



Range contraction enables harvesting to extinction

Matthew G. Burgess^{a,b,c,d,1}, Christopher Costello^{a,b,c}, Alexa Fredston-Hermann^b, Malin L. Pinsky^e, Steven D. Gaines^{a,b,c}, David Tilman^{b,d,1}, and Stephen Polasky^{d,f}

^aSustainable Fisheries Group, University of California, Santa Barbara, CA 93106; ^bBren School of Environmental Science and Management, University of California, Santa Barbara, CA 93106; ^cMarine Science Institute, University of California, Santa Barbara, CA 93106; ^dDepartment of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108; ^eDepartment of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, NJ 08901; and ^fDepartment of Applied Economics, University of Minnesota, St. Paul, MN 55108

Contributed by David Tilman, February 7, 2017 (sent for review May 11, 2016; reviewed by Franck Courchamp and Hugh P. Possingham)

Economic incentives to harvest a species usually diminish as its abundance declines, because harvest costs increase. This prevents harvesting to extinction. A known exception can occur if consumer demand causes a declining species' harvest price to rise faster than costs. This threat may affect rare and valuable species, such as large land mammals, sturgeons, and bluefin tunas. We analyze a similar but underappreciated threat, which arises when the geographic area (range) occupied by a species contracts as its abundance declines. Range contractions maintain the local densities of declining populations, which facilitates harvesting to extinction by preventing abundance declines from causing harvest costs to rise. Factors causing such range contractions include schooling, herding, or flocking behaviors—which, ironically, can be predator-avoidance adaptations; patchy environments; habitat loss; and climate change. We use a simple model to identify combinations of range contractions and price increases capable of causing extinction from profitable overharvesting, and we compare these to an empirical review. We find that some aquatic species that school or forage in patchy environments experience sufficiently severe range contractions as they decline to allow profitable harvesting to extinction even with little or no price increase; and some high-value declining aquatic species experience severe price increases. For terrestrial species, the data needed to evaluate our theory are scarce, but available evidence suggests that extinction-enabling range contractions may be common among declining mammals and birds. Thus, factors causing range contraction as abundance declines may pose unexpectedly large extinction risks to harvested species.

anthropogenic Allee effect | hyperstable | endangered species | poaching | biogeography

Harvesting has driven the population declines of thousands of species of animals and plants (1), but it is thought to rarely cause extinction because the increasing cost of harvesting a progressively rarer species would eventually exceed the value of the harvest, and harvesting would stop (2). However, for species harvested for high-value products, there is concern that their depletion could fuel price increases, via market demand, large enough to compensate for higher harvest costs and thereby maintain profit incentives to harvest all of the way to extinction, absent management intervention (3). Courchamp et al. (3) term this threat the “anthropogenic Allee effect.”

Species thought to face this threat include those harvested, both legally and illegally, for trophies [e.g., large terrestrial mammals including rhinoceros, elephants, and large cats (4–8)], for collections [e.g., stag beetles (9)], for body parts regarded as having medicinal or aphrodisiac properties [e.g., many large mammals (4)], or for luxury foods [e.g., sturgeons, bluefin tunas, sea cucumbers (10–12)]. Many such species are considered threatened by the Red List of the International Union for Conservation of Nature (IUCN) (1) or the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (13). Expanding human populations, coupled with economic growth in developing countries with large luxury harvest markets, may increase pressures on these species in coming decades (12).

A similar threat of extinction from overharvesting would occur if a species' harvest costs failed to rise as its abundance declined, thus maintaining harvesting profitability. One way this can occur is if the geographic area (range) occupied by the species contracts as its abundance declines, thereby maintaining its local population density. This pattern has been noted in several fish and aquatic invertebrate populations (14, 15) and may have contributed to the famous 1990s collapse of northern cod (*Gadus morhua*) (16). In fish and invertebrates, range contraction is often observed in declining populations that exhibit schooling behavior (to maintain school sizes) and/or forage in patchy environments (because populations concentrate in the preferred habitats) (14, 15, 17). Habitat destruction and climate change can also cause range contraction and thus might similarly buffer harvest costs against population declines and create incentives for harvesting to extinction.

These overharvesting threats from range contraction and market demand likely interact (Fig. 1). For example, prices would not need to be very sensitive (“flexible”) to abundance declines to allow profitable harvesting to extinction if costs were insensitive to abundance declines because of range contraction.

Here, we theoretically and empirically characterize this interaction. We use a simple model to illustrate conditions under which range contraction and price flexibility can in combination allow harvesting to extinction under open access. We then review available empirical evidence to shed light on where these biological and economic risk factors may be most acute. Whereas many harvests are now managed (18), it is nonetheless important to understand the threats posed by open-access incentives due to

Significance

Many threatened species including elephants, sturgeons, and bluefin tunas are harvested for high-value products. Species can be driven extinct if incentives to harvest do not diminish as populations decline; this occurs if harvest prices rise faster than costs with declining stock. Whereas recent conservation attention for these species has largely focused on market demand, we show—using a theoretical model and an empirical review—that contractions in species' geographic ranges, which stabilize costs and may be especially common among terrestrial species, might often play a larger role in maintaining harvest incentives. Forces impacting ranges—such as patchy and declining habitats, schooling/herding behavior, and climate change—therefore merit greater attention in assessing overharvesting threats.

Author contributions: M.G.B. designed research; M.G.B., C.C., A.F.-H., M.L.P., S.D.G., D.T., and S.P. performed research; M.G.B., A.F.-H., and M.L.P. analyzed data; and M.G.B., C.C., A.F.-H., M.L.P., S.D.G., D.T., and S.P. wrote the paper.

Reviewers: F.C., Université Paris-Sud, France; and H.P.P., University of Queensland.

The authors declare no conflict of interest.

¹To whom correspondence may be addressed. Email: mburgess@ucsb.edu or tilman@umn.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1607551114/-DCSupplemental.

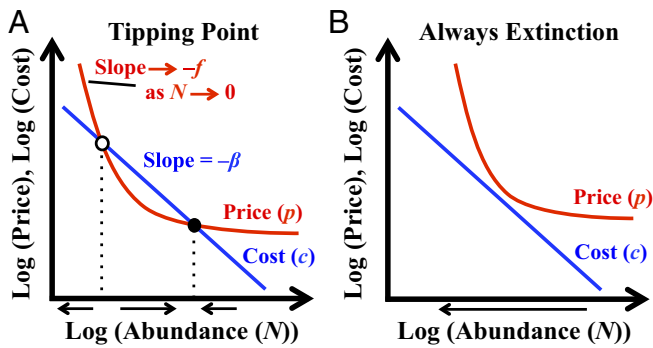


Fig. 1. Profitable harvesting to extinction [Courchamp et al.'s (3) anthropogenic Allee effect] under open access occurs when, at harvest levels at which abundance is not changing, harvest price (red, nonlinear due to density-dependent population growth) is greater than harvest cost (blue) as abundance approaches zero. Such conditions either can result in alternative stable states (A)—a tipping-point abundance (open circle) separates domains of attraction of a positive equilibrium abundance (solid circle) and extinction—or can cause profits to be positive at any abundance and make extinction the only possible outcome of open-access harvesting (B).

the pervasiveness of illegal and unreported harvesting of endangered species (4, 7, 8).

Theory

We consider the following model of open-access harvesting on a single population with abundance N . The population has a per-capita growth rate, denoted $g(N)$, which follows negative density dependence ($g'[N] < 0$) and has a maximum of r ($g[0] = r$). The population is harvested at rate Y , which is a function of the current harvest effort, E , and abundance (N); there is no harvest if either abundance or effort is zero:

$$Y = Y(N, E), Y(0, E) = Y(N, 0) = 0. \quad [1]$$

The population's rate of change, denoted $\dot{N} \equiv dN/dt$, is

$$\dot{N} = Ng(N) - Y. \quad [2]$$

Under open access, the rate of change in effort, $\dot{E} \equiv dE/dt$, has the same sign as harvest profits (2); i.e.,

$$\dot{E} > (<) 0 \text{ if } p > (<) c, \dot{E} = 0 \text{ if } p = c, \quad [3]$$

where p and c are, respectively, the price and average cost of a unit of harvest received/incurred by harvesters.

Extinction Condition. Harvesting to extinction can occur in this model if and only if, as abundance (N) approaches 0, there is still upward pressure on effort (i.e., $\dot{E} > 0$) when harvest rates (Y) exactly balance population growth ($Ng[N]$) (i.e., abundance is not changing, $\dot{N} = 0$) (illustrated in Fig. S1). Formally, this means that extinction can occur if and only if

$$\lim_{N \rightarrow 0} \left(\frac{p}{c} \right) \Big|_{Y=Ng(N)} > 1. \quad [4]$$

Prices, Costs, and Abundance. We assume that the sensitivity of the price (p) to changes in abundance (N) is mediated by changes in the supply of harvest in the market—equal to the harvest rate, Y . The sensitivity of a harvest product's price to its supply is commonly measured by the "price flexibility of demand" (19, 20), denoted f , defined as

$$\frac{\partial p}{\partial Y} \left(\frac{Y}{p} \right) = -f; \quad [5]$$

i.e., price increases by $f\%$ when supply (Y) declines by 1%. Price flexibility is related to, but distinct from, the more widely known

concept of demand elasticity; they are reciprocals in a market with only one good, but not otherwise (19). We use price flexibility, because it is considered a more appropriate empirical demand measure for harvests (e.g., ref. 20).

Assuming constant price flexibility (f), Eq. 5 implies that the price (p) is given by

$$p = \rho Y^{-f}, \quad [6]$$

where ρ is either a constant or a function of variables other than supply (Y). In the analysis that follows, we assume ρ is constant, but discuss alternate assumptions in *Theory, Other Considerations* and in *SI Materials and Methods*.

To model the relationship between average costs (c) and abundance (N), we assume the harvest rate (Y) at a given time is proportional to the harvesting effort (E) (i.e., constant returns to scale) multiplied by the population abundance (N) raised to a constant power, β (*sensu* refs. 21 and 22):

$$Y = qN^\beta E. \quad [7]$$

q is also a constant. β represents the percentage of change in catch-per-unit effort (CPUE = Y/E) resulting from a 1% change in abundance (N) and thus can be thought of as the "catch flexibility." If $\beta < 1$, then CPUE is "hyperstable" because it changes proportionally more slowly than abundance (21).

For simplicity we assume that effort has a constant cost and that the units of effort are such that they have unit costs (i.e., total cost = E). The average unit cost of harvest ($c = E/Y$) is then given by (from Eq. 7)

$$c = q^{-1} N^{-\beta}. \quad [8]$$

We briefly discuss alternate assumptions in *Theory, Other Considerations* and in *SI Materials and Methods*.

Extinction Condition Revisited. With Eqs. 6 and 8 for p and c , extinction condition 4 becomes

$$\lim_{N \rightarrow 0} \left(\frac{p}{c} \right) \Big|_{Y=Ng(N)} = \begin{cases} 0 & f < \beta \\ \rho q r^{-f} & f = \beta \\ \infty & f > \beta \end{cases} > 1, \quad [9]$$

implying (Fig. S1; intuition discussed below and illustrated in Fig. 1) that extinction can occur if and only if

$$f > \beta, \text{ or } f = \beta \text{ and } \rho q r^{-f} > 1. \quad [10]$$

If price flexibility exceeds catch flexibility ($f > \beta$), then two scenarios are possible (depending on parameter values) under open access: (i) Extinction is the only possible outcome (Fig. 1B and light-red E isocline in Fig. S1D) and (ii) there is an unstable equilibrium acting as a tipping point separating a basin of attraction of extinction and a basin of attraction of either a stable (positive) equilibrium or a limit cycle (Fig. 1A and dark-red E isocline in Fig. S1D). In contrast, if $f = \beta$ and $\rho q r^{-f} > 1$, only extinction is possible (light-red E isocline in Fig. S1E).

Range Contraction. Under random search, CPUE would be proportional to population density (abundance [N]/range area [A]), i.e., $Y \propto \left(\frac{N}{A} \right) E$, and catch flexibility (β) would then be determined solely by the relationship between abundance (N) and range area (A): $\beta = 1 - \frac{\partial A}{\partial N} \left(\frac{N}{A} \right)$. In practice, other factors (e.g., technology, harvester search skill) tend to further buffer CPUE as abundance declines (15, 23) (see Fig. 2 and Dataset S1 for many examples), meaning that

$$\beta \leq 1 - \frac{\partial A}{\partial N} \left(\frac{N}{A} \right). \quad [11]$$

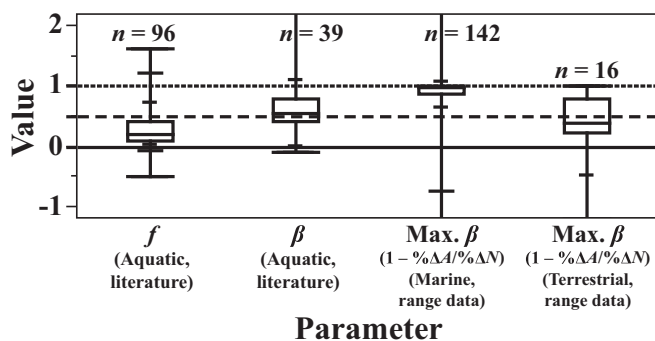


Fig. 2. Comparison of ranges of estimates of price flexibility (f : the percentage of increase in price, p , caused by a 1% decrease in harvest rate, Y) and catch flexibility (β : the percentage of decrease in CPUE caused by a 1% decrease in abundance, N) from the published literature for aquatic species and observed range-abundance relationships [which imply upper bounds on catch flexibility ($\text{Max. } \beta$) by inequality 11] in marine fish and invertebrates, terrestrial mammals, and one terrestrial bird species (northern bobwhite). Boxes show 25th to 75th percentile range; minima, maxima, and 2.5th, 10th, 90th, and 97.5th percentiles are marked on the whiskers. See [Dataset S1](#) for all values and references. Two terrestrial mammal populations having no observed abundance change are excluded.

Intuition. The intuition of our theory is as follows: A 1% decrease in abundance (N) of a rare species increases average costs by $\beta\%$ and increases price by approximately $f\%$. If $f > \beta$, the incentive to keep harvesting only increases; if $f = \beta$, it fails to decrease (and it is positive if $\rho q r^{-f} > 1$). If range (A) contracts proportionally as fast as or faster than abundance declines [i.e., $\frac{\partial A}{\partial N} \left(\frac{N}{A}\right) \geq 1 \Rightarrow \beta \leq 0$], then incentives to harvest are maintained even with constant prices ($f = 0$), and range contraction therefore poses an extinction threat on its own (16, 23). Similarly, if prices rise proportionally as fast as or faster than supply falls (i.e., $f \geq 1$), then incentives to harvest are maintained even with no range contraction (i.e., $\beta = 1$), and price flexibility poses an extinction threat on its own. The most common case, as we will see below, is where $0 < \beta, f < 1$ —one where price flexibility and range contraction (and/or other factors making costs insensitive to declines) can pose threats only in combination.

Other Considerations. Other factors beyond price and catch flexibilities can impact the changes in costs or prices coincident with changes in abundance. These include economies of scale [meaning $\frac{\partial Y}{\partial E} \left(\frac{E}{Y}\right) > 1$] (e.g., ref. 24), technology and technological change (meaning $dq/dt > 0$) (25), supply-independent increasing trends in price (e.g., caused by income growth) (meaning $\partial \rho / \partial t > 0$), and supply-independent effects of abundance on prices caused by “rarity value” (3, 26) ($\partial \rho / \partial N < 0$).

These other effects are not the focus of the present study, but we show in *SI Materials and Methods* the direction in which each of these effects is likely to impact extinction threats: Technological change, positive supply-independent price trends, and rarity value each exacerbate the threats [although supply-independent rarity effects on prices may be negligibly small in comparison with supply effects (measured by f) for species already rare enough for their harvest products to confer status; e.g., Fig. S2]. Economies of scale have a neutral effect when $f \approx 1$ or $\beta \approx 1$ but can have a mild mitigating effect when f and β are both small (Fig. S3). We briefly discuss this effect in context with observed economies of scale in fisheries (Table S1). We also show how the existence of perfect substitutes (i.e., goods that are indistinguishable from the focal species’ harvest product to consumers) will tend to prevent profit-driven extinction altogether. Finally, we discuss the implications of nonconstant f and β —in short, extinction still requires $f \geq \beta$ [assuming constant ρ and

q and $\frac{\partial Y}{\partial E} \left(\frac{E}{Y}\right) = 1$], at the limits of f and β as abundance (N) approaches zero.

Other factors—such as intertemporal discounting (27, 28) and opportunistic or multispecies harvesting (29, 30)—can influence a species’ risk of extinction by overharvesting via different mechanisms, but these are also not the focus of this study.

Review of Empirical Evidence

Our theory suggests that profitable harvesting to extinction requires highly flexible prices, highly inflexible catch rates (implying inflexible costs), or a combination ($f \geq \beta$, which may be a conservative criterion, given the exacerbating factors not included in our model). We assume that price flexibility does not directly influence—nor is it influenced by—either catch flexibility or the range-abundance relationship, and thus we review empirical estimates of these three factors separately (Fig. 2), rather than restricting our analysis to species having estimates of each (there are very few such species).

Price Flexibility. To our knowledge, price flexibility (f) estimates for wild terrestrial harvests are rare, perhaps because few terrestrial harvests of wild animal species are legal and commercial in data-rich countries. One modeling study (31), however, assumed $f = 0.1$ for poached elephants. A second study (32) estimated demand elasticity for Serengeti bushmeat to be > 1 , which is consistent with $f < 1$ with few substitutes.

In contrast, we found 96 published price-flexibility estimates for aquatic harvest products (Fig. 2 and [Dataset S1](#))—varying widely in focal species, commodity type, position in the supply chain [ex-vessel (the price paid to harvesters), wholesale, and retail], and estimation method, including some from high-value species. Most estimated price flexibilities were low (median $f = 0.22$; $f < 0.5$ in 81% of estimates). Estimates of ex-vessel price flexibilities—of primary relevance to our theory—were especially small ($n = 46$, median = 0.12, $f < 0.5$ in 96% of estimates) ([Dataset S1](#)). Ex-vessel prices tend to be less flexible than prices farther along the supply chain (33), perhaps because of market power among some wholesale buyers and processors or because storage and preservation can buffer retail supplies against changes in harvest rates.

Some high-value aquatic species lack formal price flexibility estimates from in-depth demand analyses, but their price trends are nonetheless mostly consistent with inflexible prices ($f \ll 1$). To illustrate this point, Fig. 3 shows aggregate price-supply relationships for several populations thought to be facing (or to recently have faced) demand-related extinction threats. Bluefin tunas [Atlantic (ABF) (*Thunnus thynnus*), Pacific (PBF) (*Thunnus orientalis*), and Southern (SBT) (*Thunnus maccoyii*)] have had relatively stable prices despite abundance declines (Fig. 3A and B; data from refs. 34 and 35). Indeed, Chiang et al. (36) estimated $f = 0.19$ for wholesale fresh bluefin tuna (lumped ABF, PBF, and SBT) in Japan. Historical caviar [made from sturgeon (Acipenseriformes) roe] prices (1976–2010; Fig. 3C; data from ref. 37) have risen 0.3% on average for every 1% decline in catch. Before the International Whaling Commission’s moratorium on whaling in the late 1980s, Northeast Atlantic minke whale (*Balaenoptera acutorostrata*, a relatively data-rich whale example; data from ref. 38) prices increased by 0.65% on average for every 1% decline in catch (Fig. 3D). California abalone (*Haliotis* sp.) prices seem to have been more flexible, increasing by roughly 1% (0.98%) for every 1% decline in catch over the period 1950–1993, before the 1997 ban on fishing (Fig. 3E) (data from refs. 3 and 39). These historical trends do not necessarily reflect the magnitudes of underlying market-level price flexibilities, but they are mostly consistent with the pattern of low price flexibility ($f < 1$) seen in other aquatic harvest products (Fig. 3F). Controlling for catch, none of these species have residual prices significantly correlated with abundance (Fig. S2),

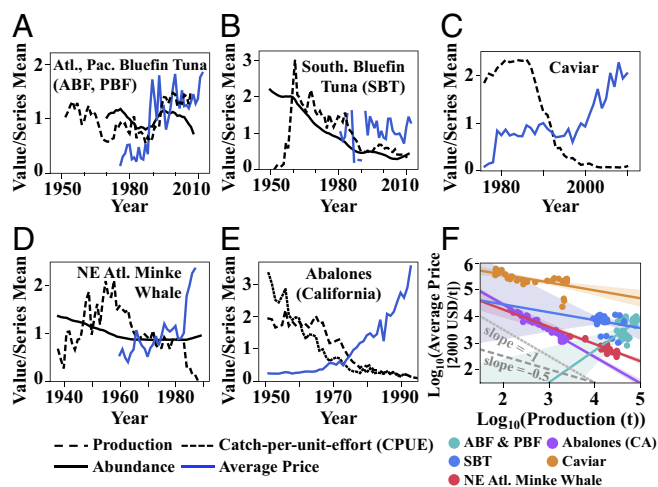


Fig. 3. Price trends in highly valued marine species: (A) ABF and PBF [production (total catch) and abundance from ref. 35; ex-vessel prices from ref. 34], (B) SBT [production (total catch) and abundance from ref. 35; ex-vessel prices from ref. 34], (C) caviar (global production, average export prices from ref. 37), (D) the Northeast Atlantic minke whale (production, abundance, prices from ref. 38), and (E) California abalones (CPUE and prices from refs. 3 and 39). All prices were converted to real USD value using the World Bank's (40) published currency exchange and inflation rates. (F) Prices of each of these harvests have historically risen as fast as catch has declined (California abalone) or slower (others). For ABF and PBF, catch and prices rose together pre-1990, creating a positive correlation, likely due to the expansion of sashimi markets. Solid lines show linear fits of log-transformed price and production (supply) data, with 95% confidence intervals shaded. Dotted and dashed gray lines, respectively, illustrate slopes of -1 (implying 1% increase in price for 1% decrease in production) and -0.5 , for reference.

suggesting that supply-independent rarity effects may indeed be negligible.

Range Contraction and Catch Flexibility. Several studies have directly estimated catch flexibility (β ; usually incorporating effects of both range and other factors) in aquatic populations (see ref. 15 for review), but to our knowledge no such literature yet exists for terrestrial populations. We found published estimates of catch flexibility from 39 aquatic populations (median $\beta = 0.56$) (Fig. 2; see Dataset S1 for values and references). Of these, 32 (82%) exhibited hyperstability ($\beta < 1$), and 14 (36%) exhibited severe hyperstability ($\beta < 0.5$), including 5 of 6 small

pelagic finfish populations—which tend to both exhibit schooling behavior and forage in patchy environments.

For comparison, we compiled estimates of coincident changes in range area and abundance in 142 harvested marine fish and invertebrate populations (Fig. 4A; see legend for references; full data available in Dataset S1). We use the ratio of coincident observed percentage of changes in range and abundance, denoted $\% \Delta A / \% \Delta N$, as a measure of average $\frac{\partial A}{\partial N} \left(\frac{N}{A} \right)$, which would bound catch flexibility (β) by inequality 11.

Most of these populations had very abundance-insensitive ranges (median $\% \Delta A / \% \Delta N = 0.03$) (Figs. 2 and 4A): For 87 (61%) of them, the range changed by less than 1/10th of the percentage by which abundance changed ($|\% \Delta A / \% \Delta N| < 0.1$) (17). We found $\% \Delta A / \% \Delta N > 0.5$ (implying $\beta < 0.5$) in only 8 (6%) of the populations, half of which were tunas or billfish (Dataset S1), and we found some evidence suggesting that abundance-sensitive range may be associated with schooling behavior among tunas (Fig. 4B). Notably, we found hyperaggregation ($\% \Delta A / \% \Delta N > 1$, implying $\beta < 0$) in both ABF and PBF (Fig. 4B), suggesting that these populations would not necessarily need any price flexibility to be profitably harvested to extinction.

In SI Materials and Methods, we compare the range–abundance relationships from these 142 harvested marine populations to a taxonomically similar sample from 247 nonharvested marine populations. In the combined sample, we find taxonomy, but not harvesting, to be a significant determinant of the range–abundance relationship (SI Materials and Methods, Tables S2 and S3, and Figs. S4 and S5), suggesting that ecology may be a more important driver. We most commonly find highly abundance-sensitive ranges ($\% \Delta A / \% \Delta N > 0.5$) among small invertebrates (molluscs, shrimps) and pelagic finfish in the combined sample (Table S3).

Our reviews of catch flexibility estimates and range–abundance relationships (Dataset S1) support the hypothesis that aggregation and patchy habitats lead to hyperstable catches in aquatic species, in part because of range contraction (14, 15). However, we find catch flexibility (β) estimates to be smaller on average than values implied by range–abundance relationships alone (Fig. 2), which suggests that other drivers besides range contraction also contribute to hyperstable catch rates. Indeed, a few studies have directly demonstrated this [e.g., refs. 16 and 41 found $\frac{\partial \text{CPUE}}{\partial D} \left(\frac{D}{\text{CPUE}} \right) \approx 0.5$, where $D = N/A$, in Atlantic cod and California kelp bass (*Paralabrax clathratus*), respectively; see refs. 15 and 23 for review].

We found estimates of coincident range and abundance trends for 17 harvested terrestrial mammals and one North American

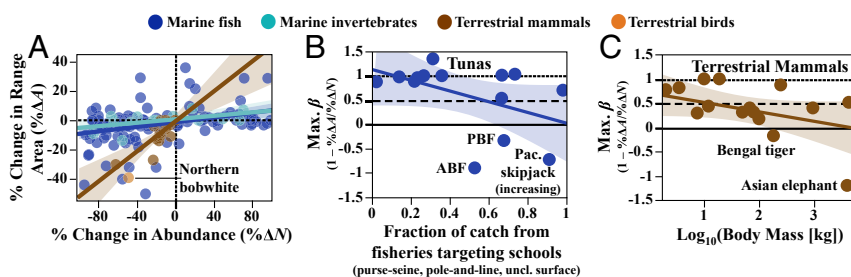


Fig. 4. Range–abundance relationships for populations of harvested US marine fish and invertebrates (1970s–2000s; from ref. 42); tuna and billfish (1960–1999; from refs. 35 and 43); harvested terrestrial mammals, mostly from the Western Ghats of India [1978/79–2008/09; from ref. 44]; also the African forest elephant (*Loxodonta cyclotis*) from 2002–2011, ref. 45]; and northern bobwhite (*Colinus virginianus*), a North American game bird (1966–1993; from ref. 46). A shows all populations. B and C show relationships between the maximum catch flexibility ($\text{Max. } \beta$) and (B) a proxy for schooling behavior in tunas and (C) adult body mass in terrestrial mammals (Dataset S1). Harvested populations exhibiting hyperaggregation ($\text{Max. } \beta < 0$) are labeled; all are declining in abundance and range over the time periods in question, except for Pacific skipjack tuna (*Katsuwonus pelamis*), which is increasing. Colored lines in all panels represent linear ordinary least-squares (OLS) fits (within large taxonomic groups in A), with 95% confidence intervals shaded. Negative slopes in B and C are nearly significant ($P < 0.1$).

game bird population [northern bobwhite (*Colinus virginianus*)] (Fig. 4A; see legend for description of sources; full data are available in Dataset S1). In most (10) of these populations, range contracted at more than half the rate that abundance declined ($\% \Delta A / \% \Delta N > 0.5$, implying $\beta < 0.5$) (Fig. 4A and C). Abundance-sensitive range was most common among large-bodied mammals; we found hyperaggregation in the Bengal tiger (*Panthera tigris*) and the Asian elephant (*Elephas maximus*)—both species threatened by poaching and habitat destruction (1, 44) (Fig. 4C).

Although this terrestrial sample is quite small, it suggests that terrestrial species might more commonly experience range contraction as they decline than marine species—a pattern that we also find in a sample of 28 nonharvested bird and mammal populations (Fig. S5, SI Materials and Methods, and Dataset S1). If, like for aquatic species, other factors besides range contraction further decrease catch flexibility (β) (Fig. 2), many terrestrial species—especially large-bodied mammals, perhaps—could be susceptible to profitable harvesting to extinction under open access.

Discussion

We find that escalating prices, stable harvest costs, or combinations of these two factors can, in theory, allow a species to be profitably harvested to extinction, absent effective protection. Our empirical review suggests that stable harvesting costs might be a surprisingly common cause of such extinction risks, but this full range of possibilities merits much further attention. Our review suggests that (i) range contraction in declining species may be common and often severe enough to allow extinction with little or no price flexibility among terrestrial species and among aquatic species that school or forage in patchy habitats, (ii) high price flexibility also occurs among some highly valued aquatic species, and (iii) other factors besides range contraction also buffer harvest costs against abundance declines. These results suggest that risk factors for abundance-insensitive costs merit greater attention in harvested species conservation.

Low price flexibility may be common because most harvested commodities have partial substitutes in the market. For example, studies have found moderate-to-high market substitutability between species within broad classes of fish products (see ref. 33 for review), including between most tuna species (36, 47). Species whose harvests have perfect substitutes are unlikely to be profitably harvested to extinction (26), because perfect substitutes cause the abundance sensitivity of a species' price to diminish as it approaches extinction (SI Materials and Methods). However, our price analyses were restricted to commercially harvested aquatic species, so the pattern of inflexibility we observed may not necessarily extend to other types of markets (e.g., black markets).

Our review suggested that range changes may be more correlated with abundance changes among terrestrial species compared with marine species (Fig. 4A and Figs. S4 and S5). This difference may be related to greater habitat destruction and space limitation on land. Space limitation positively correlates with body size in terrestrial mammals (48, 49), which may explain the especially strong relationships between range and abundance changes we found in large-bodied mammals. Thus, habitat destruction is likely a key driver of abundance-insensitive costs on land; and it also may directly and independently add to the extinction risk faced by terrestrial species. However, given our relatively small and unrepresentative terrestrial samples, these hypotheses merit further scrutiny.

Aggregating in patchy habitats is common among schooling fish, many small aquatic invertebrates, and other taxa found to have low catch flexibility, as well as some birds. Aggregation

and habitat patchiness are likely key drivers of these species' susceptibility both to range contraction as they decline [due to concentration in preferred habitats and/or need to maintain school size (14, 15)] and to some other socioeconomic factors making costs even less sensitive to abundance [e.g., aggregation predictability (15, 23), harvester coordination (e.g., ref. 50), and use of fish aggregating devices (FADs) (51)]. It is ironic that herding and schooling behaviors, which are considered adaptations for predator avoidance (52), may make such species particularly prone to extinction from human harvesting.

Together, these results suggest that the harvested species most susceptible to profitable harvesting to extinction may be those with aggregation behavior, patchy or declining habitats, large home ranges (on land), and few market substitutes (26). Moreover, our results suggest that—absent management—many high-value harvested species could potentially be threatened by these risk factors. These include Atlantic and Pacific bluefin tuna [for which we find evidence of hyperaggregation (i.e., $\beta < 0$)] and many large poached land mammals (which likely have low catch flexibility) and may include sturgeons (which face habitat destruction, e.g., ref. 53) and high-value marine invertebrates [e.g., abalones, for which we found evidence suggestive of high price flexibility (Fig. 3E and F)]. The extinct passenger pigeon (*Ectopistes migratorius*), which aggregated in large flocks and suffered both habitat destruction and overharvesting (e.g., ref. 54), possibly provides a historical case study of the interaction of these risk factors in extinction. The susceptibility of some plants [e.g., orchids in southeast Asia (55)] to overharvesting threats also merits further study. Because price and catch flexibilities (f, β) can change, a species currently having $f > \beta$ does not necessarily face extinction, absent management, but likely does face economic conditions promoting further depletion that could be severe.

Our analyses assume that species are harvested in an open-access system. Thus, a species we identify as susceptible to extinction from overharvesting would not necessarily be driven extinct if effective management or property rights that promote stewardship were implemented. Indeed, there are property rights in many harvests, including some poaching (18) and many fisheries (56). Harvests of whales (29), California abalones (39), and bluefin tunas are currently managed; and Atlantic bluefin tuna seems to be recovering (57). Trade in sturgeons and many mammals is regulated under CITES (13). It is nonetheless important to understand how open-access harvesting incentives could lead to extinction, as access restrictions are rarely perfectly enforced; high-value species are especially vulnerable to illegal harvesting (4).

Materials and Methods

SI Materials and Methods contains (i) a glossary of terms, in light of the broad range of topics discussed; (ii) brief discussions of the effects of economies of scale, technological change, rarity effects, supply-independent price trends, perfect substitutes, and nonconstant price flexibility (f) and catch flexibility (β) on overharvesting threats (Figs. S2 and S3); (iii) descriptions of the range and abundance data shown in Fig. 4; (iv) discussions of observed range–abundance relationships, in relation to taxonomy and harvesting (Tables S2 and S3 and Figs. S4 and S5); and (v) a review of returns to scale estimates in fisheries (Table S1). Dataset S1 contains all data shown in Figs. 2 and 4 and Figs. S4 and S5 and their sources.

ACKNOWLEDGMENTS. We thank P. Abrams, C. Lehman, P. Venturelli, D. Williams, and two reviewers for helpful comments and F. Courchamp, M. Pons, R. Hilborn, T. Branch, A. Scheld, and C. Anderson for assistance with price data. We acknowledge funding from a University of Minnesota Doctoral Dissertation Fellowship and a Natural Sciences and Engineering Research Council of Canada Postgraduate Scholarship-Doctoral (to M.G.B.), the Waitt Foundation, the Ocean Conservancy, and a Department of Defense National Defense Science & Engineering Graduate Fellowship (to A.F.-H.).

1. International Union for Conservation of Nature (IUCN) (2015) *IUCN Red List of Threatened Species*. Version 2016.3. Available at www.iucnredlist.org. Accessed January 14, 2017.
2. Clark CW (1976) *Mathematical Bioeconomics: The Optimal Management Resources* (Wiley, New York).
3. Courchamp F, et al. (2006) Rarity value and species extinction: The anthropogenic Allee effect. *PLoS Biol* 4(12):e415.
4. Graham-Rowe D (2011) Biodiversity: Endangered and in demand. *Nature* 480(7378):5101–5103.
5. Palazy L, Bonenfant C, Gaillard JM, Courchamp F (2011) Cat dilemma: Too protected to escape trophy hunting? *PLoS One* 6(7):e22424.
6. Palazy L, Bonenfant C, Gaillard J, Courchamp F (2012) Rarity, trophy hunting and ungulates. *Anim Conserv* 15(1):4–11.
7. Biggs D, Courchamp F, Martin R, Possingham HP (2013) Legal trade of Africa's rhino horns. *Science* 339(6123):1038–1039.
8. Wittemyer G, et al. (2014) Illegal killing for ivory drives global decline in African elephants. *Proc Natl Acad Sci USA* 111(36):13117–13121.
9. Tournant P, Joseph L, Goka K, Courchamp F (2012) The rarity and overexploitation paradox: Stag beetle collections in Japan. *Biodiversity Conserv* 21(6):1425–1440.
10. Gault A, Meinard Y, Courchamp F (2008) Consumers' taste for rarity drives sturgeons to extinction. *Cons Lett* 1(5):199–207.
11. Collette B, et al. (2011) High value and long life-double jeopardy for tunas and billfishes. *Science* 333(6040):291–292.
12. Purcell SW, Polidoro BA, Hamel JF, Gamboa RU, Mercier A (2014) The cost of being valuable: Predictors of extinction risk in marine invertebrates exploited as luxury seafood. *Proc R Soc B* 281(1781):20133296.
13. Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (2017) *The CITES Species*. Available at www.cites.org. Accessed January 14, 2017.
14. Prince JD, Loneragan NR, Okey TA (2008) Contraction of the banana prawn (*Penaeus merguensis*) fishery of Albatross Bay in the Gulf of Carpentaria, Australia. *Mar Freshw Res* 59(5):383–390.
15. Wilberg MJ, Thorson JT, Linton BC, Berkson J (2009) Incorporating time-varying catchability into population dynamic stock assessment models. *Rev Fish Sci* 18(1):7–24.
16. Rose G, Kulka D (1999) Hyperaggregation of fish and fisheries: How catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. *Can J Fish Aquat Sci* 56(5):118–127.
17. Thorson JT, Rindorf A, Gao J, Hanselman DH, Winker H (2016) Density-dependent changes in effective area occupied by sea-bottom-associated marine fishes. *Proc R Soc B* 283:20161853.
18. Harris RB, Cooney R, Leader-Williams N (2013) Application of the anthropogenic Allee effect model to trophy hunting as a conservation tool. *Conserv Biol* 27(5):945–951.
19. Houck JP (1965) The relationship of direct price flexibilities to direct price elasticities. *J Farm Econ* 47(3):789–792.
20. Eales J, Durham C, Wessells CR (1997) Generalized models of Japanese demand for fish. *Am J Ag Econ* 79(4):1153–1163.
21. Harley SJ, Myers RA, Dunn A (2001) Is catch-per-unit-effort proportional to abundance? *Can J Fish Aquat Sci* 58(9):1760–1772.
22. Clark CW, Munro GR (1975) The economics of fishing and modern capital theory: A simplified approach. *J Environ Econ Manage* 2(2):92–106.
23. Pitcher T (1995) The impact of pelagic fish behaviour on fisheries. *Sci Mar* 59(3):295–306.
24. Torres MdO, Felthoven RG (2014) Productivity growth and product choice in catch share fisheries: The case of Alaska pollock. *Mar Pol* 50:280–289.
25. Squires D, Vestergaard N (2013) Technical change and the commons. *Rev Econ Stat* 95(1):1769–1787.
26. Hall RJ, Milner-Gulland E, Courchamp F (2008) Endangering the endangered: The effects of perceived rarity on species exploitation. *Conserv Lett* 1(2):75–81.
27. Clark CW (1973) Profit maximization and the extinction of animal species. *J Poli Econ* 81: 950–961.
28. Swanson TM (1994) The economics of extinction revisited and revised: A generalised framework for the analysis of the problems of endangered species and biodiversity losses. *Oxf Econ Pap* 46:800–821.
29. Branch TA, Lobo AS, Purcell SW (2013) Opportunistic exploitation: An overlooked pathway to extinction. *Trends Ecol Evol* 28(7):409–413.
30. Burgess MG, Polasky S, Tilman D (2013) Predicting overfishing and extinction threats in multispecies fisheries. *Proc Natl Acad Sci USA* 110(40):15943–15948.
31. Hertzler G, Gomera M (2004) *Are African Elephants an Endangered Species?* (International Union for Conservation of Nature, ROSA, Harare, Zimbabwe).
32. Rentsch D, Damon A (2013) Prices, poaching, and protein alternatives: An analysis of bushmeat consumption around Serengeti National Park, Tanzania. *Ecol Econ* 91: 1–9.
33. Asche F, Bjørndal T, Gordon DV (2007) Studies in the demand structure for fish and seafood products. *Handbook of Operations Research in Natural Resources*, eds Weintraub A, Romero C, Bjørndal T, Epstein R (Springer, New York), pp 295–314.
34. Melnychuk MC, Clavelle T, Owashi B, Strauss K (2017) Reconstruction of global ex-vessel prices of fished species. *ICES J Mar Sci* 74(1):121–133.
35. Ricard D, Minto C, Jensen OP, Baum JK (2012) Examining the knowledge base and status of commercially exploited marine species with the ram legacy stock assessment database. *Fish Fish* 13(4):380–398.
36. Chiang FS, Lee JY, Brown MG, et al. (2001) The impact of inventory on tuna price: An application of scaling in the Rotterdam inverse demand system. *J Ag Appl Econ* 33(3):403–412.
37. Food and Agriculture Association of the United Nations (2016) *Fishery and Aquaculture Statistics*. Available at www.fao.org/fishery/statistics/en. Accessed April 23, 2016.
38. Amundsen ES, Bjørndal T, Conrad JM (1995) Open access harvesting of the Northeast Atlantic minke whale. *Environ Resour Econ* 6(2):167–185.
39. Hobday AJ, Tegner MJ (2000) *Status Review of White Abalone (Haliotis sorenseni) Throughout Its Range in California and Mexico* (US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Region Office, La Jolla, CA).
40. World Bank (2016) *World Development Indicators*. Available at data.worldbank.org/data-catalog/world-development-indicators. Accessed April 23, 2016.
41. Erisman BE, et al. (2011) The illusion of plenty: Hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. *Can J Fish Aquat Sci* 68(10):1705–1716.
42. Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA (2013) Marine taxa track local climate velocities. *Science* 341(6151):1239–1242.
43. Worm B, Tittensor DP (2011) Range contraction in large pelagic predators. *Proc Natl Acad Sci USA* 108(29):11942–11947.
44. Pillay R, Johnsingh A, Raghunath R, Madhusudan M (2011) Patterns of spatiotemporal change in large mammal distribution and abundance in the southern Western Ghats, India. *Biol Conserv* 144(5):1567–1576.
45. Maisels F, et al. (2013) Devastating decline of forest elephants in central Africa. *PLoS One* 8(3):e59469.
46. Rodríguez JP (2002) Range contraction in declining North American bird populations. *Ecol Appl* 12(1):238–248.
47. Sakai Y, Yagi N, Arijji M, Takahara A, Kurokura H (2009) Substitute and complement relations among various fish species in the Japanese market: Implications for fishery resource management. *Fish Sci* 75(5):1079–1087.
48. McNab BK (1963) Bioenergetics and the determination of home range size. *Am Nat* 97:133–140.
49. Ripple WJ, et al. (2014) Status and ecological effects of the world's largest carnivores. *Science* 343(6167):1241484.
50. Gaertner D, Dreyfus-Leon M (2004) Analysis of non-linear relationships between catch per unit effort and abundance in a tuna purse-seine fishery simulated with artificial neural networks. *ICES J Mar Sci* 61(5):812–820.
51. Torres-Irineo E, Gaertner D, Chassot E, Dreyfus-León M (2014) Changes in fishing power and fishing strategies driven by new technologies: The case of tropical tuna purse seiners in the eastern Atlantic Ocean. *Fish Res* 155:10–19.
52. Hamilton WD (1971) Geometry for the selfish herd. *J Theor Biol* 31(2):295–311.
53. Lenhardt M, Jaric I, Kalauzi A, Cvijanovic G (2006) Assessment of extinction risk and reasons for decline in sturgeon. *Biodiversity Conserv* 15(6):1967–1976.
54. Hung CM, et al. (2014) Drastic population fluctuations explain the rapid extinction of the passenger pigeon. *Proc Natl Acad Sci USA* 111(29):10636–10641.
55. Phelps J, Webb EL (2015) "Invisible" wildlife trades: Southeast Asia's undocumented illegal trade in wild ornamental plants. *Biodiversity Conserv* 186:296–305.
56. Worm B, et al. (2009) Rebuilding global fisheries. *Science* 325(5940):578–585.
57. Pons M, et al. (2016) Effects of biological, economic and management factors on tuna and billfish stock status. *Fish Fish* 18(1):1–21.
58. Asche F, Bremnes H, Wessells CR (1999) Product aggregation, market integration, and relationships between prices: An application to world salmon markets. *Am J Agr Econ* 81(3):568–581.
59. Natale F, Hofherr J, Fiore G, Virtanen J (2013) Interactions between aquaculture and fisheries. *Mar Pol* 38:205–213.
60. Greenville J, Hartmann J, Macauley TG (2006) Technical efficiency in input-controlled fisheries: The NSW ocean prawn trawl fishery. *Mar Resour Econ* 21:159–179.
61. Hannesson R (1983) Bioeconomic production function in fisheries: Theoretical and empirical analysis. *Can J Fish Aquat Sci* 40:968–982.
62. Sharma KR, Leung P (1999) Technical efficiency of the longline fishery in Hawaii: An application of a stochastic production frontier. *Mar Resour Econ* 13:259–274.
63. Kirkley JE, Squires D, Strand IE (1995) Assessing technical efficiency in commercial fisheries: The mid-Atlantic sea scallop fishery. *Am J Ag Econ* 77:686–697.
64. Weninger Q (1998) Assessing efficiency gains from individual transferable quotas: An application to the mid-Atlantic surf clam and ocean quahog fishery. *Am J Ag Econ* 80:750–764.
65. Esmaili A (2006) Technical efficiency analysis for the Iranian fishery in the Persian Gulf. *ICES J Mar Sci* 63:1759–1764.
66. Bjørndal T, Conrad JM (1987) The dynamics of an open access fishery. *Can J Econ* 20:74–85.
67. Bjørndal T (1989) Production in a schooling fishery: The case of the North Sea herring fishery. *Land Econ* 65:49–56.
68. Comitini S, Huang DS (1967) A study of production and factor shares in the halibut fishing industry. *J Poli Econ* 75:366–372.
69. Kompas T, Che TN (2005) Efficiency gains and cost reductions from individual transferable quotas: A stochastic cost frontier for the Australian south east fishery. *J Prod Anal* 23:285–307.
70. Campbell HF, Hand AJ (1998) Joint ventures and technology transfer: The Solomon Islands pole-and-line fishery. *J Devel Econ* 57:421–442.
71. Eggert H (2000) Technical efficiency in the Swedish trawl fishery for Norway lobster. *IIFET 2000 Proceedings*. Available at oregonstate.edu/dept/IIFET/2000/papers/eggert.pdf 448. Accessed April 25, 2016.