communities with other species and can compete for limiting resources.

267 The harvest of one species may induce cascading effects on other species because it may  
268 affect interspecific interactions and hence ecosystem processes leading to alternative stable  
269 states (Barkai & McQuaid 1988; Kirby, Beaugrand & Lindley 2009; Selkoe *et al.* 2015;  
270 Gårdmark *et al.* 2015). Surprisingly, a topic that to a large extent has been ignored is how  
271 harvesting affects the fluctuations of population size of interacting species. Jarillo *et al.*  
272 (2018) showed that proportional harvesting, in which the catches at each location are  
273 proportional to the population size, tends to synchronize fluctuations in population size of  
274 competing harvested species in space, and thus ultimately increases the probability of  
275 extinction. However, if other harvesting strategies are applied, such as *fixed quota* strategy for  
276 catches more concentrated in areas with high population sizes, the outcome can be opposite:  
277 harvesting can reduce the synchrony of the species (Engen, Cao & Sæther 2018) and thus the  
278 risk of local extinction. However, fixed quota harvest strategies are generally not sustainable  
279 on the long-run (Lande, Engen & Saether 1995; Lande, Sæther & Engen 1997). Thus,  
280 different harvesting strategies can have contrasting effects on vulnerability of interacting  
281 species over large geographical areas to changes in climate and cause spatial decoupling of  
282 ecosystem structures. Interactions imply that harvest of a given species may affect the  
283 dynamics of entire food webs, also affecting non-harvested species. The removal of species at  
284 low-trophic levels affects the dynamics of upper-trophic levels and thus the entire community  
285 (Smith *et al.* 2011). Similarly, when apex predators are removed from the ecosystem or when

286 their dynamics are modified by trophic down-grading, the entire ecosystem can be  
287 destabilized through trophic cascades, involving changes in the abundance of multiple  
288 interacting species subsequently to the change in abundance of a single species (McCann  
289 2012; Terborgh 2015). Cascades can modify the response of the entire community to  
290 changing climate conditions (Estes *et al.* 2011). For instance, the removal of carnivores might  
291 lead to high abundance in herbivores as ungulates, higher herbivory and lower frequency and  
292 intensity of wildfires (Estes *et al.* 2011). In marine systems, overfishing of large-bodied fish  
293 might reduce herbivory, increase levels of disease and prevent the recovery of corals after  
294 cyclones (Hughes *et al.* 2003). In this later example, interactions among species are essential  
295 to the resilience of the community (Loreau 2010), and when some species decline or are  
296 removed from the system, interactions are broken and the ability of the entire community to  
297 recover from disturbances such as changing climate conditions decreases. Understanding such  
298 interactions has received an increasing interest in the recent years and multi-species  
299 interactions are now included in models for sustainable harvest of exploited populations  
300 (Leslie & McLeod 2007; Persson, Van Leeuwen & De Roos 2014). Ecosystem-based  
301 approaches are crucial to gain a comprehensive understanding of harvest-induced effects at  
302 the community level.

303

## 304 **7 | CONCLUSIONS**

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

311 increase environmentally-induced fluctuations in population size and thus extinction risk. In  
312 terrestrial environments, studies evaluating the “harvest-interaction hypothesis” have mainly  
313 developed theoretical approaches to evaluate how contrasting harvesting strategies might  
314 enhance or reduce environmentally-induced fluctuations in population size. Surprisingly,  
315 empirical evidence is lacking. Few field experiments have been conducted and little is known  
316 on the combined effect of hunting and climate on population fluctuations in terrestrial species.  
317 Available studies have measured the relative contributions of climate, density dependence and  
318 harvesting on the population growth rate fluctuations (Koons *et al.* 2015 for a study on  
319 American bison *Bison bison*; López-Montoya, Moro & Azorit 2017 for a study on red *Cervus*  
320 *elaphus hispanicus* and fallow deer *Dama dama*) whereas other studies have evaluated the  
321 effect of different harvesting strategies on population dynamics (McGowan 1975; Mentis &  
322 Bigalke 1985; Connelly *et al.* 2003; Gervasi *et al.* 2015). Other studies have compared the  
323 dynamics of harvested vs. natural populations in similar environments (Palmer & Bennett Jr  
324 1963; Pedersen *et al.* 2004). Tests of how harvesting enhances or dampens environmentally-  
325 induced fluctuations in population sizes by comparing the dynamics of harvested vs. natural  
326 populations in similar environments have not yet been conducted. We strongly encourage  
327 analyses of this question on a large range of species with contrasting life histories (slow  
328 versus fast species), with contrasting abilities to face environmental fluctuations (mobile  
329 versus resident species, ectotherms versus endotherms), at different trophic levels (carnivores  
330 versus herbivores) by using some of the existing long-term field studies of exploited  
331 populations. Long-term individual-based studies with capture-mark-recapture data and  
332 population counts are available for many exploited bird and mammalian populations.  
333 Analyses of time series of classified counts and harvest data can be complicated by hunting  
334 regulations and hunter preferences and also by covariation between abundance and  
335 regulations. As stated by Festa-Bianchet *et al.* (2017) “*It remains unclear, therefore, whether*

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

343

#### 344 **ACKNOWLEDGEMENTS**

345 We thank Marco Festa-Bianchet, John Fryxell, one anonymous referee and the Editor for their  
346 helpful comments on previous drafts of this paper. Our study was funded by the Research  
347 Council of Norway as part of the Centre of Excellence-grant to CBD (SFF-III 223257/F50)  
348 and to SUSTAIN (244647/E10).

349

#### 350 **AUTHORS’ CONTRIBUTIONS**

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

353

#### 354 **DATA ACCESSIBILITY**

355 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

357 **REFERENCES**

- 358  
359 Aanes, S., Engen, S., Sæther, B.-E., Willebrand, T. & Marcström, V. (2002) Sustainable  
360 harvesting strategies of willow Ptarmigan in a fluctuating environment. *Ecological*  
361 *Applications*, **12**, 281–290.
- 362 Allendorf, F.W. & Hard, J.J. (2009) Human-induced evolution caused by unnatural selection  
363 through harvest of wild animals. *Proceedings of the National Academy of Sciences*,  
364 **106**, 9987–9994.
- 365 Anderson, C.N.K., Hsieh, C., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J., May,  
366 R.M. & Sugihara, G. (2008) Why fishing magnifies fluctuations in fish abundance.  
367 *Nature*, **452**, 835–839.
- 368 Apollonio, M., Andersen, R. & Putman, R. (2010) European ungulates and their management  
369 21st century
- 370 Barbraud, C. & Weimerskirch, H. (2003) Climate and density shape population dynamics of a  
371 marine top predator. *Proceedings of the Royal Society B: Biological Sciences*, **270**,  
372 2111–2116.
- 373 Barkai, A. & McQuaid, C. (1988) Predator-Prey Role Reversal in a Marine Benthic  
374 Ecosystem. *Science*, **242**, 62–64.
- 375 Barnett, L.A.K., Branch, T.A., Ranasinghe, R.A. & Essington, T.E. (2017) Old-growth fishes  
376 become scarce under fishing. *Current Biology*, **27**, 2843-2848.e2.
- 377 Berkeley, S.A., Chapman, C. & Sogard, S.M. (2004) Maternal age as a determinant of larval  
378 growth and survival in a marine fish, *Sebastes melanops*. *Ecology*, **85**, 1258–1264.
- 379 Berryman, A. & Lima, M. (2006) Deciphering the effects of climate on animal populations:  
380 diagnostic analysis provides new interpretation of Soay sheep dynamics. *The*  
381 *American Naturalist*, **168**, 784–795.
- 382 Birkeland, C. & Dayton, P.K. (2005) The importance in fishery management of leaving the  
383 big ones. *Trends in Ecology & Evolution*, **20**, 356–358.
- 384 Bonenfant, C., Gaillard, J., Coulson, T., Festa-Bianchet, M., Loison, A., Garel, M., Loe, L.E.,  
385 Blanchard, P., Pettorelli, N., Owen-Smith, N., Du Toit, J. & Duncan, P. (2009)  
386 Empirical evidence of density-dependence in populations of large herbivores.  
387 *Advances in Ecological Research* (ed H. Caswell), pp. 313–357. Academic Press.
- 388 Boyce, M.S., Sinclair, A.R.E. & White, G.C. (1999) Seasonal compensation of predation and  
389 harvesting. *Oikos*, **87**, 419–426.
- 390 Brander, K.M. (2007) Global fish production and climate change. *Proceedings of the National*  
391 *Academy of Sciences of the United States of America*, **104**, 19709–19714.
- 392 Breau, C., Cunjak, R.A. & Bremset, G. (2007) Age-specific aggregation of wild juvenile  
393 Atlantic salmon *Salmo salar* at cool water sources during high temperature events.  
394 *Journal of Fish Biology*, **71**, 1179–1191.
- 395 Bunnefeld, N., Reuman, D.C., Baines, D. & Milner-Gulland, E.J. (2011) Impact of  
396 unintentional selective harvesting on the population dynamics of red grouse. *The*  
397 *Journal of Animal Ecology*, **80**, 1258–1268.
- 398 Cameron, T.C., O’Sullivan, D., Reynolds, A., Hicks, J.P., Piertney, S.B. & Benton, T.G.  
399 (2016) Harvested populations are more variable only in more variable environments.  
400 *Ecology and Evolution*, **6**, 4179–4191.
- 401 Ciannelli, L., Fisher, J.A.D., Skern-Mauritzen, M., Hunsicker, M.E., Hidalgo, M., Frank, K.T.  
402 & Bailey, K.M. (2013) Theory, consequences and evidence of eroding population  
403 spatial structure in harvested marine fishes: a review. *Marine Ecology Progress*  
404 *Series*, **480**, 227–243.

- 405 Connelly, J.W., Reese, K.P., Garton, E.O. & Commons-Kemner, M.L. (2003) Response of  
 406 greater sage-grouse *Centrocercus urophasianus* populations to different levels of  
 407 exploitation in Idaho, USA. *Wildlife Biology*, **9**, 335–340.
- 408 Corten, A. (2002) The role of conservatism in herring migrations. *Reviews in Fish Biology*  
 409 *and Fisheries*, **11**, 339–361.
- 410 Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock,  
 411 T.H., Crawley, M.J. & Grenfell, B.T. (2001) Age, sex, density, winter weather, and  
 412 population crashes in Soay sheep. *Science*, **292**, 1528–1531.
- 413 Courchamp, F., Berec, L. & Gascoigne, J. (2008) *Allee Effects in Ecology and Conservation*.  
 414 OUP Oxford, Oxford ; New York.
- 415 Drinkwater, K. (2002) A review of the role of climate variability in the decline of  
 416 northern cod. *Fisheries in a changing climate*, American Fisheries Society, pp. 113–  
 417 129. N.A. McGinn, Bethesda, Maryland.
- 418 Earn, D.J.D., Levin, S.A. & Rohani, P. (2000) Coherence and Conservation. *Science*, **290**,  
 419 1360–1364.
- 420 Engen, S. (2007) Stochastic growth and extinction in a spatial geometric Brownian population  
 421 model with migration and correlated noise. *Mathematical Biosciences*, **209**, 240–255.
- 422 Engen, S. (2017) Spatial synchrony and harvesting in fluctuating populations: relaxing the  
 423 small noise assumption. *Theoretical Population Biology*, **116**, 18–26.
- 424 Engen, S., Cao, F.J. & Sæther, B.-E. (2018) The effect of harvesting on the spatial synchrony  
 425 of population fluctuations. *Theoretical Population Biology*, **123**, 28–34.
- 426 Engen, S., Lande, R. & Sæther, B.-E. (1997) Harvesting strategies for fluctuating populations  
 427 based on uncertain population estimates. *Journal of Theoretical Biology*, **186**, 201–  
 428 212.
- 429 Engen, S., Lande, R. & Saether, B.-E. (2002) The spatial scale of population fluctuations and  
 430 quasi-extinction risk. *The American Naturalist*, **160**, 439–451.
- 431 Engen, S., Lee, A.M. & Sæther, B.-E. (2018) Spatial distribution and optimal harvesting of an  
 432 age-structured population in a fluctuating environment. *Mathematical Biosciences*,  
 433 **296**, 36–44.
- 434 Engen, S., Sæther, B.-E., Armitage, K.B., Blumstein, D.T., Clutton-Brock, T.H., Dobson,  
 435 F.S., Festa-Bianchet, M., Oli, M.K. & Ozgul, A. (2013) Estimating the effect of  
 436 temporally autocorrelated environments on the demography of density-independent  
 437 age-structured populations. *Methods in Ecology and Evolution*, **4**, 573–584.
- 438 Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter,  
 439 S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L.,  
 440 Oksanen, T., Paine, R.T., Pickett, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M.,  
 441 Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R. & Wardle,  
 442 D.A. (2011) Trophic downgrading of planet Earth. *Science*, **333**, 301–306.
- 443 Fauchald, P., Mauritzen, M. & Gjøsaeter, H. (2006) Density-dependent migratory waves in  
 444 the marine pelagic ecosystem. *Ecology*, **87**, 2915–2924.
- 445 Festa-Bianchet, M., Douhard, M., Gaillard, J.-M. & Pelletier, F. (2017) Successes and  
 446 challenges of long-term field studies of marked ungulates. *Journal of Mammalogy*, **98**,  
 447 612–620.
- 448 Foley, P. (1994) Predicting Extinction Times from Environmental Stochasticity and Carrying  
 449 Capacity. *Conservation Biology*, **8**, 124–137.
- 450 Frank, K.T., Petrie, B., Leggett, W.C. & Boyce, D.G. (2016) Large scale, synchronous  
 451 variability of marine fish populations driven by commercial exploitation. *Proceedings*  
 452 *of the National Academy of Sciences*, **113**, 8248–8253.

- 453 Fryxell, J.M., Packer, C., McCann, K., Solberg, E.J. & Sæther, B.-E. (2010) Resource  
454 management cycles and the sustainability of harvested wildlife populations. *Science*,  
455 **328**, 903–906.
- 456 Gaillard, J.-M., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of large  
457 herbivores: variable recruitment with constant adult survival. *Trends in Ecology &*  
458 *Evolution*, **13**, 58–63.
- 459 Gaillard, J.-M., Lemaître, J.-F., Berger, V., Bonenfant, C., Devillard, S., Douhard, M.,  
460 Gamelon, M., Plard, F. & Lebreton, J.-D. (2016) Axes of variation in life histories.  
461 *Encyclopedia of Evolutionary Biology*, Elsevier, pp. 312–323. R. M. Kliman, Oxford,  
462 UK.
- 463 Gaillard, J.-M. & Yoccoz, N.G. (2003) Temporal variation in survival of mammals: a case of  
464 environmental canalization? *Ecology*, **84**, 3294–3306.
- 465 Gamelon, M., Gaillard, J.-M., Servanty, S., Gimenez, O., Toïgo, C., Baubet, E., Klein, F. &  
466 Lebreton, J.-D. (2012) Making use of harvest information to examine alternative  
467 management scenarios: a body weight-structured model for wild boar. *Journal of*  
468 *Applied Ecology*, **49**, 833–841.
- 469 Gamelon, M., Gimenez, O., Baubet, E., Coulson, T., Tuljapurkar, S. & Gaillard, J.-M. (2014)  
470 Influence of life-history tactics on transient dynamics: a comparative analysis across  
471 mammalian populations. *The American Naturalist*, **184**, 673–683.
- 472 Gamelon, M., Grøtan, V., Nilsson, A.L.K., Engen, S., Hurrell, J.W., Jerstad, K., Phillips,  
473 A.S., Røstad, O.W., Slagsvold, T., Walseng, B., Stenseth, N.C. & Sæther, B.-E.  
474 (2017) Interactions between demography and environmental effects are important  
475 determinants of population dynamics. *Science Advances*, **3**, e1602298.
- 476 Gårdmark, A., Casini, M., Huss, M., Leeuwen, A. van, Hjelm, J., Persson, L. & de Roos,  
477 A.M. (2015) Regime shifts in exploited marine food webs: detecting mechanisms  
478 underlying alternative stable states using size-structured community dynamics theory.  
479 *Phil. Trans. R. Soc. B*, **370**, 20130262.
- 480 Gervasi, V., Brøseth, H., Nilsen, E.B., Ellegren, H., Flagstad, Ø. & Linnell, J.D.C. (2015)  
481 Compensatory immigration counteracts contrasting conservation strategies of  
482 wolverines (*Gulo gulo*) within Scandinavia. *Biological Conservation*, **191**, 632–639.
- 483 Hansen, B.B., Gamelon, M., Albon, S.D., Lee, A.M., Stien, A., Irvine, R.J., Sæther, B.-E.,  
484 Loe, L.E., Ropstad, E., Veiberg, V. & Grøtan, V. (2019) More frequent extreme  
485 climate events stabilize reindeer population dynamics. *Nature Communications*,  
486 **10**:1616.
- 487 Heino, M., Kaitala, V., Ranta, E. & Lindström, J. (1997) Synchronous dynamics and rates of  
488 extinction in spatially structured populations. *Proceedings of the Royal Society of*  
489 *London B: Biological Sciences*, **264**, 481–486.
- 490 Hollowed, A.B. & Sundby, S. (2014) Change is coming to the northern oceans. *Science*, **344**,  
491 1084–1085.
- 492 Hsieh, C., Reiss, C.S., Hewitt, R.P. & Sugihara, G. (2008) Spatial analysis shows that fishing  
493 enhances the climatic sensitivity of marine fishes. *Canadian Journal of Fisheries and*  
494 *Aquatic Sciences*, **65**, 947–961.
- 495 Hsieh, C., Reiss, C.S., Hunter, J.R., Beddington, J.R., May, R.M. & Sugihara, G. (2006)  
496 Fishing elevates variability in the abundance of exploited species. *Nature*, **443**, 859–  
497 862.
- 498 Hsieh, C., Yamauchi, A., Nakazawa, T. & Wang, W.-F. (2010) Fishing effects on age and  
499 spatial structures undermine population stability of fishes. *Aquatic Sciences*, **72**, 165–  
500 178.
- 501 Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg,  
502 R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P.,

- 503 Nyrström, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B. & Roughgarden, J. (2003)  
504 Climate Change, Human Impacts, and the Resilience of Coral Reefs. *Science*, **301**,  
505 929–933.
- 506 Hutchings, J.A. & Myers, R.A. (1994) What can be learned from the collapse of a renewable  
507 resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian*  
508 *Journal of Fisheries and Aquatic Sciences*, **51**, 2126–2146.
- 509 Jarillo, J., Sæther, B.-E., Engen, S. & Cao, F.J. (2018) Spatial scales of population synchrony  
510 of two competing species: effects of harvesting and strength of competition. *Oikos*,  
511 **127**, 1459–1470.
- 512 Jenouvrier, S. (2013) Impacts of climate change on avian populations. *Global Change*  
513 *Biology*, **19**, 2036–2057.
- 514 Jenouvrier, S., Desprez, M., Fay, R., Barbraud, C., Weimerskirch, H., Delord, K. & Caswell,  
515 H. (2018) Climate change and functional traits affect population dynamics of a long-  
516 lived seabird. *Journal of Animal Ecology*, **87**, 906–920.
- 517 Jesmer, B.R., Merkle, J.A., Goheen, J.R., Aikens, E.O., Beck, J.L., Courtemanch, A.B.,  
518 Hurley, M.A., McWhirter, D.E., Miyasaki, H.M., Monteith, K.L. & Kauffman, M.J.  
519 (2018) Is ungulate migration culturally transmitted? Evidence of social learning from  
520 translocated animals. *Science*, **361**, 1023–1025.
- 521 Jonzen, N., Ranta, E., Lundberg, P., Kaitala, V. & Lindén, H. (2003) Harvesting-induced  
522 population fluctuations? *Wildlife Biology*, **9**, 59–65.
- 523 Kirby, R.R., Beaugrand, G. & Lindley, J.A. (2009) Synergistic Effects of Climate and Fishing  
524 in a Marine Ecosystem. *Ecosystems*, **12**, 548–561.
- 525 Koons, D.N., Colchero, F., Hersey, K. & Gimenez, O. (2015) Disentangling the effects of  
526 climate, density dependence, and harvest on an iconic large herbivore's population  
527 dynamics. *Ecological Applications*, **25**, 956–967.
- 528 Kuo, T.-C., Mandal, S., Yamauchi, A. & Hsieh, C. (2016) Life history traits and exploitation  
529 affect the spatial mean-variance relationship in fish abundance. *Ecology*, **97**, 1251–  
530 1259.
- 531 Kuparinen, A. & Festa-Bianchet, M. (2017) Harvest-induced evolution: insights from aquatic  
532 and terrestrial systems. *Philosophical Transactions of the Royal Society B: Biological*  
533 *Sciences*, **372**, 20160036.
- 534 Lande, R., Engen, S. & Saether, B.-E. (1995) Optimal harvesting of fluctuating populations  
535 with a risk of extinction. *The American Naturalist*, **145**, 728–745.
- 536 Lande, R., Engen, S. & Saether, B.-E. (2003) *Stochastic Population Dynamics in Ecology and*  
537 *Conservation*. Oxford University Press, Oxford ; New York.
- 538 Lande, R., Sæther, B.-E. & Engen, S. (1997) Threshold Harvesting for Sustainability of  
539 Fluctuating Resources. *Ecology*, **78**, 1341–1350.
- 540 Lefebvre, J., Gauthier, G., Giroux, J.-F., Reed, A., Reed, E.T. & Bélanger, L. (2017) The  
541 greater snow goose *Anser caerulescens atlanticus*: Managing an overabundant  
542 population. *Ambio*, **46**, 262–274.
- 543 Leslie, H.M. & McLeod, K.L. (2007) Confronting the challenges of implementing marine  
544 ecosystem-based management. *Frontiers in Ecology and the Environment*, **5**, 540–  
545 548.
- 546 Lindegren, M., Checkley, D.M., Rouyer, T., MacCall, A.D. & Stenseth, N.C. (2013) Climate,  
547 fishing, and fluctuations of sardine and anchovy in the California Current.  
548 *Proceedings of the National Academy of Sciences*, **110**, 13672–13677.
- 549 López-Montoya, A.J., Moro, J.G.M. & Azorit, C. (2017) Drivers of population growth  
550 variations for two Mediterranean sympatric Deer. *Ecological Research*, **32**, 703–712.
- 551 Loreau, M. (2010) *From Populations to Ecosystems: Theoretical Foundations for a New*  
552 *Ecological Synthesis (MPB-46)*. Princeton University Press.

- 553 MacCall, A.D. (1990) *Dynamic Geography of Marine Fish Populations*. University of  
554 Washington Press, Seattle, Washington.
- 555 Marshall, C.T. & Frank, K.T. (1995) Density-dependent habitat selection by juvenile haddock  
556 (*Melanogrammus aeglefinus*) on the southwestern Scotian Shelf. *Canadian Journal of*  
557 *Fisheries and Aquatic Sciences*, **52**, 1007–1017.
- 558 May, R.M., Beddington, J.R., Horwood, J.W. & Shepherd, J.G. (1978) Exploiting natural  
559 populations in an uncertain world. *Mathematical Biosciences*, **42**, 219–252.
- 560 McCann, K. (2012) *Food Webs*. Princeton University Press.
- 561 McGowan, J.D. (1975) Effect of autumn and spring hunting on ptarmigan population trends.  
562 *The Journal of Wildlife Management*, **39**, 491–495.
- 563 Mentis, R.C. & Bigalke, M.T.&. (1985) Experimental hunting of grassland francolins in the  
564 Natal Drakensberg. *South African Journal of Wildlife Research*, **15**, 12–16.
- 565 Milner-Gulland, E.J., Fryxell, J.M. & Sinclair, A.R.E. (2011) *Animal Migration: A Synthesis*.  
566 Oxford University Press, Oxford, New York.
- 567 Morris, W.F. & Doak, D.F. (2004) Buffering of life histories against environmental  
568 stochasticity: accounting for a spurious correlation between the variabilities of vital  
569 rates and their contributions to fitness. *The American Naturalist*, **163**, 579–590.
- 570 Myers, R.A., Hutchings, J.A. & Barrowman, N.J. (1997) Why do fish stocks collapse? The  
571 example of cod in Atlantic Canada. *Ecological Applications*, **7**, 91–106.
- 572 Mysterud, A. & Sæther, B.E. (2010) Climate change and implications for the future  
573 distribution and management of ungulates in Europe. *Ungulate management in*  
574 *Europe: problems and practices*, 349–375.
- 575 Nøttestad, L., Holst, J.C., Giske, J. & Huse, G. (1999) A length-based hypothesis for feeding  
576 migrations in pelagic fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**,  
577 26–34.
- 578 Palmer, W.L. & Bennett Jr, C.L. (1963) Relation of season length to hunting harvest of ruffed  
579 grouse. *The Journal of Wildlife Management*, 634–639.
- 580 Paniw, M., Ozgul, A. & Salguero-Gómez, R. (2018) Interactive life-history traits predict  
581 sensitivity of plants and animals to temporal autocorrelation. *Ecology Letters*, **21**,  
582 275–286.
- 583 Pedersen, H.C., Steen, H., Kastdalen, L., Brøseth, H., Ims, R.A., Svendsen, W. & Yoccoz,  
584 N.G. (2004) Weak compensation of harvest despite strong density-dependent growth  
585 in willow ptarmigan. *Proceedings. Biological Sciences*, **271**, 381–385.
- 586 Péron, G. (2013) Compensation and additivity of anthropogenic mortality: life-history effects  
587 and review of methods. *Journal of Animal Ecology*, **82**, 408–417.
- 588 Persson, L., Van Leeuwen, A. & De Roos, A.M. (2014) The ecological foundation for  
589 ecosystem-based management of fisheries: mechanistic linkages between the  
590 individual-, population-, and community-level dynamics. *ICES Journal of Marine*  
591 *Science*, **71**, 2268–2280.
- 592 Planque, B., Fromentin, J.-M., Cury, P., Drinkwater, K.F., Jennings, S., Perry, R.I. & Kifani,  
593 S. (2010) How does fishing alter marine populations and ecosystems sensitivity to  
594 climate? *Journal of Marine Systems*, **79**, 403–417.
- 595 Post, E., Langvatn, R., Forchhammer, M.C. & Stenseth, N.Chr. (1999) Environmental  
596 variation shapes sexual dimorphism in red deer. *Proceedings of the National Academy*  
597 *of Sciences of the United States of America*, **96**, 4467–4471.
- 598 Rijnsdorp, A.D. & Pastoors, M.A. (1995) Modelling the spatial dynamics and fisheries of  
599 North Sea plaice (*Pleuronectes platessa* L.) based on tagging data. *ICES Journal of*  
600 *Marine Science*, **52**, 963–980.

- 601 Rouyer, T., Sadykov, A., Ohlberger, J. & Stenseth, N.C. (2012) Does increasing mortality  
602 change the response of fish populations to environmental fluctuations? *Ecology*  
603 *Letters*, **15**, 658–665.
- 604 Royama, T. (1992) *Analytical Population Dynamics*. Springer Science & Business Media.
- 605 Sæther, B.-E. (1997) Environmental stochasticity and population dynamics of large  
606 herbivores: a search for mechanisms. *Trends in Ecology & Evolution*, **12**, 143–149.
- 607 Sæther, B.-E., Engen, S., Persson, J., Brøseth, H., Landa, A. & Willebrand, T. (2005)  
608 Management strategies for the wolverine in Scandinavia. *The Journal of Wildlife*  
609 *Management*, **69**, 1001–1014.
- 610 Sæther, B.-E., Engen, S. & Solberg, E.J. (2001) Optimal harvest of age-structured populations  
611 of moose *Alces alces* in a fluctuating environment. *Wildlife Biology*, **7**, 171–179.
- 612 Sæther, B.-E., Grøtan, V., Engen, S., Coulson, T., Grant, P.R., Visser, M.E., Brommer, J.E.,  
613 Grant, B.R., Gustafsson, L., Hatchwell, B.J., Jerstad, K., Karell, P., Pietiäinen, H.,  
614 Roulin, A., Røstad, O.W. & Weimerskirch, H. (2016) Demographic routes to  
615 variability and regulation in bird populations. *Nature Communications*, **7**, 12001.
- 616 Sæther, B.-E., Tufto, J., Engen, S., Jerstad, K., Røstad, O.W. & Skåtan, J.E. (2000)  
617 Population dynamical consequences of climate change for a small temperate songbird.  
618 *Science*, **287**, 854–856.
- 619 Sandercock, B.K., Nilsen, E.B., Brøseth, H. & Pedersen, H.C. (2011) Is hunting mortality  
620 additive or compensatory to natural mortality? Effects of experimental harvest on the  
621 survival and cause-specific mortality of willow ptarmigan. *Journal of Animal Ecology*,  
622 **80**, 244–258.
- 623 Selkoe, K.A., Blenckner, T., Caldwell, M.R., Crowder, L.B., Erickson, A.L., Essington, T.E.,  
624 Estes, J.A., Fujita, R.M., Halpern, B.S., Hunsicker, M.E., Kappel, C.V., Kelly, R.P.,  
625 Kittinger, J.N., Levin, P.S., Lynham, J.M., Mach, M.E., Martone, R.G., Mease, L.A.,  
626 Salomon, A.K., Samhuri, J.F., Scarborough, C., Stier, A.C., White, C. & Zedler, J.  
627 (2015) Principles for managing marine ecosystems prone to tipping points. *Ecosystem*  
628 *Health and Sustainability*, **1**, 1–18.
- 629 Shelton, A.O. & Mangel, M. (2011) Fluctuations of fish populations and the magnifying  
630 effects of fishing. *Proceedings of the National Academy of Sciences of the United*  
631 *States of America*, **108**, 7075–7080.
- 632 Smith, A.D.M., Brown, C.J., Bulman, C.M., Fulton, E.A., Johnson, P., Kaplan, I.C., Lozano-  
633 Montes, H., Mackinson, S., Marzloff, M., Shannon, L.J., Shin, Y.-J. & Tam, J. (2011)  
634 Impacts of Fishing Low-Trophic Level Species on Marine Ecosystems. *Science*, **333**,  
635 1147–1150.
- 636 Stenseth, N.C., Viljugrein, H., Saitoh, T., Hansen, T.F., Kittilsen, M.O., Bølviken, E. &  
637 Glöckner, F. (2003) Seasonality, density dependence, and population cycles in  
638 Hokkaido voles. *Proceedings of the National Academy of Sciences*, **100**, 11478–  
639 11483.
- 640 Sugihara, G., Beddington, J., Hsieh, C., Deyle, E., Fogarty, M., Glaser, S.M., Hewitt, R.,  
641 Hollowed, A., May, R.M., Munch, S.B., Perretti, C., Rosenberg, A.A., Sandin, S. &  
642 Ye, H. (2011) Are exploited fish populations stable? *Proceedings of the National*  
643 *Academy of Sciences*, **108**, E1224–E1225.
- 644 Takashina, N. & Mougi, A. (2015) Maximum sustainable yields from a spatially-explicit  
645 harvest model. *Journal of Theoretical Biology*, **383**, 87–92.
- 646 Terborgh, J.W. (2015) Toward a trophic theory of species diversity. *Proceedings of the*  
647 *National Academy of Sciences*, **112**, 11415–11422.
- 648 Tu, C.-Y., Chen, K.-T. & Hsieh, C. (2018) Fishing and temperature effects on the size  
649 structure of exploited fish stocks. *Scientific Reports*, **8**, 7132.

650 Turchin, P. (1995) Population regulation: old arguments and a new synthesis. *Population*  
651 *Dynamics*, Academic Press, pp. 19–40. N. Cappucino & P.W. Price, New York.  
652