The role of costs in price-related extinction threats

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Abstract.

As a harvested species is depleted, its harvest price often rises due to falling supply, rarity value, or both. There is concern that high price flexibility can cause extinction by buffering harvest profits against abundance declines. However, harvest costs also tend to increase as a population declines. Here, I derive a simple rule of thumb for determining whether prices might rise faster than costs as a population is depleted – indicating susceptibility to severe overharvesting under open-access.

Comparing this rule of thumb to a review of empirical evidence from marine species, I find that conditions leading costs to be insensitive to abundance declines – particularly catch rates insensitive to abundance declines, termed ‘hyperstable’, usually as a result of range contraction – are much more common than high price flexibility, even in highly valued species such as bluefin tunas, sturgeons, whales and abalones. My analysis suggests that factors potentially causing coincident range contraction as a population declines – including herding or schooling behavior and habitat destruction – may be important but underappreciated factors contributing to price-related extinction threats.
Introduction

There is concern that a number of species may be threatened with extinction by the market values of their harvest products. These include species hunted for trophies (e.g., Biggs et al. 2013), collections (e.g., Tournant et al. 2012), body parts regarded as having medicinal or aphrodisiac properties (e.g., Angulo & Courchamp 2009), or luxury foods (e.g., Gault et al. 2008; Collette et al. 2011; Purcell et al. 2014). Many of these species have already suffered substantial population declines, prompting listing by the International Union for the Conservation of Nature (IUCN) Red List (IUCN 2013), the Convention on International Trade of Endangered Species (CITES 2014), or both. Expanding human populations coupled with rapid economic growth in developing countries with large luxury harvest markets may increase pressures on these species in the coming decades (Graham-Rowe 2011; Purcell et al. 2014).

Some are concerned that the market value of these rare species’ harvests might increase as they become rarer, leading to an extinction spiral in which profits – and by extension incentives to harvest – are buffered against rising search costs as the populations are depleted. Courchamp et al. (2006) termed this ‘the Anthropogenic Allee Effect’ (AAE). Recent studies have provided empirical evidence of rising prices coinciding with declining abundance in sturgeons (Gault et al. 2008), mammals (Palazy et al. 2011, 2012a,b), and beetles (Tournant et al. 2012) (see Angulo & Courchamp 2009; Angulo et al. 2009 for more general experiments) – citing these trends as evidence of extinction threats from AAE.

However, others (e.g., Mysterud 2012; Harris et al. 2013; Lyons & Natutsch 2013) have disputed the strength of this evidence, pointing out that: (i) rising prices in response to declines are not a sufficient condition for extinction, as costs also rise; (ii) the AAE framework is built on an assumption of open-access harvesting, which is likely to be violated in harvests that have some form of central management, cooperative governance, or property rights; and (iii) in cases where only a specific segment of the population is targeted (e.g. trophy hunting of only large males), the population as a whole may not be as susceptible to collapse.
Here, I address the first of these concerns. I derive a simple rule of thumb that provides a first approximation of whether the harvest prices of a species or population are likely to rise faster than harvest costs as they are depleted – an indication of AAE susceptibility under open-access.

Prices will be sensitive (‘flexible’) to abundance declines if consumer demand is inelastic (Asche et al. 2007) – meaning quantities demanded are relatively insensitive to prices; if rarity itself fuels increases in demand (Courchamp et al. 2006; Hall et al. 2008); or both. Moreover, any flexibility of prices driven by consumer demand must be transmissible through the supply chain to the harvesters themselves (Asche et al. 2007). Costs will be insensitive to abundance declines if catch-rates are insensitive (often termed ‘hyperstable’ (Harley et al. 2001)) to abundance, or if there are economies of scale – meaning that larger harvest quantities come at lower average costs, holding abundance constant (Torres & Felthoven 2014). The rule of thumb I propose compares the strengths of these relationships.

I then review past empirical estimates of price flexibility, catch hyperstability, and returns to scale in marine species, emphasizing species thought to be threatened by their rising harvest prices currently or in the past. Drawing on this evidence, I argue that prices, even of the most valued species, are rarely responsive enough to declining abundance to allow profits to be maintained unless catch hyperstability or returns to scale is significant. Significantly hyperstable catch rates are quite common however – caused by aggregation behavior (e.g. schooling or herding) (Winters & Wheeler 1985; Bjorndal & Conrad 1987; Mackinson et al. 1997), technology or communication among harvesters (Hilborn & Walters 1987; Gaertner & Dreyfus-Leon 2004; Thorson & Berkson 2010; Torres-Irino et al. 2014), and also, I hypothesize, by habitat destruction.

The AAE mechanism, which is the focus of my analysis, is one of many possible mechanisms of extinction by overharvesting (see Dulvy et al. 2003 for review of some of the others). For example, a species might also be driven extinct if it is caught opportunistically or accidentally in a harvest targeting other species that can support large harvest efforts (Branch et al. 2013; Gaines & Costello 2013). A species might be driven extinct if its growth rate is smaller than the market interest rate or the
discount rate of harvesters; harvesters would then have an economic incentive to harvest the entire population as quickly as possible in order to convert it into a more productive asset (Clark 1973; Swanson 1994). Extinction would be likely if a population experienced either depensation (Courchamp et al. 1999) or extinction from stochastic forces (Lande et al. 2003) at population sizes large enough for harvesting to still be profitable (Berck 1979). These other overharvesting threats are beyond the scope of my analysis, but the development of integrated approaches to assess combinations of harvesting and other threats is an important area of future research.

Methods

Model

I derive a rule-of-thumb test for AAE susceptibility using simple but fairly standard models of harvest productivity, price formation, and population dynamics. The rule of thumb is designed to provide a simple indication of whether harvest prices might rise faster than harvest costs as a population of interest is depleted. The models are kept quite simple to maximize the breadth of empirical applicability, but aim to capture as many important aspects as possible.

I assume the following general model of the population’s dynamics:

\[
\frac{dN}{dt} = Ng(N) - Y \tag{1}
\]

Here, \(g(N)\) is the per-capita growth rate of the population, and is subject to negative density dependence \((g'(N) < 0)\) with no depensation \((g(N) \geq 0)\); \(Y\) is the harvest (yield).

I assume that harvest \((Y)\) is a function of harvest effort expenditure \((E)\) (in monetary units (e.g., dollars), not search time, traps, hooks, or other raw effort units), and population size \((N)\), with constant elasticities to each sensu Clark & Munro (1975),

\[
Y = qE^\alpha N^\beta \tag{2a}
\]
Here, \( q, \alpha, \) and \( \beta \) are non-negative constants. Parameters \( \alpha \) and \( \beta \) are ‘elasticities’ because they measure the percent change in yield resulting from a one percent change in expenditure (\( \alpha \)) or abundance (\( \beta \)), all else equal (i.e. \( (\delta Y/\delta E)(E/Y) = \alpha \), \( (\delta Y/\delta N)(N/Y) = \beta \)). Elasticity \( \alpha \) represents the returns to scale and \( \beta \) is the elasticity of production to the stock size. The cost, \( C \), of obtaining a unit of harvest, as a function of abundance, can be derived by setting \( Y = 1 \) in equation (2a) and solving for \( E \):

\[
C(N) = q - 1 \alpha N - \beta \alpha (2b).
\]

I assume that the price of a unit of catch, \( p \), in a given time period is a function of the total supply of catch in that time period \( Y \) and other unspecified factors, \( X (X = \{X_i\}) \). I again assume a constant elasticity of price \( (p) \) to supply \( (Y) \) and that factors \( X \) (e.g., size of the economy, supplies of related goods, etc.) are not directly related to either abundance \( (N) \) or supply \( (Y) \) (i.e. \( \delta X_j/\delta N = 0, \delta X_j/\delta Y = 0 \) for all \( j \)).

\[
p(Y, X) = p_0Y^{-f}P_X(X) \quad (3).
\]

Here, \( p_0 \) is a positive constant, and \( f \), assumed here to be a non-negative constant, represents the elasticity of price to supply, which economists term the ‘price flexibility of demand’ (Houck 1965; Barten & Bettendorf 1989; Schrank & Roy 1991; Eales et al. 1997). The price flexibility is related to, but distinct from, the demand elasticity (see Appendix S1 in Supporting Information for brief discussion) \((\delta p/\delta Y)(Y/p) = f\)). \( P_X(.) \) is an unspecified function.

Though perceptions of rarity, which might be directly related to abundance \( (N) \) more than supply, are thought to be important in driving price increases (Courchamp et al. 2006), I posit that these rarity effects can most likely be captured by estimates of price flexibility in practice for the following reasons. First, if abundance \( (N) \) is not known, then perceptions of rarity likely come from observations of supply \( (Y) \) (e.g., Gault et al. 2008), and would thus be incorporated into \( f \). Second, if abundance \( (N) \) is known, but strongly correlated with supply \( (Y) \), estimation of \( f \) alone would capture
the perceived rarity effect on prices; and $f$ would probably be more reliably estimated than separate
effects mediated by supply and abundance, due to high multicollinearity. If rarity influences consumer
demand through discrete (rather than continuous) perceptions (i.e., a species is perceived to be ‘rare’ or
‘not rare’), then rarity effects on demand could be accounted for empirically within a price flexibility
($f$) estimation framework that allows for discrete shifts in the demand function (see Asche & Zhang
(2013) for an example and estimation method).

The core question in this study is whether prices should be expected to rise faster than costs as
the population’s abundance declines. It makes sense to ask this question under biological equilibrium
conditions (i.e. $dN/dt = 0$). In other words, we are asking what the resulting unit price equilibrium ($p^*$)
and unit harvest cost equilibrium ($C^*$) would be if abundance was fixed at $N^*$; and we are asking how
changing $N^*$ would affect $p^*$ relative to $C^*$. Fixing $N$ without assuming biological equilibrium would be
self-contradictory because $dN/dt \neq 0$ would mean $N$ was changing. At biological equilibrium, $N^*$,

$$Y = N^* g(N^*) \quad (4a).$$

This implies that,

$$p^*(N^*, X) = p_0 N^{*−f} g(N^*)^{−f} P_{X}(X) \quad (4b).$$

Putting equations (2b) and (4b) together gives the following equation for the ratio of
equilibrium unit price and unit cost ($p^*/C^*$):

$$\frac{p^*(N^*, X)}{C^*(N^*)} = N^* \left(\frac{p_0}{\alpha}\varepsilon\right)^{−f} g(N^*)^{−f} \frac{1}{q\rho} P_{X}(X) \quad (5),$$

Thus, the percent change in the equilibrium ratio of price and cost ($p^*/C^*$) resulting from a one percent
change in abundance ($N^*$), $(\delta(p^*/C^*)/\delta N^*)(N^*/(p^*/C^*))$, is given by:

$$\frac{\partial (p^*/C^*)}{\partial N^*}\left(\frac{N^*}{(p^*/C^*)}\right) = \frac{\beta}{\alpha} - f \left(1 + N^* \left(\frac{g'(N^*)}{g(N^*)}\right)\right) \quad (6).$$
The population’s equilibrium harvest price \( (p^*) \) rises faster than the equilibrium harvest cost \( (C^*) \) as abundance \( (N^*) \) is depleted if \( (\delta(p^*/C^*)/\delta N^*) < 0 \). Because abundance \( (N) \), price \( (p) \), and cost \( (C) \) all must be non-negative, \( (\delta(p^*/C^*)/\delta N^*) < 0 \) implies \( (\delta(p^*/C^*)/\delta N^*)(N^*/(p^*/C^*)) < 0 \), and vice-versa, meaning AAE requires:

\[
\frac{\beta}{\alpha} < f \left( 1 + N^* \frac{g'(N^*)}{g(N^*)} \right) \quad (7a).
\]

Moreover, because \( g'(N) < 0 \) and \( g(N) \geq 0 \); implying \( Ng'(N)/g(N) \leq 0 \); inequality \((7a)\) can only be satisfied if:

\[
\frac{\beta}{\alpha} < f \quad (7b).
\]

If \( (\beta/\alpha) > f \), equation \((5)\) implies that the ratio of price to cost \((p/C)\) approaches 0 (equivalent to profits \((\pi = Y(p - C))\) approaching 0) as the population declines to extinction \((N \to 0)\).

Thus, the AAE is only possible in this model if inequality \((7b)\) is satisfied. The assumption of constant elasticities \((\alpha, \beta, f)\) is unrealistic, though likely as accurate and complex of an approximation as can be supported by data in most harvests. Moreover, even if these elasticities \((\alpha, \beta, f)\) were dynamic, inequality \((7b)\) might still need to be satisfied for AAE, which would still require prices to consistently rise faster than costs as abundance declines, even if the magnitude of the difference varied.

In Appendices S2 and S3 (Supporting Information), respectively, I briefly discuss the impacts of incorporating substitute goods and technical change in the model. I refer the reader to Squires & Vestergaard (2013a,b) for excellent summaries of the impacts of technical change in harvests in general. Briefly, the main results (inequalities \((7a,b)\)) are robust to these complexities, provided there are no perfect substitutes (goods that are indistinguishable from the harvest product of interest to consumers) and technical change is either unrelated to expenditure (e.g., learning by doing (Squires & Vestergaard 2013b)) or related to expenditure in a manner that can be captured by measuring returns to
scale ($\alpha$). The existence of perfect substitutes negates the possibility of an AAE threat unless equation (7b) is satisfied for all species within a group of perfect substitutes. Though relevant to extinction in general (see Clark 1973; Swanson 1994), discounting is not included in the model because it is irrelevant to the question of whether prices rise faster than costs as a population is depleted.

\textit{Application}

The available data for a species or population of interest determine how rule of thumb (7b) might be most precisely and accurately tested. At a bare minimum, estimating price flexibility requires price ($p$) and quantity ($Y$) data; but additional data – on incomes, consumer expenditures, and quantities of related goods – is preferable to guard against omitted variable bias. The simplest regression equation for estimating price flexibility ($f$), assuming it is constant, can be derived by taking the log of both sides of equation (3), which yields equation (8):

\[
\log(p_t) = a - f \log(Y_t) + \log(P_x(X_t)) \tag{8}
\]

Here, $a$ is the intercept ($a = \log(p_0)$). More sophisticated estimation methods also exist, but tend to have larger data requirements. For example, most modern methods jointly estimate systems of inverse demand equations for groups of related harvest products (e.g., fresh and frozen tunas in Chiang et al. 2001) to estimate $f$, rather than separately estimating separate equations for each product. This typically requires short time-scale market-level price and quantity data for all products, as well as other data deemed relevant (e.g., household expenditures or income) (e.g., Eales et al. 1997).

If effort expenditure ($E$), total harvest ($Y$) and abundance ($N$) data are available, then elasticities $\beta$ and $\alpha$, or their ratio ($\beta / \alpha$) can be estimated from the regression equations (9a,b) (derived from equations (2a,b)) (e.g., Amundsen et al. 1995),

\[
\log(Y_i) = b + \alpha \log(E_i) + \beta \log(N_i) \tag{9a}
\]
where $b$ and $c$ are constant intercepts ($b = \log(q)$; $c = \log(q^{1/\alpha})$).

Detailed expenditure data are often not available, however (e.g., see Lam et al. 2011 for a recent review in fisheries). If expenditure data ($E$) are not available, but abundance data ($N$) and catch-per-unit-effort (CPUE) data (in units of catch-per-days harvesting or -hooks, -trips, -traps, etc.) are, then estimating the elasticity of CPUE to $N$ (here denoted $\gamma$), from equation (9c) below, can provide a useful proxy for either $\beta$ or $(\beta/\alpha)$, depending on how scale affects costs (measured by $\alpha$):

$$\log(\text{CPUE}_t) = c + \gamma \log(N_t) \quad (9c).$$

Harley et al. (2001) discuss more sophisticated methods for estimating $\gamma$ from equation (9c), which they call $\beta$, and is often measured or approximated in fisheries. If scale affects the average costs of effort (hooks, days, etc.) (e.g., bait and fuel is cheaper in bulk quantities), but CPUE is impacted mostly by the population dynamics, then CPUE $\equiv Y/E^\alpha$, and $\gamma$ and $\beta$ can indeed be treated as equivalent.

However, if scale primarily affects the relationship between the quantity of effort (hooks, days, etc.) and catch rates, with costs of effort being mostly constant, then CPUE $\equiv Y/E$, implying that $\gamma \equiv (\beta/\alpha)$, not $\beta$. A species’ catch rates are said to be ‘hyperstable’ if $\gamma < 1$ (Harley et al. 2001).

Abundance data are also often not available. In such cases, I hypothesize that $\beta$ can be effectively approximated as follows, if fractional changes between two time periods (denoted 1 and 2) in both abundance ($\Delta N = (N_2 - N_1)/N_1$) and geographic range size (denoted $A$) ($\Delta A = (A_2 - A_1)/A_1$) are known for the population of interest:

$$\beta \approx \frac{\% \text{ change in density}}{\% \text{ change in abundance}} = \frac{1 + \Delta N}{1 + \Delta A - 1} / \Delta N \quad (9d).$$

As a proof of concept, I apply this approximation method to tunas in Appendix S4 (Supporting Information). Estimates of $\beta$ from equation (9d) are consistent with $\beta$-values from the literature.
Equation (9d) makes use of the fact that range contraction in declining populations is thought to be one of the main drivers of hyperstable catch rates ($\gamma < 1$) (Winters & Wheeler 1985; Mackinson et al. 1997). Range contraction buffers population density (the main biological determinant of CPUE) against reductions in overall abundance (see Brown 1984; Lawton 1993 for theoretical discussion; Ceballos & Ehrlich 2002; Laliberte & Ripple 2004 for terrestrial examples; Winters & Wheeler 1985; Worm & Tittensor 2011 for marine examples). Aggregating species (forming schools or herds) often manifest declines to a greater extent as range contractions than density reductions (Winters & Wheeler 1985; Mackinson et al. 1997), for example. Other factors (besides range contraction) can also cause hyperstable relationships between CPUE and abundance, including technological improvement, learning, and information sharing among harvesters (e.g. Hilborn & Walters 1987; Gaertner & Dreyfus-Leon 2004; Thorson & Berkson 2010; Torres-Irineo et al. 2014). However, these might more likely be components of $\alpha$ than $\beta$.

Elasticities of scale ($\alpha$) may be difficult to estimate in low-data situations, particularly when illegal harvests are involved; there are no easy ways around requirements of cost ($E$) and abundance ($N$) data (e.g., Amundsen et al. 1995). In such cases, I suggest assuming either constant returns to scale ($\alpha = 1$), or assuming a value of $\alpha$ estimated from a related harvest type. If estimates or approximations of $\beta$ and $f$ are available, then inequality (7b) can be used to determine the threshold value of $\alpha$ that would signal a potential threat ($\alpha > f\beta$). This allows the rule of thumb to be applied even with large potential uncertainty in $\alpha$ (or analogously, in one of the other parameters).

**Results**

**Review of Empirical Evidence**

Estimates of price flexibility of demand ($f$) for fish products have varied among species, commodity types, and estimation methods, but have mostly been 0.5 or smaller, even for high-value
products (e.g. Schrank & Roy 1991; Eales et al. 1997; Jaffry et al. 1999; Chiang et al. 2001; Asche et al. 2007; Asche & Zhang 2013; Scheld & Anderson 2014), suggesting an often proportionally small response of fish prices to falling supply. Moreover, studies of fish demand have found ex-vessel prices to be less flexible than retail prices (Asche et al. 2007). Studies of market integration (substitutability) have found high substitutability between species within broad classes of fish products, including salmon, whitefish – including cod, haddock, saithe, hake and pollock (see Asche et al. 2007 for review; Scheld & Anderson 2014) – and substitutability, but not perfect substitutability, between most tuna species (Chiang et al. 2001; Sakai et al. 2009).

Even the most highly valued aquatic species seem to have relatively inflexible prices ($f << 1$). To illustrate this point, Figure 1 shows aggregate price-supply relationships for several populations believed to be threatened by high and rising values currently or in the past: bluefin tunas (Atlantic bluefin tuna – ABF – *Thunnus thynnus*, Pacific bluefin tuna – PBF – *Thunnus orientalis*, and Southern bluefin tuna – SBT – *Thunnus maccocyii*) (data from Ricard et al. 2012; Sea Around Us Project 2014; R. Hilborn, pers. comm.), caviar-producing sturgeons (Acipenseriformes) (data from FAO 2014), the Northeast Atlantic minke whale (*Balaenoptera acutorostrata*) (a relatively data-rich whale example; data from Amundsen et al. 1995), and abalone species (*Haliotis sp.*) harvested in California (data from Hobday & Regner 2000; Courchamp et al. 2006).

The price flexibility, $f$, of fresh bluefin tuna (lumped ABF, PBF, and SBT) in Japan was estimated by Chiang et al. (2001) to be 0.19, indicating a 0.19% increase in price for every 1% decrease in supply, with low to moderate substitutability between bluefin and bigeye (*Thunnus obesus*) and yellowfin (*Thunnus albacares*) tunas. This is consistent with relative historical stability observed in aggregate prices (Figure 1A,B). Historical caviar prices (1976-2010; Figure 1C; FAO 2014) have risen more than those of bluefin tunas (~0.3% for every 1% decline in catch), but are still consistent with the common finding that harvest prices tend to rise by half of the percentage by which harvest supplies decline, or less. Northeastern minke whale prices showed a stronger price trend (~0.65% increase on
average for every 1% decline in catch (Figure 1D)), before the International Whaling Commission’s moratorium on whaling came into effect in the late 1980s (Amundsen et al. 1995). Abalone prices in California seem to have been more flexible, increasing by roughly 1% (0.98%) for every 1% decline in abundance over the period 1950-1993, before the 1997 ban on fishing (Figure 1E) (Hobday & Tegner 2000; Courchamp et al. 2006). These historical trends do not necessarily reflect the magnitudes of underlying market-level price flexibilities, but they are mostly consistent with the pervading pattern of low price flexibility (f < 1) seen in other marine harvest products (Figure 1F). Controlling for catch, the residual prices of none of these species (for which data are available) are significantly correlated with abundance (Figure 1G), suggesting that rarity effects in these species may indeed be more strongly associated with supply than abundance, and thus likely captured by price flexibility.

The pervasive observation of low price flexibility (f < 1, often < 0.5), even in highly valued aquatic species, suggests that threats of AAE may be uncommon except among species that have exceptionally stable harvest costs in the face of declining abundance ((β/α) < 0.5) – via hyperstable catch rates, economies of scale, or both.

However, combinations of hyperstable catch rates and economies of scale of this severity are quite common in marine systems. For example, across 15 fisheries for which estimates of either scale elasticity (α) or an equivalent measure of returns to scale (RTS – a composite measure used in studies of multiple factors of production (e.g., see Torres & Felthoven 2014)) were available, returns to scale were on average 1.40 (s.d. = 0.50) (1.40 = RTS ≅ α) (Table S1, Supporting Information). This implies that a population with price flexibility of 0.5 would need an elasticity of production to abundance (β) of on average about 0.7 or smaller to be susceptible to AAE; a population with price flexibility of 0.2 (e.g., ABF, PBF, or SBT) would need β of on average about 0.3 or smaller.

In fact, estimates of β or γ among schooling species have often been <0.5 and frequently not significantly different from 0, meaning that CPUE is nearly uncorrelated with abundance. This
includes lower-trophic level forage fish, such as the Peruvian anchovy (*Engraulis ringens*) Pacific sardine (*Sardinops sagax caerulea*) and Atlantic herring (*Clupea harengus harengus*) (MacCall 1976; Winters & Wheeler 1985; Bjorndal & Conrad 1987; Bjorndal 1988; Mackinson *et al.* 1997), in addition to some larger species. For example, Pintassilgo & Duarte (2002) assume $\alpha = 1$ and $\beta = 0.2$ for most gears in a model of ABF. Amundsen *et al.* (1995) estimate $\alpha = 0.86\text{--}0.87$ and $\beta = 0.12\text{--}0.14$ (though not significantly different from 0) for the Northeast Atlantic minke whale.

If $\beta = 0$ (or $\gamma = 0$), then any price flexibility whatsoever (i.e. $f > 0$) can result in extinction, termed ‘catchability-led stock collapse’ in fisheries (Pitcher 1995). Other tunas (e.g., SBT, skipjack (*Katsuwonus pelamis*) and yellowfin) are thought to have moderate hyperstability ($\beta \approx 0.3\text{--}0.7$) in their surface fisheries (e.g. purse-seine, pole-and-line), which target schools, but little hyperstability ($\beta \approx 1$) in longline fisheries (Kennedy 1999; Gaertner & Dreyfus-Leon 2004; Ward 2008; Campbell & Kennedy 2010; Campbell *et al.* 2010).

A meta-analysis of flatfish (megrim, plaice, sole) and gadiformes (cod, haddock, hake, pollock, whiting), mostly from trawl fisheries, estimated $\gamma$ values averaging 0.64-0.75 (Harley *et al.* 2001). There have been few estimates of $\beta$ or $\gamma$ for commercial fisheries for diadromous species (e.g. salmonids, sturgeons), but recent estimates of $\gamma$ from anglers have ranged from $\sim$ 0.6-1 for salmonids (Tsuboi & Endou 2008; Ward *et al.* 2013). Though there is little information with which to estimate $\beta$ for sturgeons, there may be reason to believe that catches are quite hyperstable (i.e. $\beta << 1$), because many of the most severely depleted caviar-producing sturgeons (e.g. Beluga sturgeon (*Huso huso*), Russian sturgeon (Osetr) (*Acipenser gueldenstaedtii*)) have suffered significant habitat destruction caused by pollution, hydroelectric dams, and other forms of encroachment (IUCN 2013), which has likely led to range contraction. There have been no estimates of $\beta$ in abalones to my knowledge, but their mostly sessile nature may suggest $\beta \approx 1$. 
Discussion

Several studies have empirically demonstrated that harvest prices of rare species rise in response to falling supply and rarity value (Courchamp et al. 2006; Gault et al. 2008; Angulo et al. 2009; Palazy et al. 2011, 2012a,b; Tournant et al. 2012), sparking concerns about possible AAE threats. However, it was unknown whether rarity value or other factors could drive prices up fast enough to maintain harvest profits as a population was depleted (Harris et al. 2013). This study derives a simple rule of thumb for answering this question: the harvest profits of a population will only be robust to declining abundance if the own-price flexibility of demand of the population’s harvest is larger than the ratio of the elasticities of production to abundance and scale (i.e. $f > \beta/\alpha$).

To date, the literature on AAE has mostly focused on price trends (Courchamp et al. 2006; Hall et al. 2008). However, the evidence reviewed in this study suggests that, at least in marine species, AAE threats are likely to be driven to a greater extent by hyperstable catch rates than rising prices; prices generally rise proportionally more slowly than catches decrease ($f < 0.5$ in most studies). Economies of scale are also common (Table S1), and may exacerbate populations’ susceptibilities to AAE.

There are several possible reasons for the pervasiveness of low price flexibilities. One possibility is that even the most highly valued luxuries have at least partial substitutes. Populations whose harvests have perfect substitutes are very unlikely to be threatened by AAE (Hall et al. 2008), because perfect substitutability causes the impact of declines in a population’s abundance on its price to diminish as it approaches extinction (see Appendix S2). A second possibility is that processors and other market intermediaries may buffer prices against supply shocks (Asche et al. 2007). More research is needed to estimate price flexibilities and substitutability between highly valued harvest products. Greater collection and dissemination market- and ex-vessel level price and quantity data for such products is important to advancing this research agenda.
Because price flexibilities are often smaller than 0.5, most harvested populations would likely need small catch elasticities ($\beta < 0.5$) or significant returns to scale to be threatened by AAE. Among harvested fish populations, those with catch elasticities this small have been predominantly schooling species, which manifest population declines largely as range contractions, thereby maintaining population densities (Winters & Wheeler 1985; Mackinson et al. 1997). Some schooling populations have catch rates that are seemingly uncorrelated with abundance ($\beta \approx 0$) (Mackinson et al. 1997), which can lead to population collapses regardless of demand or substitutability (‘catchability-led stock collapse’ (Pitcher 1995)).

Thus, highly valued species that aggregate should be of particular concern for AAE threats. For example, based on $f$- and $\beta$-values from the literature, Atlantic and Pacific bluefin tuna may be susceptible to AAE (Chiang et al. 2001 estimate $f = 0.19$, Pintassilgo & Duarte 2002 assume $\beta = 0.2$; small $\beta$ is consistent with observed abundance and range trends Appendix S4, Figure S1)). This possibility merits careful further study, as there are good data in these fisheries – likely sufficient to quite rigorously estimate $\beta$ and returns to scale ($\alpha$). Though seldom studied, it is likely that many terrestrial harvested species that aggregate have hyperstable catch rates as well. Estimating $\beta$ in terrestrial harvests has likely been hindered by difficulty in obtaining catch-per-unit-effort (CPUE) data, particularly in illegal harvests. I offer one possible approach (equation (9d)) to approximating $\beta$ from range data, and provide some empirical support for this approach (Appendix S4).

Because range contraction is an important driver of hyperstable catch rates, habitat destruction could exacerbate overharvesting threats, by buffering population densities against declines in abundance, and shrinking the search area for harvesters. Habitat destruction is unlikely to be a major issue for high-seas marine species (Worm & Tittensor 2011), but may be an important consideration for terrestrial, freshwater, reef, and diadromous species, likely including sturgeons (Lenhardt et al. 2006). Investigating extinction threats posed by catch hyperstability in harvested land animals, and
interactions between threats of habitat destruction and overharvesting, are important areas of future research. The extinct passenger pigeon (*Ectopistes migratorius*), which aggregated in large flocks and suffered both habitat destruction and overharvesting (e.g. Bucher 1992; Hung *et al.* 2014), is one potentially interesting historical case study. Climate change could possibly also lead to range contraction-related overharvesting threats to some species.

This study focuses on AAE, which is an open-access mechanism of extinction. There are property rights in many harvests, including some poaching (Harris *et al.* 2013) and many fisheries (Worm *et al.* 2009). There is currently some form of management governing harvests of whales (International Whaling Commission (IWC 2014)), bluefin tunas (CCSBT 2011a,b; IATTC 2012; ISC 2012), and California abalones (Hobday & Tegner 2000). Trade in sturgeons is regulated under the Convention on International Trade in Endangered Species (CITES 2014). Cooperation, governance, or management can prevent extinction of a harvested population under many circumstances, but it is nonetheless important to understand open-access incentives, as access restrictions are rarely perfectly enforced, particularly in the oceans. There is significant illegal and unreported fishing of southern bluefin tuna, for example (Polachek 2012), despite a very strong recent tradition of management, led by the Commission for the Conservation of Southern Bluefin Tuna (CCSBT).

This study considers one type of overharvesting threat (AAE), among many. Direct threats of incentive-driven extinction due to high discounting (Clark 1973) are not considered; nor are indirect threats from ecological interactions with other species (e.g. Estes *et al.* 1998), stochastic forces (Lande *et al.* 2003), market interactions (e.g. Sakai *et al.* 2009), or multispecies or opportunistic harvesting (e.g. Branch *et al.* 2013; Gaines & Costello 2013). Future work expanding or combining the rule of thumb approach presented here with other approaches considering these other factors is a fruitful area of future research. For example, the indirect threat posed by AAE to bycatch species might be assessed by comparing their depletion rates (e.g., sensu Burgess *et al.* 2013) to those of species estimated to be susceptible to AAE by the approach presented here.
Overharvesting threatens many species worldwide (Millennium Ecosystem Assessment 2005). Highly-valued, rare species, such as caviar-producing sturgeon species (Lenhardt et al. 2006; Gault et al. 2008), land-animals hunted for trophies (Johnson et al. 2010; Palazy et al. 2012a), large whales (Clark 1973; see also Branch et al. 2013), marine invertebrates (Purcell et al. 2014), and highly valued tunas (Collette et al. 2011), are rapidly declining and are thought to be threatened with extinction as a result of their rarity-value (Courchamp et al. 2006). This study provides a rule-of-thumb approximation method for empirically evaluating this threat; and provides evidence suggesting that hyperstable catch rates resulting from aggregation, range contraction, and possibly habitat destruction, may be larger drivers of AAE than rising prices, at least in marine species. More research is needed to evaluate the possible threat of hyperstable catch rates to hunted land-mammals (e.g. rhinos, elephants, ungulates, large cats), and this study illustrates one possible method that does not require catch data. The possible synergy between habitat destruction and overharvesting highlighted here merits further study and conservation attention.

Acknowledgements
I thank Stephen Polasky, David Tilman, Steven Gaines, Christopher Costello, Peter Abrams, Clarence Lehman and Paul Venturelli for useful discussions, and Franck Courchamp, Maite Pons, Ray Hilborn, and Trevor Branch for assistance with price data. This work was supported by a University of Minnesota Doctoral Dissertation Fellowship, a Natural Sciences and Engineering Research Council of Canada (NSERC) Postgraduate Scholarship, and the Waitt Family Foundation.

Supporting Information
Brief discussions of price flexibility in relation to other economic demand measures (Appendix S1), the and effects of substitutes (Appendix S2) and technical change (Appendix S3) on extinction threats; a proof-of-concept test of equation (9d) in tunas (Appendix S4, Figure S1); and a list of studies
estimating returns to scale in fisheries are available online (Table S1). The author is solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Figure Legends
**Figure 1. Price trends in highly valued marine species.** Panels (A)-(E) illustrate trends in supplies and prices of (A) ABF and PBF (production (total catch) and abundance from Ricard *et al.* 2012; average ex-vessel prices calculated from Sea Around Us Project 2014), (B) SBT (production (total catch) and abundance from Ricard *et al.* 2012; prices (averaged across Tokyo auction markets) from R. Hilborn (pers. comm.)), (C) caviar (global production, average export prices from FAO 2014), (D) the Northeast Atlantic minke whale (production, abundance, prices from Amundsen *et al.* 1995), and (E) California abalones (CPUE and prices from Hobday & Tegner 2000; Courchamp *et al.* 2006). All prices were converted from nominal to real USD value using data on currency exchange rates and annual inflation from the World Bank (2014). (F) Prices of each of these harvests have historically declined as fast as catch (abalone) or slower (others). Solid lines show linear fits of log transformed price and production (supply) data, with 95% confidence intervals shaded. Dotted and dashed grey lines respectively illustrate slopes of -1 (implying 1% decrease in price for 1% increase in production) and -0.5, for reference. (G) Controlling for price, none of these species, for which data was available, had a significant historical relationship between price and abundance, suggesting price flexibility may capture rarity effects for these products.
*CPUE used as an abundance proxy for abalone.
Supporting Information for:

The role of costs in price-related extinction threats

Matthew G. Burgess

Contents:

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Appendix S2. Substitutes

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Figure S1. Estimates of catch elasticity ($\beta$) from range in tunas

Table S1. Estimates of returns to scale ($\alpha$, RTS) in fisheries.

Literature Cited

Appendix S1. Price flexibility vs. demand elasticity

Throughout this study, I use price flexibility ($f$) as a measure of the price-quantity relationship. It is worth briefly justifying this choice, in relation to the more common measure of quantity-price relationships, own-price elasticity of demand (usually denoted $\varepsilon$), which measures the percentage decrease in the quantity of a product demanded in response to a 1% increase in its price. Price flexibility, $f$, is related to $\varepsilon$, but not an exact reciprocal for most goods (i.e. $f \neq 1/\varepsilon$; see Houck 1965; Schrank & Roy 1991; Eales et al. 1997; Asche et al. 2007). Price flexibility ($f$) is considered a more appropriate measure of the quantity-price relationship than $\varepsilon$ for harvested products, because quantity is determined before price, in contrast to many other types of markets (Houck 1965; Barten & Bettendorf 1989). There is also empirical support (e.g., Eales et al. 1997) for price flexibility being a better measure of quantity-price relationships in harvested species than demand elasticity.
Appendix S2. Substitutes

The existence of substitute goods impacts the sensitivity of a population’s harvest price to its supply because it potentially reduces a consumer’s willingness to pay a higher price (when they could shift demand to the substitute instead) (Asche et al. 2007). Substitutes can be incorporated into inverse demand models (those estimating price-dependencies on supplies) by including the substitute supply quantities in the regression model estimating price flexibility (f) (e.g., Scheld & Anderson 2014). As a simple example, suppose the price flexibility of population i’s harvest was estimated from an equation of form (S2.1):

\[
\log(p_i) = a - f_i \log(Y_i) + \sum_k f_{ik} \log(Y_k) + \log(P_X(X_i)) \tag{S2.1}
\]

Here, \( P_X(X) \) is again an unspecified function (e.g., of income, etc.), \( Y_{kt} \) is the supply of good \( k \) in time period \( t \), and \( f_{ik} \) is the cross-price flexibility (the elasticity of the price of population \( i \) to supply changes in good \( k \)). Good \( k \) is a substitute if \( f_{ik} < 0 \). Provided all \( Y_{kt} \) are independent of \( Y_{it} \), and no good, \( k \), is a perfect substitute of \( i \), the relationship, \( (\delta p/\delta Y)(Y/p) = -f \), and by extension rule of thumb (7b), still hold.

However, it is important, for the purposes of both estimating \( f \) and more generally predicting extinction threats to a population, to identify any other species or products that are perfect substitutes, meaning that consumers do not distinguish between the two products. Perfect substitutes are defined, for the purpose of my analysis, by the Law of One Price (LOP), which states that perfect substitutes must either have identical or proportional equilibrium prices (where any proportional differences result from differences in quality or transportation costs that are immune to arbitrage) (Hotelling 1929; Asche et al. 1999, 2007). The simplest test for perfect substitutability between two products, 1 and 2, involves estimating the parameters in the following equation:

\[
\log(p_1) = a + b \log(p_2) \tag{S2.2}
\]
and testing the hypothesis that $b = 1$ (perfect substitutability). This equation can also be used to test a hypothesis of no market interaction ($b = 0$). Asche et al. (1999, 2007) review other methods for testing for substitutability (often referred to more broadly as ‘market integration’ in economic studies, as the LOP depends on both equivalence of products for consumers and ease of arbitrage between markets in a spatial sense) that can allow for non-stationarity in prices and other dynamic complexities, when longer unbroken time-series data are available.

Identifying perfect substitutes is important for two reasons. First, if a good, $k$, is a perfect substitute for harvest of a population, $i$ (i.e. the LOP holds), then treating them as separate products creates bias in estimating $f_i$ (even if $\log(Y_k)$ is included in the regression, for example), as the ‘true’ $f_i$ will vary with the supply of the perfect substitute good at each time period. Second, and more fundamentally, if harvest of population $i$ is part of a set of populations producing equivalent harvests (denoted $S$), then the price responds to changes in the total supply of harvest of all populations in $S$. In other words, price flexibility, $f_i$, would really describe:

$$f_i = \frac{\partial p_i}{\partial \left( \sum_{k=1}^{S} Y_k \right)} \left( \frac{\sum_{k=1}^{S} Y_k}{p_i} \right) \neq \frac{\partial p_i}{\partial Y_i} \left( \frac{Y_i}{p_i} \right) \quad (S2.3).$$

Under biological equilibrium conditions, $Y_i = N_i g_i(N_i)$, it follows from equation (S2.3) that $(\partial p_i/\partial N_i)$ approaches 0 as abundance $(N_i)$ approaches 0, eliminating the threat of price-driven extinction, if there are other more common populations or products which are perfect substitutes (i.e. $Y_k > 0$, for at least one $k$). Thus, with respect to price-driven extinction threats, a group of populations whose harvests are perfect substitutes are only as weak as their strongest (i.e. most slowly depleted) member. This result may have important implications for rare fish species that are aquacultured. However the assumption that aquaculture is a perfect substitute for wild harvest remains untested for most species, and evidence so far suggests that perfect substitutability may be rare (Asche et al. 2001; Natale et al. 2013).
Appendix S3. Technical change

I briefly consider very simple extensions of the modeling framework in this study to account for technical change, but I refer the reader to Squires & Vestergaard (2013a,b) for a much richer treatment of technical change in fisheries and other harvests. Recall that the main text assumes a Cobb-Douglas harvest function \( Y \) of effort expenditure \( E \) and population abundance \( N \):

\[
Y = qE^\alpha N^\beta \quad (2a),
\]

which results in the following equation for the costs of obtaining a unit of catch:

\[
C(N) = q \frac{1}{\alpha} N^\frac{\beta}{\alpha} \quad (2b).
\]

Technical changes can either be exogenous to capital investments by the harvesters (termed ‘disembodied’ by economists), making them a function of time (e.g., learning by doing); or they can endogenous (‘embodied’), and therefore functions of capital investment (e.g., better equipment) (Squires & Vestergaard 2013a,b). Thus, a simple way of incorporating technical change into this model is adding a function representing technology, \( T(t,K) \), of time, \( t \), and capital formation, \( K \), into equation (2a), such that:

\[
Y = qE^\alpha N^\beta T(t,K) \quad (S3.1).
\]

Setting \( Y = 1 \) in equation (S3.1), and solving for \( E \), the cost per-unit-catch, \( C \), is given by:

\[
C = q \frac{1}{\alpha} N^\frac{\beta}{\alpha} [T(t,K)]^\frac{1}{\alpha} \quad (S3.2).
\]

If capital formation, \( K \), and overall expenditure, \( E \), are independent (i.e. \( K \) does not depend on \( E \)); or if technical change is strictly disembodied (i.e. \( T(t,K) = T(t) \)); then \((\delta C/\delta N)/(N/C) = - (\beta/\alpha)\), and rule of thumb (7b) applies.

However, things are less straightforward if capital formation is dependent on expenditure (i.e. \( K = K(E) \)) (most likely the case) and technical change is embodied \((\delta T/\delta K) \neq 0\). In this case, in order for effective elasticity of scale \((\delta Y/\delta E)/(E/Y)\), denoted \( s \), to still be constant, the technology effect, \( T \),
would also need to have a constant elasticity to expenditure \((\delta T/\delta E)/(E/T)\), denoted \(\tau\). With this assumption, \((\delta C/\delta N)/(N/C) = - (\beta/s)\), where \(s = \alpha + \tau\), and rule of thumb (7b) could apply provided the estimation of returns to scale included embodied technical change (i.e. \(s\), not \(\alpha\), was being estimated). However, embodied technical change with non-constant elasticity to total expenditure \((E)\) would not be captured by rule of thumb (7b) and merits explicit consideration when appropriate data are available.

Appendix S4. Proof of concept for equation (9d)

As a proof of concept for equation (9d), I approximate average (i.e. across all gears) \(\beta\) values for tunas by combining the average observed 1960-1999 range change across the Atlantic, Pacific, and Indian Oceans estimated by Worm & Tittensor (2011), with estimates from the RAM Legacy Stock Assessment Database (Ricard et al. 2012) of the abundance change in each population (in units of total biomass) over the same period. Multiple populations of the same species in the same ocean were aggregated to be compatible with Worm & Tittensor’s (2011) range change estimates. Estimated range changes in SBT were averaged across all 3 oceans (Atlantic, Pacific, Indian).

Estimates of \(\beta\) using equation (9d) for tunas are fairly consistent with existing hypotheses (Figure S1A, B) (e.g., Kennedy 1999; Pintassilgo & Duarte 2002; Campbell & Kennedy 2010; Campbell et al. 2010). Species caught mostly in longline fisheries (albacore \((Thunnus alalunga)\), bigeye, SBT) had average \(\beta\) estimates close to 1, while species caught mostly in purse-seine, pole-and-line and other surface fisheries targeting schools (ABF, PBF, skipjack, yellowfin), had mostly low to moderate average \(\beta\) estimates (Figure S1B). Estimates of average \(\beta\) for both ABF and PBF using this method were close to or below 0, as their ranges have contracted as much or more than their abundances (Worm & Tittensor 2011; Ricard et al. 2012). It is possible, though unlikely, that the true \(\beta\)s for these species are negative (this would mean CPUE increases as abundance decreases), but likely that they are indeed very low. This analysis suggests that range contraction may indeed be a key driver
of catch hyperstability, and equation (9d) may provide a useful tool for empirically estimating catch elasticities ($\beta$) when CPUE data is difficult to obtain.

**Fig. S1**

**Figure S1. Estimates of catch elasticity ($\beta$) from range in tunas.** Panel (A) compares 1960-1999 abundance and range trends in marine tunas (data from Worm & Tittensor 2011; Ricard et al. 2012). When range does not change with abundance, $\beta$ would be expected to be 1 (solid grey line). When range changes proportionally with abundance, density is not correlated with abundance, and $\beta$ would be expected to be 0 (dashed grey line). Panel (B) shows estimates of average $\beta$ for tuna species calculated using equation (9d) plotted against the fraction of total catch from purse-seine, pole-and-line, and other surface fisheries (data from FAO 2014). The solid line is fit to all points, and suggests an average $\beta$ of 1.13 in tunas with no catch in surface fisheries, and an average $\beta$ of 0.03 in tunas caught exclusively in surface fisheries. The dashed line is fit excluding negative $\beta$ estimates, and suggests average $\beta$s of 1.04 and 0.79 with no surface fisheries and exclusively surface fisheries, respectively. These values, and their differences across fishery types, are consistent with estimated ranges of $\beta$ for tunas from the literature.
Table S1. Estimates of returns to scale (\( \alpha \), RTS) in fisheries.

| Fishery                                           | Parameter | Value | Reference                       |
|---------------------------------------------------|-----------|-------|---------------------------------|
| NE Atlantic minke whale                           | \( \alpha \) | 0.865 | Amundsen et al. 1995            |
| Mid-Atlantic sea scallop                          | RTS       | 1.73  | Kirkley et al. 1995             |
| Hawaii longline                                    | RTS       | 1.87  | Sharma & Leung 1999             |
| Alaska pollock (pre-American Fisheries Act)       | RTS       | 1.95  | Torres & Felthoven 2014         |
| Alaska pollock (post-American Fisheries Act)      | RTS       | 1.07  | Torres & Felthoven 2014         |
| Mid-Atlantic surf clam                            | RTS       | 1.04  | Weninger 1998                   |
| Mid-Atlantic ocean quahog                          | RTS       | 1.51  | Weninger 1998                   |
| Lofoten (Norway) saithe                            | RTS       | 1.94  | Hannesson 1983                  |
| Lofoten (Norway) cod                               | RTS       | 1.06  | Hannesson 1983                  |
| North Sea herring (1975)                           | RTS       | 1.44  | Bjorndal 1989                   |
| Australian Southeast trawl fishery                | RTS       | 0.99  | Kompas & Che 2005               |
| Swedish trawl fishery for Norway lobster           | RTS       | 0.92  | Eggert 2000                     |
| Solomon Islands pole and line fishery             | RTS       | 0.96  | Campbell & Hand 1998            |
| Pacific halibut                                    | RTS       | 1     | Comitini & Huang 1967           |
| NSW Ocean prawn trawl fishery                     | RTS       | 2.6   | Greenville et al. 2006          |
| Iranian Persian Gulf fishery                       | RTS       | 1.42  | Esmaeili 2006                   |
| **Mean (S.D.)**                                   |           | **1.40 (0.50)** |
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