Simple solutions to complex problems in fisheries

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Dedication

For Megan. Here's to the start of a new adventure.

Abstract

Fisheries science faces a challenging combination of complexity and data limitation that places opposing pressures on theoretical research - which seeks to describe the complexity - and empirical research - which is constrained to simplicity by the limitations of available data. In this volume, I present studies aiming to reconcile theoretical and empirical approaches to assessing the current status of fished populations and designing management plans in two ways: i) by using concise mechanistic theories rooted in measurable parameters to develop new predictive assessment tools; and ii) by using ecological and economic theory to develop insights whose applications are not data-dependent or system specific. My research provides several important insights for assessment and management in fisheries: 1) Combinations of biological and socioeconomic conditions that eventually lead to extinction or overfishing can often be empirically identified decades before high harvest rates and large population declines occur, allowing for preventative management. 2) Though there is concern that harvest value, which rises as a harvested species is depleted, can allow profits to be maintained it is driven extinct, this threat most often also requires catch-rates to be substantially robust to declining abundance. Because range contraction often buffers population densities against abundance declines, habitat destruction may exacerbate threats of overharvesting. 3) Assessments based on single-species population models in multispecies fisheries can often provide reliable estimates of sustainable yields and harvest rates in populations with high vulnerability to overfishing, but often significantly overestimate sustainable yields and harvest rates in populations with lower vulnerability. However, single-species assessment frameworks can nonetheless be used to identify conditions leading to such bias, and estimate bounds on its magnitude. 4) Diversifying technologies and efficiencies within fishing fleets often leads to fewer population collapses in both managed and unmanaged fisheries; and increases the positive impact management can make on fishery yields and profits. The studies in this volume provide new perspectives on theoretical-empirical synergies in fisheries research, and maximizing the information value of fisheries data through theoretical concision and ecological abstraction.

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Chapter 1

Introduction

Effectively managing the world's fisheries is important to food security, livelihoods, and sustaining diverse and productive marine ecosystems (Worm et al. 2009; Costello et al. 2012; Halpern et al. 2012; Sumaila et al. 2012). Fisheries management is guided by fitting models to data to assess the current health of target populations, and to predict the impacts of future fishing efforts or management strategies on these populations and their ecosystems (Hilborn & Walters 1992; Cadima et al. 2003). However, modeling efforts in fisheries face a challenging combination of complexity and data-limitation: marine ecosystems are complex (e.g. Link 2002), and oceans are difficult and expensive to sample (Hilborn 2011).

Data-limitation makes fitting complex models with many parameters difficult and unreliable. Consequently, the combination of complexity and data-limitation in fisheries has led to a significant disconnect between advances in theory and empirical approaches to assessment and modeling. For example, despite numerous recent calls for 'ecosystem-based fishery management' (Pikitch et al. 2004), most fishery management organizations still fit data to single-species growth models to predict future population responses to fishing pressure, ignoring species interactions (Cadima et al. 2003; Hilborn 2011; Hilborn & Ovando 2014). Approaches to assessing threats of extinction and overfishing to populations are often correlative or phenomenological - deducing a threat from past declines in abundance or from combinations of life-history traits that correlate with susceptibility to overfishing in other species (Dulvy 2004; Cheung et al. 2005; Mace et al. 2008; Le Quesne & Jennings 2012; Costello et al. 2012), rather than using predictive models based on the ecological and socio-economic mechanisms driving overfishing. Theoretical models in fisheries science often use parameters or conceptualizations that are difficult to match with collectible data (Hilborn 2011).

The research I present in this volume aims to reconcile theory with empirical approaches to fisheries assessment, modeling, and management in two ways. First, I use simple mechanistic theories rooted in commonly measured parameters to develop new

empirical approaches to predicting extinction and overfishing threats. Second, I explore ecological and economic fisheries theory to extract practical insights for fisheries management, which are not data-dependent or system-specific.

Chapters 2 and 3 present mechanistic approaches to identifying combinations of biological and socioeconomic conditions that would eventually cause a harvested population to be driven extinct or severely depleted, before high harvest rates and resulting population declines occur. Chapter 2 focuses on identifying threats to weak stocks and by-catch species in multispecies fisheries. Multispecies fisheries, which catch multiple species simultaneously, pose severe threats (e.g. Hall et al. 2000; Lewison et al. 2004a, 2014) because more resilient species can support profits at high effort while more vulnerable species are depleted (Gaines & Costello 2013). The assessment approach presented is built on the premise that the shared threat of fishing effort in a multispecies fishery links the fates of the species caught in a predictable way. The fates of some 'key' species can be predicted as a result of their influence on economic or regulatory factors driving maximum effort in the fishery. The approach presented predicts threats to other species by measuring their average vulnerability to depletion relative to these key species. In a case study of Western and Central Pacific tunas and billfish, it is shown that threats to 4 populations recently identified as threatened with overfishing could have been identified in the 1950s.

Chapter 3 presents an approach to identifying threats to target populations as a result of profits that are robust to declining abundance. Several recent studies (e.g. Courchamp et al. 2006; Gault et al. 2008; Collette et al. 2011; Palazy et al. 2011; 2012a,b; Purcell et al. 2014) have provided empirical evidence that harvest prices of species tend to rise as their abundances decline. If prices rise faster than the costs of obtaining harvest, a species could be profitably harvested to extinction (Courchamp et al. 2006). I present an approach to empirically estimating whether current bioeconomic conditions would allow profitable harvesting to extinction. The approach illustrates that profitable harvesting to extinction requires a combination of price flexibility in response to declining abundance and catch rates that are 'hyperstable', meaning that they decline more slowly than abundance (Harley et al. 2001). Drawing on evidence from bluefin

tunas, caviar producing sturgeons, whales, and other valuable harvested aquatic species, it is argued that, even for rare and highly valued species, prices are often relatively inflexible, but catch rates can be highly hyperstable – in some cases even uncorrelated with abundance – particularly in species that aggregate (e.g. in herds or schools) (Mackinson et al. 1997). Thus, more conservation and management attention to catch hyperstability is merited, particularly in terrestrial species, where very little attention has been paid to this phenomenon. It is also argued that habitat destruction may exacerbate threats of overharvesting by buffering population densities against declines in abundance.

Chapters 4 and 5 are theoretical studies, seeking to provide practical general insights for fisheries management. Chapter 4 explores the idea that single-species assessment models in fisheries, though not explicitly considering species interactions, may nonetheless effectively capture the true relationship between yield and fishing effort for a population when fit to data. This idea has not been widely explored, but has recently been challenged in predator-prey models (Abrams 2009a,b,c) and economically-inspired 'general equilibrium ecosystem models' (GEEM), designed to capture effects of dynamic foraging behavior (Tschirhart 2012). Understanding ecological contexts under which single-species assessment models can produce reliable estimates of sustainable harvests is important for prioritizing ecological data collection and implementation of ecosystem-based fishery management (Pikitch et al. 2004). I focus on the effect of competitive interactions on the reliability of single-species assessment models in multispecies fisheries. It is likely that species caught in multispecies fisheries compete ecologically with one another because multispecies fishing methods tend to select species with similar ecological niches as a result of using bait, size-selective gear, and spatial and temporal targeting. I find evidence suggesting that sustainable yields of species with high susceptibility to overfishing (weak stocks) will often be reliably estimated, but sustainable yields of species least susceptible to overfishing (strong stocks) will often be significantly overestimated. However, I also illustrate how single-species assessment frameworks can be reliably used to identify conditions under which such overestimates are likely to occur, as well as bounds on estimation bias. I discuss how existing management solutions addressing the problem of unbalanced exploitation in multispecies

fisheries – the 'weak stock problem' (Gaines & Costello 2013) – can also reduce the likelihood of overestimation of sustainable strong stock yields.

Chapter 5 illustrates opportunities and pitfalls presented by the diversity of technologies, strategies and technical efficiencies in fishing fleets. Biological diversity is known to play an important role in driving the productivity and stability of ecosystems, along with other functions (e.g. Tilman & Downing 1994; McCann 2000; Loreau et al. 2001; Isbell et al. 2011; Reich et al. 2012). However, despite theoretical parallels, the role of fleet diversity in driving the productivity, profitability, and ecological impacts of fisheries has received little attention. In multispecies fisheries, it is shown that diversity in relative catch rates of different species, as a result of diversity in gear or spatial/temporal targeting for example, leads to higher yields and less overfishing in both well-managed and unmanaged fisheries. Diversity in technical efficiency is shown to be a double-edged sword – creating opportunities for higher profits in well-managed fisheries, but leading to greater overfishing threats in unmanaged fisheries.

In the concluding chapter, I discuss the information-driven tradeoff in assessment methods in fisheries between reach, or breadth of applicability (which correlates with informational simplicity), and predictive power (which correlates with mechanistic accuracy and detail). I argue that this tradeoff underlies many debates between simplistic and holistic assessment approaches, and that the most effective assessment method is likely to be highly context-dependent. Instead, more attention should be paid to maximizing the information value of the data that are collected. The studies presented in this volume demonstrate that: i) making mechanistic theory more concise to allow for predictive assessments with limited data, and ii) understanding when complex realities can and cannot be effectively abstracted by fitting simple models to data, are potentially promising avenues toward this goal that deserve further attention. iii) Interpolating missing data using data from similar species or fisheries (e.g. Cheung et al. 2005; Costello et al. 2012; Le Quesne & Jennings 2012), and iv) making use of recent advances in non-linear non-parametric forecasting methods (e.g. Sugihara & May 1990; Sugihara et al. 2012; Deyle et al. 2013), are other avenues that have shown recent promise. Future

approaches to fisheries science and management combining these four avenues are likely to be highly successful in the face of data limitations.

Chapter 2

Predicting overfishing and extinction threats in multispecies fisheries

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Abstract

Threats to species from commercial fishing are rarely identified until species have suffered large population declines, by which time remedial actions can have severe economic consequences, such as closure of fisheries. Many of the species most threatened by fishing are caught in multispecies fisheries, which can remain profitable even as populations of some species collapse. Here we show for multispecies fisheries that the biological and socioeconomic conditions that would eventually cause species to be severely depleted or even driven extinct can be identified decades before those species experience high harvest rates or marked population declines. Because fishing effort imposes a common source of mortality on all species in a fishery, the long-term impact of a fishery on a species is predicted by measuring its loss rate relative to that of species that influence the fishery's maximal effort. We tested our approach on eight Pacific tuna and billfish populations, four of which have been identified recently as in decline and threatened with overfishing. The severe depletion of all four populations could have been predicted in the 1950s, using our approach. Our results demonstrate that species threatened by human harvesting can be identified much earlier, providing time for adjustments in harvesting practices before consequences become severe and fishery closures or other socioeconomically disruptive interventions are required to protect species.

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2.1 Introduction

Marine fisheries are an important global source of food and livelihoods (Beddington et al. 2007; Worm et al. 2009; Godfray et al. 2010; Costello et al. 2012), but there are concerns that current fishing practices threaten some marine species with severe depletion or eventual extinction (Hutchings & Reynolds 2004; Beddington et al. 2007; Worm et al. 2009; Costello et al. 2012). Many of the largest commercial fishing methods, such as trawling, longlining, and seining, unavoidably catch multiple species simultaneously (Clark 1976; Hilborn 1985a; Boyce 1996; Hall et al. 2000; Lewison et al. 2004a). Multispecies fisheries pose a particular threat of extinction or severe depletion because fishing can remain profitable as long as some valuable species remain abundant, even while others collapse (Clark 1976, 1985; Hilborn 1985a; Boyce 1996; Hall et al. 2000; Lewison et al. 2004a). In contrast, in a single-species fishery profits tend to fall as the target population declines, thereby removing the incentive to fish before extinction occurs (Clark 1976). Multispecies fisheries pose a threat to two types of species or stocks (populations): (i) commercially valued species, called "weak stocks", which are more vulnerable to overharvesting than are other commercially valuable species (Hilborn 1985a), and (ii) by-catch species, which are caught accidentally and create little economic incentive to cease fishing as their populations collapse because they have little or no commercial value (Boyce 1996; Hall et al. 2000; Lewison et al. 2004a).

Failure to prevent collapse of weak stocks and by-catch species can impose substantial long-term environmental and economic costs. Slow-growing populations are most likely to collapse, but can take several decades to recover (Hutchings & Reynolds 2004). Recovery often requires long-term fishery closures or reductions in effort, having substantial economic and social consequences (Hutchings & Reynolds 2004; Worm et al. 2009). Moreover, population declines caused by one fishery can diminish yields and profits in other commercial or artisanal fisheries that depend on the same species (e.g., Whitmarsh et al. 2003).

Despite these costs, species threatened by fishing have rarely been identified until after their populations have declined substantially (Hall et al. 2000; Hutchings & Reynolds 2004; Lewison et al. 2004a; Beddington et al. 2007; Worm et al. 2009; Costello

et al. 2012). Assessments of fishery impacts on species mostly focus on estimating current exploitation rates or past population trends (Cadima et al. 2003; Mace et al. 2008; International Union for the Conservation of Nature (IUCN) 2011), which identifies already declining species rather than predicting future declines. Data limitations have made empirical prediction of future threats from fishing challenging, particularly for weak stocks and by-catch species. Oceans are difficult to sample extensively, and few economic incentives exist to gather data on species other than the most commercially valued species (Hall et al. 2000; Lewison et al. 2004a). Some predictive models (e.g. Christen & Walters 2004) have been developed to forecast the impacts of some fisheries, but these are often data intensive. Some of the characteristics that make a population susceptible to overfishing are well known—for example, low population growth rates (Roberts & Hawkins 1999; Dulvy et al. 2004; Lewison et al. 2004a; Cheung et al. 2005; Collette et al. 2011), high value and/or low fishing costs (Clark 1976, 1985; Roberts & Hawkins 1999; Courchamp et al. 2006; Collette et al. 2011), and schooling behavior (Roberts & Hawkins 1999). Recently, some correlative approaches based on these characteristics have been developed for assessing likely relative threats to data-poor species (Dulvy et al. 2004; Cheung et al. 2005; Costello et al. 2012; Le Quesne & Jennings 2012). However, predicting the severity of future threats in absolute terms with this type of approach can be challenging.

Here, we present a mechanistic approach that uses readily available data to predict the potential of current fishing practices, if maintained, to eventually cause a population to be driven extinct or "overfished", here defined as depletion below its maximum sustainable yield (MSY) abundance (N_{MSY}) (Worm et al. 2009). Our approach identifies combinations of biological and socioeconomic conditions that are likely to eventually lead to high mortality rates and population declines. As we show, these conditions can be identified long before either occurs.

We test the predictive power of our approach on eight tuna and billfish populations of the Western and Central Pacific Ocean fisheries. High-seas tuna and billfish have elicited recent conservation concern due to significant population declines and range contractions found in many species (Collette et al. 2011; Juan-Jorda et al.

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2011; Worm & Tittensor 2011). Three of the populations in our study, bigeye tuna (*Thunnus obesus*) and both the northern and the southern striped marlin (*Tetrapturus audax*) populations, have been recently identified as experiencing overfishing—meaning their exploitation rates have exceeded the MSY exploitation rate (F_{MSY}) (Langley et al. 2006; Brodziak & Piner 2010; Harley et al. 2010; Juan-Jorda et al. 2011). A fourth, blue marlin (*Makaira nigricans*), whose overfishing status has been subject to considerable uncertainty (Kleiber et al. 2003), has undergone a significant population decline and range contraction (Kleiber et al. 2003; IUCN 2011; Worm & Tittensor 2011). We determine whether our approach could have predicted threats to these four populations, using data from as early as the 1950s, and assess the threats predicted by the latest available data to all populations.

2.2 The Eventual Threat Index (*T*)

The central premise of our approach is that the shared threat of effort in a given multispecies fishery links the fates of species in a way that allows the fates of all species to be predicted if the fate of any one species can be predicted. The fates of some "key" species can be predicted based on their influence on the economic or regulatory factors that determine maximum fishing effort in the fishery. Other species' fates can be predicted by measuring their vulnerabilities to long-term depletion by the fishery relative to the key species. For the purposes of our approach, we define a "species" at the population level and a "fishery" as a group of fishermen using a particular type of gear to target a particular group of species in a particular region, with roughly uniform relative catch rates of the species (Branch et al. 2005).

For each fishery, *j*, we measure the "vulnerability" to long-term depletion of species *i* at time *t* [denoted $V_{ij}(t)$], using three population-specific pieces of data that are readily available for many fisheries: population size [$N(t)$] (e.g., Ricard et al. 2012), average catch-per-unit effort [CPUE(t)] (e.g., Western and Central Pacific Fisheries Commission (WCPFC) 2012), and maximum per-capita growth rate (*r*) (e.g., Myers et al. 1999; Ricard et al. 2012):

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$$V_{ij}(t) = \frac{CPUE_{ij}(t)}{r_i N_i(t)} \quad (2.1).$$

Vulnerability measures the fraction of species i's maximum population growth rate $[r_i N_i(t)]$ lost on average to each unit of fishing effort (e.g., hooks, days fished, etc.) (Clark 1976, 1985). Because fishing effort is shared by all species, the fishery's relative long-term impacts on different species can be predicted by measuring their relative vulnerabilities as defined in Eq. 2.1 (Fig. 2.1A). We derive the mathematical properties of relative vulnerabilities in a general theoretical model in SI Materials and Methods. In general, effort levels greater than $1/V$ put a species on a path to extinction, as this implies the total catch rate (CPUExEffort) is larger than the maximum population growth rate (rN).

If a fishery is profitable, effort increases until either profit declines to zero because commercially valued species become depleted (Clark 1976, 1985) or regulations prevent further increase because species protected by management become depleted (Fig. 2.1B and C). Profitability or regulations thus impose an upper bound on fishing effort in the fishery that determines which species will likely experience a severe decline or extinction.

Except in rare cases (Clark 1973; Courchamp et al. 2006), a fishery would be expected to cease operation before all of its commercially valued species are driven extinct, due to a lack of profitability, regulatory intervention, or both (e.g., Hutchings & Myers 1996). Thus, there is at least one species in most fisheries whose importance to the fishery's profits or regulations ensures that the fishery will close before this species is driven extinct. Because high profits and nonbinding limits on the exploitation of managed species in a fishery tend to lead to increases in effort (Clark 1976, 1985), most fisheries also have one or more commercially valued or managed species that are likely to be exploited at least at a minimum rate. Species having both of these properties are key species because their long-term fates are most easily predicted or bounded. We predict the long-term threat of current fishing practices to a given species by calculating its vulnerability relative to a key species in each fishery in which it is caught.

In a managed fishery, the most vulnerable species targeted by management is a

likely key species, as fishing effort is likely to increase only until this species reaches the minimum population size or maximum exploitation rate allowed by management (Fig. 2.1C). In an unmanaged fishery, the species generating the most revenue is a likely key species, as its importance to the fishery's profits will likely prevent it from being either driven extinct or underexploited (Clark 1976, 1985). In the analysis presented here, we identify key species in this manner. However, our approach to threat prediction is robust to many other approaches to identifying key species (SI Materials and Methods). For instance, if a key species could be profitably driven extinct due to the presence of another valued species that is more robust, the other valued species would become the key long before the first was near extinction.

Fish species are typically caught in multiple fisheries so to be practical the threat measure must capture the vulnerability to harvest of each species across all of the fisheries in which it is caught. For each fishery, we measure its impact on species i relative to that fishery's key species at time t, using the ratio, $V_{ij}(t)/V_{key,j}(t)$. This ratio can also be measured by replacing measures of CPUE in Eq. 2.1 with total catch in the fishery, if this is easier to measure, as effort will cancel out (Catch = CPUExEffort). We measure the combined threat of all fisheries to species i at time t by calculating the "eventual threat index", $T_i(t)$,

$$T_i(t) = \sum_j \left[\left(\frac{V_{ij}(t)}{V_{key,j}(t)} \right) \left(\frac{Catch_{key,jj}(t)}{\sum_k Catch_{key,jk}(t)} \right) \right] \quad (2.2).$$

$T_i(t)$ sums the $V_{ij}(t)/V_{key,j}(t)$ ratios for all fisheries catching species i, including where species i is a key species, and weights the $V_{ij}(t)/V_{key,j}(t)$ for each fishery j by the catch of its key species in year t ($Catch_{key,jj}(t)$) as a fraction of its key species' total catch from all fisheries in year t ($\sum_k Catch_{key,jk}(t)$).

If fishing practices and relative efforts in different fisheries do not change, then $T_i(t)$ becomes a constant through time, denoted T_i^*, even as total effort changes (SI Materials and Methods). Fishery managers commonly evaluate threats to populations by comparing their estimated abundances (N) and mortality rates (F, where $F = Catch/N$) to those producing MSY (N_{MSY} and F_{MSY}) (e.g., Kleiber et al. 2003; Langley et al. 2006;

Brodziak & Piner 2010; Worm et al. 2009; Harley et al. 2010; Juan-Jorda et al. 2011; Costello et al. 2012; Ricard et al. 2012). With the common assumption in fisheries that the fishing mortality rate, F at MSY for a species, F_{MSY}, is half of its maximum growth rate, r (Schaefer 1954), T_i^* can be shown (SI Materials and Methods) to have the useful property,

$$\frac{F_i^*}{F_{i,MSY}} = T_i^* \overline{\left(\frac{F_{key}^*}{F_{key,MSY}}\right)} \text{ (2.3a),}$$

where F_i^* is species i's long-term fishing mortality rate, and $\overline{\left(\dfrac{F_{key}^*}{F_{key,MSY}}\right)}$ is a weighted

average of the long-term fishing mortality rates of the key species of fisheries catching species i. Thus, $T_i(t)$ predicts the long-term mortality rate (F) that current fishing practices at time t would eventually impose on species i relative to the key species of the fisheries in which it is caught, were these fishing practices to continue indefinitely (Fig. 2.1D).

Managed fisheries often aim to maintain their target species at their MSY populations (Beddingtom et al. 2007; Worm et al. 2009; Costello et al. 2012). This would

mean that $\overline{\left(\dfrac{F_{key}^*}{F_{key,MSY}}\right)}$ =1 if all fisheries were well managed, and consequently the fishing

mortality rate of species i ($F_i/F_{i,MSY}$) would approach T_i^* in the long term (i.e., $F_i^*/F_{i,MSY} = T_i^*$). Fig. 2.1E illustrates this property in a simulation model (Materials and Methods). Unmanaged fisheries tend to overfish their target species (Clark 1976, 1985) [i.e.

$\overline{\left(\dfrac{F_{key}^*}{F_{key,MSY}}\right)} > 1$]. Because key species are unlikely to be driven extinct by their fisheries

(Clark 1976, 1985; Hutchings & Myers 1996), it can be assumed that an upper bound on fishing effort is set by $F_{key}^* \leq r$ (i.e., harvest rate $\leq$ maximum growth rate) for all key

species. Because we are assuming $F_{MSY} = r/2$, this implies, $\overline{\left(\dfrac{F_{key}^*}{F_{key,MSY}}\right)} < 2$. Thus, it is

reasonable to assume that

$$T_i^* \leq \frac{F_i^*}{F_{i,MSY}} < 2T_i^* \text{ (2.3b)}.$$

Under these assumptions, measured $T_i(t)$ values should be interpreted as implying that current fishing practices at time t pose a high threat of species i's eventual extinction if $T_i(t) \geq 2$ (because this implies $F_i^* \geq r_i$), a high threat of eventual overfishing and a possible threat of extinction with poor management if $1 < T_i(t) < 2$, a possible threat of overfishing with poor management if $0.5 < T_i(t) \leq 1$, and a very low threat of overfishing if $T_i(t) \leq 0.5$ (Fig. 2.1D). Fishing gear, targeting behaviors, and management often change in response to evolving technology (e.g., Gilman et al. 2006), markets (e.g., Delgado et al. 2003), or political climate. Thus, $T_i(t)$ should be re-measured on a regular basis.

If assuming that $r = 2F_{MSY}$ or that MSY is a measurable and desired target for management is inappropriate (e.g., Johannes 1998), our index, $T_i(t)$, can still be used to predict threats, but the threshold values for interpretation ($T_i(t) = 2, 1, 0.5$) would need to be adjusted (SI Materials and Methods). Our approach can also be adapted to incorporate age structure, by altering the procedure for measuring vulnerabilities (SI Materials and Methods).

2.3 Case Study: Western and Central Pacific Tuna and Billfish

To test our approach, we use historical data for eight tuna and billfish populations of the Western and Central Pacific (WCPFC 2013) to estimate yearly T values from the 1950s to the present time, using Eqs. 2.1 and 2.2. We compare each population's earliest possible T and V estimates (1953–1967, depending on the population) to their observed abundance and exploitation trends from these early years up until the most recent year for which data are available (1997–2009, depending on the population) (Figs. 2.2, 2.3, 2.4) (Kleiber et al. 2003; Langley et al. 2006, 2009; Brodziak & Piner 2010; Worm et al. 2009; Brodziak & Ishimura 2010; Harley et al. 2010; International Scientific Committee for Tuna and Tuna-Like Species in the North-Pacific Ocean (ISC) 2011; Hoyle 2011; Juan-Jorda et al. 2011; Costello et al. 2012; Ricard et al. 2012) (SI Materials and Methods). These populations are the northern and southern populations of Pacific albacore tuna (*Thunnus alalunga*), bigeye tuna (*T. obesus*), blue marlin (*M. nigricans*),

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the northern and southern Pacific striped marlin (*T. audax*), North Pacific swordfish (*Xiphias gladius*), and yellowfin tuna (*Thunnus albacares*). Northern and southern populations of some species are treated separately because they are considered ecologically distinct (Langley et al. 2006; Brodziak & Piner 2010; Brodziak & Ishimura 2010; Hoyle 2011; ISC 2011). We use international catch data from longline, purse-seine, and pole-and-line fisheries (WCPFC 2012) (Fig. 2.3), together accounting for 92% of all reported tuna and swordfish catch in this region in 2010 (WCPFC 2011). For the purposes of estimating *T*, we define "fisheries" spatially by dividing the WCPFC Convention area (WCPFC 2013) into 15 regions (Fig. 2.S1) (~30° × 30°), having roughly uniform relative catch rates within fisheries (WCPFC 2011). We also distinguish between shallow- and deep-set longline catch and between purse-seine catch from schools associated and unassociated with floating objects, as these are known to have different catch rates (Crowder & Myers 2001; Secretariat of the Pacific Community (SPC) 2012). We also tried other ways of distinguishing fisheries for our analysis and found our predictions were robust to these alternatives (SI Materials and Methods and Fig. 2.S2). We estimate historical *T* values, assuming open access, as there was little international management of these fisheries before the 1980s (SPC 2012). For all populations, we find our *T* estimates robust to considerations of older data limitations (SI Materials and Methods). We use 3-y moving geometric averages of *T* to reduce noise. We compare *T* values to average annual fishing mortality rates (denoted *U*) (Ricard et al. 2012) from the fisheries studied ($U_{Combined}$ = combined catch/average population biomass) (Fig. 2.2 and SI Materials and Methods) instead of instantaneous fishing mortality (*F*), as the latter is difficult to estimate without seasonal and size- or age-structured catch and population data, which are not publicly available for these fisheries (WCPFC 2012). For the same reason, we also use average annual measures of CPUE and maximum per-capita growth rate in estimating *V* and *T* (SI Materials and Methods).

Longline fishing effort began to expand rapidly in the 1950s and 1960s, using predominantly shallow sets targeting bigeye and yellowfin tuna in northern and equatorial regions and albacore tuna in southern regions (WCPFC 2012, Kleiber et al. 2009) (Fig. 2.3 and Table 2.S1). There was little effort in the purse-seine and pole-and-

line fisheries (WCPFC 2012). At this time, T estimates (Fig. 2.2) predicted that North Pacific swordfish and all three marlin populations were on paths toward extinction ($T >$ 2), South Pacific albacore and bigeye tuna were on paths toward overfishing ($1 < T < 2$), and there were low threats to yellowfin and North Pacific albacore tuna ($T \leq 0.5$). In the mid-1970s, the tuna-targeting longline fishery largely shifted toward using deeper sets, with many of the remaining shallow sets targeting swordfish (Kleiber et al. 2009) (Fig. 2.3 and Table 2.S1). This shift in fishing technology led to reductions in the threat level predicted by T for most species (Figs. 2.2 and 2.3) because the profits from the shallow-set longline fishery were now heavily dependent in many places on swordfish, which has high vulnerability relative to other species (Table 2.S1). This limited the capacity of the shallow-set swordfish fishery to threaten other species. Additionally, the catch rates of swordfish and albacore tuna were lower in the deep-set longline fisheries that were targeting bigeye and yellowfin. As a result of this technological shift, T estimates for North Pacific swordfish, South Pacific albacore tuna, and blue marlin no longer indicated a threat beginning in the late 1970s and continuing to the early 1990s (Figs. 2.2, 2.3, 2.4). Also in the 1970s, the purse-seine and pole-and-line fisheries began to expand, targeting primarily skipjack tuna (*Katsuwonus pelamis*), with yellowfin and bigeye tuna as significant by-catch (ISC 2011; WCPFC 2012), particularly in purse-seine sets targeting schools associated with floating objects (ISC 2011). This led to increases in T values for yellowfin and bigeye tuna. An eventual threat to yellowfin is predicted beginning in the early 1990s ($T > 1$) (Figs. 2.2 and 2.4) as an increasing fraction of purse-seine landings came from purse-seine sets targeting associated schools (Fig. 2.3).

T values from as early as the 1950s have consistently predicted threats of eventual extinction ($T \geq 2$) or overfishing ($T > 1$) from then-current fishing technologies for both northern and southern striped marlin populations (extinction), for blue marlin (extinction, pre-1975, and overfishing until the 1990s), and for bigeye tuna (overfishing) (Figs. 2.2 and 2.4). As predicted, all four of these populations eventually did experience mortality rates from these fisheries ($U_{Combined}$) exceeding U_{MSY}, but not until decades after T values predicted this (Fig. 2.2). Our predictions provided a warning beginning 40 y before this occurred for bigeye tuna and South Pacific striped marlin. These four populations also

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suffered significant population declines and have abundances currently either at (bigeye tuna) or below (striped marlin) N_{MSY} (Langley et al. 2006; Brodziak & Piner 2010; Harley et al. 2010) (Fig. 2.4). Blue marlin's N_{MSY} is unknown (Kleiber et al. 2003). These depletions were only recognized three or more decades after they could have been predicted by measuring T (Fig. 2.4). Blue marlin has also experienced a significant range contraction in this region (Worm & Tittensor 2011). The first stock assessments identifying these populations as overfished ($N < N_{MSY}$) or experiencing overfishing ($F > F_{MSY}$ or $U > U_{MSY}$) came out in the 1980s or later (Yuen & Miyake 1980; Miyabe 1989; Kleiber et al. 2003; Langley et al. 2006; Brodziak & Piner 2010; Harley et al. 2010) (Fig. 2.4).

T values from the last two decades predict a threat of eventual overfishing to yellowfin tuna (Fig. 2.2). Although it has not yet become overfished ($N > N_{MSY}$, $U_{Combined} < U_{MSY}$) (Figs. 2.2 and 2.4) (Langley et al. 2009), its mortality rate is steadily increasing (Fig. 2.2), and it has undergone a marked population decline since T predicted a threat (Fig. 2.4). Early T values (1950–1970) indicated a threat to South Pacific albacore tuna (Fig. 2.2), and it suffered a significant decline during that period, leading to concern for an overfishing threat in an early stock assessment (Skillman 1975) (Fig. 2.4). More recent T values (post-1970s) have not indicated a threat (Fig. 2.2), and it is not currently considered to be overfished or experiencing overfishing (Hoyle 2011; Juan-Jorda et al. 2011). Its population has been relatively stable (Fig. 2.4). Similarly, more recent T values for North Pacific swordfish and albacore tuna do not indicate a threat and neither population appears to be on a trajectory toward overfishing (Brodziak & Ishimura 2010; ISC 2011) (Figs. 2.2 and 2.4).

Our most recent estimates of T, under the assumption of open access, suggest that the northern and southern striped marlin population and yellowfin and bigeye tuna face severe overfishing, and the striped marlin populations may face extinction (Figs. 2.2 and 2.4), if these fisheries are poorly managed and current technologies remain the same. The striped marlin populations are particularly threatened by deep-set longline fisheries; and yellowfin and bigeye tuna are particularly threatened by purse-seine fisheries targeting schools associated with floating objects (Fig. 2.3). Purse-seine fisheries targeting

associated schools have received recent conservation attention (SPC 2001). However, shallow-set longline fisheries have received far more conservation attention than deep-set fisheries, as shallow sets tend to have higher bycatch rates (Crowder & Myers 2001). Because of the key species' (bigeye and yellowfin tuna) relatively lower vulnerabilities in the deep-set fishery, our results suggest that effort in the deep-set fishery has a greater potential to profitably increase in the future. If this occurs, striped marlin would be highly impacted. Although a continued expansion of purse-seine fishing might mitigate some of the threat to the striped marlin by depleting yellowfin and bigeye tuna, the possible threat of deep-set longline fisheries merits further study.

2.4 Discussion

For each of the four populations currently believed to be experiencing or to have recently experienced overfishing ($F > F_{MSY}$ or $U > U_{MSY}$) (Kleiber et al. 2003; Langley et al. 2006; Brodziak & Piner 2010; Harley et al. 2010; Juan-Jorda et al. 2011), our approach was able to predict a threat of eventual overfishing or extinction starting from as early as the 1950s (Figs. 2.2 and 2.4), before each began its dramatic population decline (Fig. 2.4). Moreover, for all populations except North Pacific albacore tuna, which has a very low mortality rate, estimates of T and $U_{Combined}/U_{MSY}$ appear to be converging (Fig. 2.2), consistent with the theory underlying the use of T as an eventual threat predictor (SI Materials and Methods). Because these results suggest that our approach can predict threats well in advance of high mortality rates and declines in abundance (Figs. 2.2 and 2.4), its use in these and other fisheries may provide time to adopt preventative management before fishery closures or other highly disruptive interventions are needed. Of the four populations predicted by our approach to be currently threatened, only the striped marlins are already severely overfished ($N < N_{MSY}$) (Langley et al. 2006, 2009; Brodziak & Piner 2010; Harley et al. 2010). Thus, it could be possible to avoid severe depletion of yellowfin and bigeye tuna in this region.

Multispecies tuna fisheries are also known to significantly impact sharks, sea turtles, and other by-catch species in the Pacific and elsewhere (Lewison et al. 2004a,b; Clarke et al. 2013; Worm et al. 2013). The slow population growth and high recent catch

rates of these species suggest they likely have high vulnerabilities, and many could be threatened with extinction (Lewison et al. 2004a,b; Clarke et al. 2013; Worm et al. 2013). Our approach, along with recent advances in by-catch monitoring and data-poor abundance estimation methods (Lewison et al. 2004b; Clarke et al. 2013; Worm et al. 2013), could be used to rapidly assess future extinction threats posed by current fishing practices to by-catch species worldwide.

Internationally cooperative management of large high-seas fisheries can be challenging (Beddington et al. 2007; Worm et al. 2009), but will be critical to protecting weak stocks and by-catch species in tuna and billfish fisheries (Lewison et al. 2004a,b; Collette et al. 2011; Juan-Jorda et al. 2011; Worm & Tittensor 2011; Clarke et al. 2013; Worm et al. 2013). Managing each fishery to protect its most vulnerable species is one possible solution (Hilborn et al. 2004). However, such "weak-stock management" can cause faster-growing populations to be underexploited, which lowers profits and decreases food supplies (Hilborn et al. 2004). Trade-offs between conservation and yield could be mitigated by improving the species selectivity of fishing technologies (Lewison et al. 2004a; Gilman et al. 2006). Measurements of T and V/V_{key} can be used to set selectivity goals and monitor progress. Marine protected areas or other spatial fishing restrictions, which can provide refuges or reduce impacts on species' spawning grounds, are also useful management tools that have been implemented in some fisheries, including some Pacific tuna fisheries (Sibert et al. 2012). Another option is to manage the relative sizes of different fisheries with different catch rates, for example the deep-set longline and purse-seine fisheries. This type of management could mitigate both over- and underharvesting without requiring technological advances by equalizing species' aggregate catch rates. Recent studies suggest that some spatial management strategies, such as maritime zoning (Sibert et al. 2012) or setting regional catch quotas for fishery-wide goals (Dougherty et al. 2013), could accomplish this in Pacific tuna (Sibert et al. 2012) and groundfish (Dougherty et al. 2013) fisheries.

Our approach, like all other approaches to threat assessment, is subject to uncertainties associated with measurement of populations' sizes, growth rates, and catch rates (Ricard et al. 2012) and should be interpreted accordingly. Moreover, we strongly

encourage the incorporation of size- or age-structure data when using our approach, whenever possible, and describe a possible method for incorporating age structure in SI Materials and Methods.

Our approach is designed to identify direct threats to populations from fisheries in which the populations of interest are not the key species. It is not relevant to a species that is the key species in most or all of the fisheries in which it is caught. It is for this reason that we do not present T values for skipjack tuna. Although many species severely threatened by fishing are weak stocks or by-catch species in multispecies fisheries (Hilborn 1985a; Boyce 1996; Hall et al. 2000; Lewison et al. 2004a), a few target species, such as southern bluefin tuna (Collette et al. 2011) and caviar-producing sturgeons (Courchamp et al. 2006), are threatened by their high and increasing rarity value (Courchamp et al. 2006). Our approach is also not designed to predict indirect threats from fishing mediated by species interactions. If $T_i > 2$, current practices are likely to lead to a harvest rate of species i that exceeds its maximum growth rate, guaranteeing extinction. However, extinction or severe depletion can be caused indirectly by fishing at a much lower level. For example, a recent sea otter decline in Alaska may be linked to a trophic cascade caused by offshore fisheries (Estes et al. 1998) – a threat our approach would not have detected. Further research is needed to develop preventative approaches for threats from species interactions and rarity value.

Growing human populations and rising food demands are putting increasing pressure on marine ecosystems (Beddington et al. 2007; Worm et al. 2009; Costello et al. 2012). Long-term costs and societal impacts of conservation could be substantially reduced by shifting resources toward preventative measures, instead of rescuing already threatened species (Wilson et al. 2011). Developing cost-effective approaches that can predict future threats to species is a valuable tool for conservation. Our results illustrate that a simple mechanistic theory has the potential to effectively predict species threats well into the future, thus allowing time for preventative management actions.

2.5 Materials and Methods

Mathematical derivations of the properties and generalizations of the eventual

threat index, *T*, can be found in SI Materials and Methods. A detailed description of our data sources and methods for the case study can also be found in SI Materials and Methods (Figs. 2.S1, 2.S2, 2.S3, 2.S4). This includes population, catch, effort, and price data; estimates of population growth rates; estimates of populations' vulnerabilities; methods for determining the key species in each fishery; and an analysis exploring the sensitivity of our case study results to older data limitations and different means of defining key species and fisheries.

Simulation Model: Fig. 2.1E.

Fig. 2.1E shows the results of a simulated model designed to illustrate the properties of *T* in fisheries managed to exploit their target species at MSY. The model simulates two fisheries each catching three species. Fishery 1 targets species 1 and fishery 2 targets species 2, but both fisheries catch both species 1 and 2, as well as a by-catch species, *i*. All three species are assumed to have logistic growth and linear catch rates, such that the instantaneous rate of population change of species *x* (where *x* = 1, 2, *i*) at time *t* is given by,

$$\frac{dN_x(t)}{dt} = r_x N_x(t)\left(1 - \frac{N_x(t)}{2N_{x,MSY}}\right) - q_{x1}N_x(t)E_1(t) - q_{x2}N_x(t)E_2(t) \quad (2.4).$$

Here, $E_j(t)$ is the level of effort in fishery *j* at time *t*, and q_{xj} is the per-capita per-unit-effort catch rate of species *x* in fishery *j*, which we assume is constant in this model. Vulnerability, $V_{xj}(t) = q_{xj}/r_x$ is constant. Fishing effort in both fisheries (*j, k* = 1, 2; *k* ≠ *j*) grows according to Eq. 2.5:

$$\frac{dE_j(t)}{dt} = aE_j(t)\left(0.5r_j - q_{jj}E_j(t) - q_{jk}E_k(t)\right) \quad (2.5).$$

Here, *a* is a constant determining the adjustment rate of effort to the target species exploitation rate relative to its target rate (F_{MSY}). We use the following parameter values: {$N_{x,MSY}$ = 1, $N_x(0)$ = 2 for all *x*; $E_1(0)$ = $E_2(0)$ = 0.1; r_1 = r_2 = 1; r_i = 0.5; q_{11} = q_{22} = q_{i1} = q_{i2} = 0.1; q_{12} = q_{21} = 0.05; *a* = 0.35}. Species 1 is the key species in fishery 1, and species 2 is the key species in fishery 2 for the calculation of $T_i(t)$.

Acknowledgements
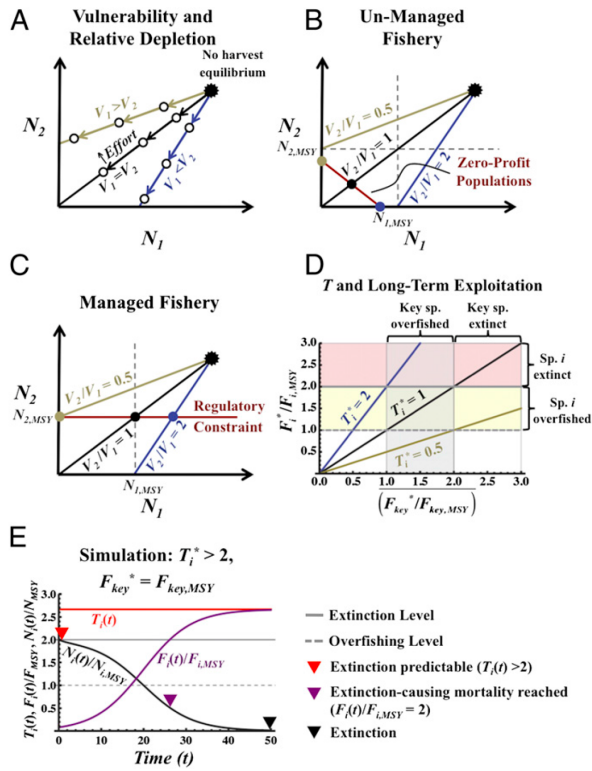
Figure 2.1. General theory and simulated example. A–D illustrate the theoretical framework and E provides an illustrated example. Each panel assumes $r = 2F_{MSY}$ for all species, and all but D assume constant vulnerabilities (V). A illustrates how species' relative vulnerabilities determine relative depletion, which combined with effort determines long-term abundances for populations (open circles). Higher effort pushes the outcome farther down the set of possible abundances determined by species' relative vulnerabilities (blue, black, and yellow lines). B and C illustrate how relative vulnerabilities and profitability (B) or regulatory constraints (C) (dark red lines) jointly determine long-term species abundances (solid circles). C assumes that the fishery is managed to harvest species 2 at MSY. D illustrates the theoretical relationship between the long-term exploitation rate of species i ($F_i^*/F_{i,MSY}$) and the average long-term exploitation rate of the key species ($\overline{F_{key}^* / F_{Key,MSY}}$), as determined by the long-term T_i value (T_i^*), shown for $T_i = 2$ (blue), $T_i = 1$ (black), and $T_i = 0.5$ (yellow). For $T_i = 2$, species i will be harvested to extinction when the key species is harvested at MSY or overfished. In contrast, for $T_i = 0.5$, the key species would be harvested to extinction before species i would be overfished. E shows time trends of the eventual threat index ($T_i(t)$), mortality ($F_i(t)/F_{i,MSY}$), and abundance ($N_i(t)/N_{i,MSY}$) for the case of a bycatch species (i) caught in two fisheries whose technologies and relative fleet sizes do not change and where the key species in each fishery is harvested at MSY. Extinction of species i is predictable in year 0 whereas extinction causing mortality does not occur until year 26. Growth equations and parameter values for E are provided in Materials and Methods.

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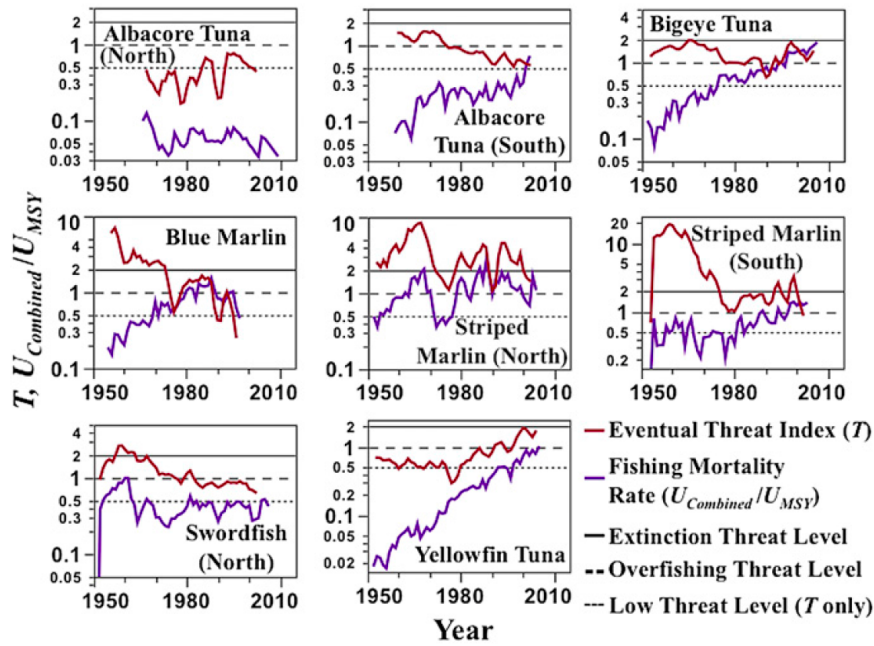
Figure 2.2. Exploitation histories and estimable T values. A comparison of eventual threat index values [T (3-y geometric mean), red] to the combined fishing mortality rates ($U_{Combined}$) from longline, purse-seine, and pole-and-line fisheries as a fraction of the mortality rate producing MSY (UMSY), ($U_{Combined}/U_{MSY}$, purple), for each population. Levels indicating high extinction threats (T, $U_{Combined}/U_{MSY}$ = 2) (solid black lines), high overfishing threats (T, $U_{Combined}/U_{MSY}$ = 1) (dashed black lines), and low overfishing threats (T = 0.5) (dotted black lines) are shown.
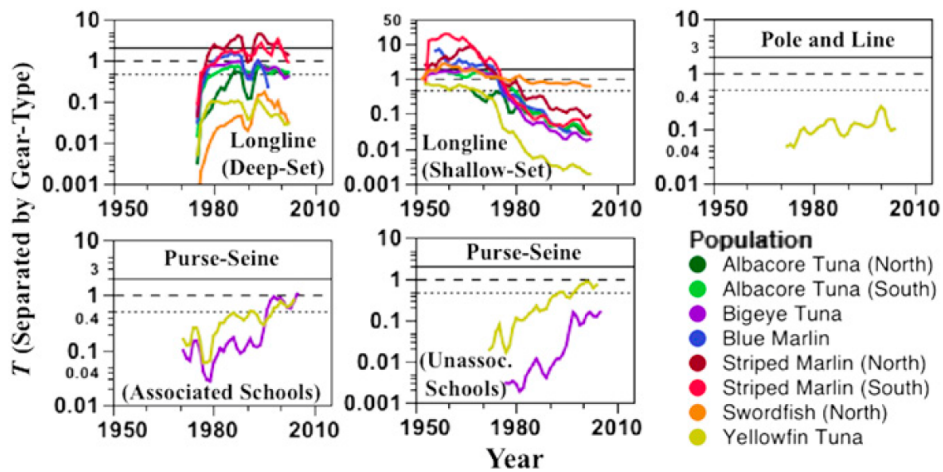
Figure 2.3. Gear-specific threats. Fishing gear-specific estimates of threats (3-y geometric mean T values summed only over fisheries within each gear type) are shown. T values of 2 (solid line) (high extinction threat), 1 (dashed line) (high overfishing threat), and 0.5 (dotted line) (low overfishing threat) are highlighted. The shift in longline fishing toward deeper sets beginning in the 1970s led to a reduction in the threat caused by the shallow-set longline fishery to all populations and introduced a threat from the deep-set fishery to striped marlin populations. Purse-seine fisheries have recently begun to pose a threat to bigeye and yellowfin tuna.
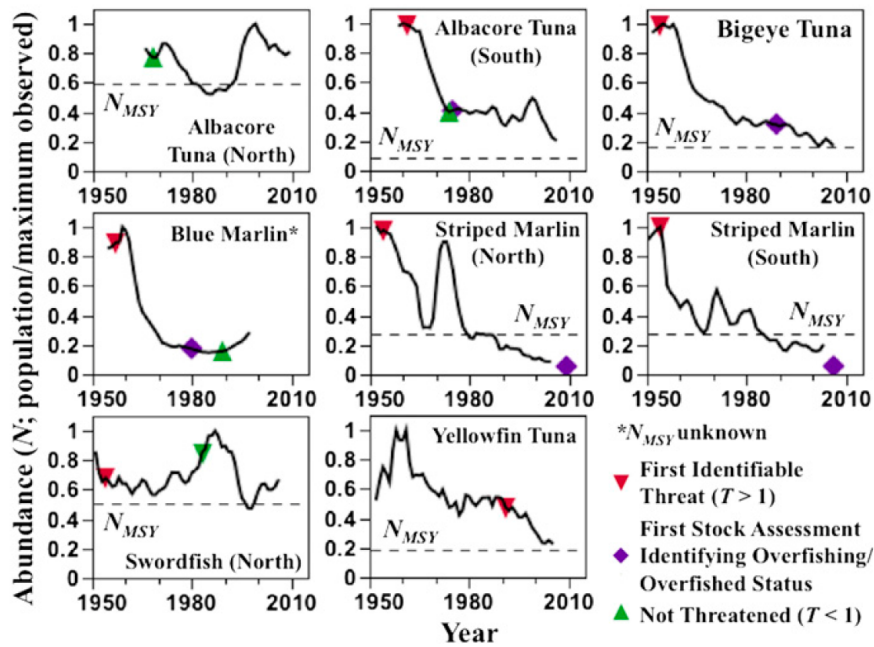
Figure 2.4. Assessment histories and earliest identifiable threats. Shown is a comparison of when threats could have been identified by estimating T ($T > 1$: red triangles) vs. when populations were first assessed as overfished ($N < N_{MSY}$) or subject to overfishing ($F > F_{MSY}$) in stock assessments (purple diamonds). The populations' abundance trends are shown (black curves), each scaled to its maximum value in the series. Estimates of N_{MSY} (dashed lines) and dates when the eventual threat index no longer would have predicted an overfishing threat ($T < 1$) (green triangles) are also shown.

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2.6 Supporting Information

SI Materials and Methods

1.$V_{ij}/V_{key,\,j}$ and T and Generalizations of Their Interpretation.

      Our approach is based on the fact that the shared threat of effort in a multispecies fishery links the fates of species in a way that allows the fates of all species to be predicted if the fate of any one species can be predicted. Specifically, we assert that in any multispecies fishery there is at least one identifiable species, which, due to its socioeconomic importance to the fishery, will not be driven extinct without first triggering the closure of the fishery (Clark 1976, 1985; Hutchings & Myers 1996), but will be depleted to at least a certain level. On the basis of this assumption of a bounded threat of depletion to this "key species", we introduce an approach to bounding the likely threats to all other species, using the measurable threat index, *T*. This threat index can be used under highly general assumptions regarding population growth and species interactions to predict direct threats from multispecies fishing, although it does not assess indirect threats via species interactions. Additionally, although we give fairly specific criteria with which to identify the key species, our approach is quite robust to different identifications in practice. We illustrate these points below.

1.1. Vulnerability, relative long-term impacts, and T.

      In a general model of a group of *S* species caught in a single fishery, with $\vec{\mathbf{N}}(t)$ as the vector-form representation of the population sizes of all species at time t, $\vec{\mathbf{N}}(t) \equiv \left(N_1(t),...,N_S(t) \right)$, and general population growth function, $f_i\!\left(\vec{\mathbf{N}}(t)\right)$, with ($f_i(.) \leq 1$), the instantaneous rate of change of species *i*'s population at time *t* is given by:

$$\frac{dN_i(t)}{dt} = N_i\!\left(r_i f_i\!\left(\vec{\mathbf{N}}(t)\right) - q_i(t)E(t) \right) \text{ (2.S1.1a),}$$

which can be rewritten equivalently as:

$$\frac{dN_i(t)}{dt} = r_i N_i\!\left(f_i\!\left(\vec{\mathbf{N}}(t)\right) - V_i(t)E(t) \right) \text{ (2.S1.1b),}$$

because $V_i(t) = q_i(t)/r_i$ (Clark 1976, 1985; Holt 1977). Vulnerability is constant when *q* is

constant, which implies species' per-capita catch rates are constant [i.e., average catch-per-unit effort (CPUE) is proportional to abundance], but unlike in the simulated example in Fig. 2.1E, we now assume that q may change. In reality, per-capita catch rates (q) are likely to change through time as technology or the behavior of fishermen changes, and q may also change if schooling behavior or other biological factors cause catch rates to be hyperstable (i.e., they decline more slowly than abundance) (Harley et al. 2001). Thus, $V_i(t)$ can be thought of as measuring the impact of current fishing practices at time t on species i, provided biologically caused hyperstability is small (i.e., q is constant if technology and the behavior of fisherman do not change).

Setting the right-hand side (RHS) of Eq. 2.S1.1b equal to 0, we see that for any species i having positive abundance at equilibrium, the following relationship must hold,

$$f_i\left(\vec{\mathbf{N}}^*\right) = V_i^* E^* \quad (2.\text{S}1.2),$$

where V_i^* is the equilibrium vulnerability of species i, N_i^* is the equilibrium population size of species i, and $\vec{\mathbf{N}}^* \equiv \left(N_1^*, ..., N_S^*\right)$. From Eq. 2.S1.2, it follows that for any two species, x and y, that both have positive abundances at equilibrium, the following relationship must hold:

$$\frac{f_x\left(\vec{\mathbf{N}}^*\right)}{f_y\left(\vec{\mathbf{N}}^*\right)} = \frac{V_x^*}{V_y^*} \quad (2.\text{S}1.3a).$$

Substituting current vulnerability measures, $V(t)$, for V^* in Eq. 2.S1.3a predicts the long-term relative impacts of current fishing practices at time t on species x and y. If vulnerabilities (V) are constant, then Eq. 2.S1.3a defines a curve that represents all of the possible equilibrium population sizes ($\vec{\mathbf{N}}^*$) at different effort levels. This curve, determined by species' relative vulnerabilities, is illustrated in Fig. 1A–C. For example, with logistic growth (Schaefer 1954) (Eq. 2.4), Eq. 2.S1.3a would become

$$\frac{1 - \left(N_x^* / K_x\right)}{1 - \left(N_y^* / K_y\right)} = \frac{V_x^*}{V_y^*} \quad (2.\text{S}1.3b),$$

which is a straight line emanating from the point where $N_i = K_i$ for all i, the no-harvest equilibrium, as illustrated in Fig. 2.1A–C, because vulnerabilities are constant.

Suppose that a "key" species can be identified in the fishery, which will not be driven extinct without first triggering the fishery's closure, but socioeconomic forces will allow the fishery's effort to increase until this key species has at least a certain fishing mortality rate, $F_{key,MIN}$. Suppose that the fishing mortality rate, F, needed to just drive the key species extinct is $F_{key,MAX}$. Noting that $F_i(t) = r_i V_i(t) E(t)$, the bounds on mortality of the key species can be written as

$$\frac{F_{key,MIN}}{r_{key}} \leq V_{key}^* E^* < \frac{F_{key,MAX}}{r_{key}} \quad (2.S1.4),$$

Rearranging [2.S1.4], we get bounds on equilibrium effort, E^*,

$$\frac{F_{key,MIN}}{V_{key}^* r_{key}} \leq E^* < \frac{F_{key,MAX}}{V_{key}^* r_{key}} \quad (2.S1.5).$$

Finally, by combining Eq. 2.S1.2 with Eq. 2.S1.5, we get bounds on the equilibrium fishing mortality rate of species i, F_i^*, given by

$$\left(\frac{V_i^*}{V_{key}^*}\right)\left(\frac{F_{key,MIN}}{r_{key}}\right) \leq \frac{F_i^*}{r_i} < \left(\frac{V_i^*}{V_{key}^*}\right)\left(\frac{F_{key,MAX}}{r_{key}}\right) \quad (2.S1.6a)$$

If F_{key}^*/r_{key} values are exactly predictable, then Eq. 2.S1.6a becomes

$$\frac{F_i^*}{r_i} = \left(\frac{V_i^*}{V_{key}^*}\right)\left(\frac{F_{key}^*}{r_{key}}\right) \quad (2.S1.6b).$$

Note that inequality [2.S1.6a] and Eq. 2.S1.6b are derived without any specific assumptions about population growth or species interactions. Essentially, they imply that the direct threat of a multispecies fishery to all species can be finitely bounded by measuring V/V_{key} because the long-term harvest rates of at least one socioeconomically important species can be bounded. With the assumptions that $r = 2F_{MSY}$ for all species (MSY, maximum sustainable yield) (Schaefer 1954), directly caused extinction requires $F \geq r$, and $F_{key,MIN} \geq F_{key,MSY}$, inequality [2.S1.6a] and Eq. 2.S1.6b become

$$\left(\frac{V_i^*}{V_{key}^*}\right) \leq \frac{F_i^*}{F_{i,MSY}} < 2\left(\frac{V_i^*}{V_{key}^*}\right) \quad (2.S1.7a)$$

$$\frac{F_i^*}{F_{i,MSY}} = \left(\frac{V_i^*}{V_{key}^*}\right)\left(\frac{F_{key}^*}{F_{key,MSY}}\right) \quad (2.S1.7b).$$

The same logic in a model with multiple fisheries is used to derive Eq. 2.3a in place of [2.S1.7b] and Eq. 2.3b in place of [2.S1.7a]. If there are M fisheries instead of one, the instantaneous rate of change of species i's population is given by

$$\frac{dN_i(t)}{dt} = r_i N_i\left(f_i\left(\vec{\mathbf{N}}(t)\right) - \sum_{j=1}^{M} V_{ij}(t)E_j(t)\right) \quad (2.S1.8).$$

For any species i having positive abundance at equilibrium, the following relationship must hold:

$$f_i\left(\vec{\mathbf{N}}^*\right) = \sum_{j=1}^{M} V_{ij}^* E_j^* \quad (2.S1.9).$$

For any two species, x and y, that both have positive abundances at equilibrium, the following relationship must hold:

$$\frac{f_x\left(\vec{\mathbf{N}}^*\right)}{f_y\left(\vec{\mathbf{N}}^*\right)} = \frac{\sum_{j=1}^{M} V_{xj}^* E_j^*}{\sum_{j=1}^{M} V_{yj}^* E_j^*} \quad (2.S1.10).$$

If vulnerabilities and relative efforts do not change [i.e., $E_j(t)/E_k(t)$ is constant for all j and k], then the ratio on the RHS of Eq. 2.S1.10 is constant.

Assuming a key species can be identified for fishery j, which will not be driven extinct (occurring at mortality rate $F_{key,j,MAX}$) without first triggering the closure of fishery j, but socioeconomic forces will likely allow effort in fishery j to expand until this key species has at least a fishing mortality rate of $F_{key,j,MIN}$, the following will hold:

$$\left\{\frac{F_{key,j,MIN}}{r_{key,j}} \le \sum_{k=1}^{M} V_{key,jk}^* E_k^* < \frac{F_{key,j,MAX}}{r_{key,j}}\right\} \vee E_j^* = 0 \quad (2.S1.11).$$

Similarly to Eq. 2.S1.5 in the single-fishery case, we can derive bounds on equilibrium fishing effort E_j^*, in any fishery j having positive effort at equilibrium (i.e., its key species is not extinct), by multiplying $\sum_{k=1}^{M} V_{key,jk}^* E_k^*$ in inequality [2.S1.11] by

$$\frac{F_{key,j,MIN}}{r_{key,j}}\left(\frac{V_{key,j}^* E_j^*}{V_{key,j}^*\left(\sum_{k=1}^{M} V_{key,jk}^* E_k^*\right)}\right) \le E_j^* < \frac{F_{key,j,MAX}}{r_{key,j}}\left(\frac{V_{key,j}^* E_j^*}{V_{key,j}^*\left(\sum_{k=1}^{M} V_{key,jk}^* E_k^*\right)}\right) \quad (2.S1.12a).$$

If we multiply the outer terms in inequality [2.S1.12a] by $(r_{key,j}N_{key,j}*)/(r_{key,j}N_{key,j}*)$ and note that, for species i and fishery j, $r_iV_{ij}N_i* = Catch_{ij}*$, the equilibrium catch (per unit time), we get

$$\frac{F_{key,j,MIN}}{r_{key,j}}\left(\frac{Catch_{key,jj}^{*}}{V_{key,j}^{*}\sum_k Catch_{key,jk}^{*}}\right) \le E_j^{*} < \frac{F_{key,j,MAX}}{r_{key,j}}\left(\frac{Catch_{key,jj}^{*}}{V_{key,j}^{*}\sum_k Catch_{key,jk}^{*}}\right) \quad (2.\text{S}1.12b).$$

Finally, by combining Eq. 2.S1.9 with Eq. 2.S1.12b, we get bounds on the equilibrium fishing mortality rate of species i, F_i*:

$$T_i^{*}\overline{\left(\frac{F_{key,MIN}}{r_{key}}\right)} \le \frac{F_i^{*}}{r_i} < T_i^{*}\overline{\left(\frac{F_{key,MAX}}{r_{key}}\right)} \quad (2.\text{S}1.13a)$$

Here, $\overline{\left(\dfrac{F_{key,MIN}}{r_{key}}\right)}$ and $\overline{\left(\dfrac{F_{key,MAX}}{r_{key}}\right)}$ are weighted averages of F_{MIN}/r and F_{MAX}/r for all key species, weighted by their relative catch shares and vulnerabilities relative to species i (precise weights can be derived from inequality [2.S1.12b]). If vulnerabilities and relative efforts do not change, $T_i(t)$ is constant, meaning $T_i(t) = T_i*$ for all t. If $F_{key}*/r_{key}$ values are known, then Eq. 2.S1.13a becomes

$$\frac{F_i^{*}}{r_i} = T_i^{*}\overline{\left(\frac{F_{key}^{*}}{r_{key}}\right)} \quad (2.\text{S}1.13b)$$

With the assumptions that $r = 2F_{MSY}$ for all species (Schaefer 1954), directly caused extinction requires $F \ge r$, and $F_{key,MIN} \ge F_{key,MSY}$, inequality [2.S1.13a] becomes inequality [2.3b] and Eq. 2.S1.13b becomes Eq. 2.3a from the main text, which imply the interpretations of measured T values presented in the text (i.e., $T \le 0.5$, $T > 1$, and $T \ge 2$ imply, respectively, a low threat of overfishing, a high overfishing threat, and a high extinction threat). However, if these assumptions about F_{MSY} and extinction are known to not be valid for a particular species, then thresholds for interpreting T should be adjusted. T can still be used to measure threats because Eqs. 2.S1.13a and 2.S1.13b do not require these assumptions.

1.2. The key species: Practical definitions and sensitivity.

In the text, we recommended that the key species in a managed fishery should be identified as the species with the highest vulnerability among those that are targeted by management to not be depleted beyond a specific abundance. This particular manner of identifying the key species in a managed fishery is based on the assumption that managed species with higher vulnerabilities reach their management thresholds at the lowest effort. In an unmanaged fishery, we recommended identifying the key species as the species generating the most revenue.

In practice, using T to predict threats is insensitive to different approaches to identifying the key species. This insensitivity is particularly high in unmanaged fisheries, as we demonstrate in our case study (Fig. 2.S2). The essential property of the key species in a particular fishery, as illustrated in section 1.1 of this SI, is that it is a species that cannot be driven extinct without the fishery closing first and that effort in the fishery will expand to at least the level that causes the key species to experience a certain minimum long-term mortality rate (we assume this minimum mortality rate is F_{MSY} in the text). In most unmanaged fisheries, these assumptions should hold for the highest-revenue– generating species (Clark 1976, 1985). The highest-revenue–generating species is also easy to identify with few data, which is why we propose using this criterion for defining the key species in practice. In some fisheries, it is possible for these assumptions to be violated, for example if (*i*) a fishery is highly profitable and there are enough less vulnerable species to support it even at an effort level that causes this most profitable species to go extinct (1, 2) or (*ii*) the fishery is marginally profitable enough that the profitability constraint binds even before the key species is depleted to N_{MSY}. In case *i*, interpreting T using thresholds (0.5, 1, 2) would likely underestimate the threat to all species (because the assumption that the key species will not be profitably driven extinct would be violated). However, before this occurred, the highest-revenue–generating species would change (because extinct species generate no revenue). Thus, T's underestimation of threats would still be corrected potentially long before other species became threatened, assuming T was re-measured on a regular basis. In case *ii*, interpreting T using thresholds (0.5, 1, 2) would likely overestimate the threat. This should be corrected by appropriately adjusting the thresholds for interpreting T.

In a managed fishery, the assumption that determines the upper bound on threats – that the key species will not be driven extinct without the closure of the fishery – is likely a safe assumption as long as one of the species targeted by management is considered the key species when measuring T. The lower bound on threats, determined by the assumed depletion of the key species to its management target abundance (e.g., N_{MSY}), is more sensitive to which species is considered the key species. If the species considered the key species is not the species that is depleted to its management target with the least effort, then interpreting T using its management target as a reference point will overestimate threats. Furthermore, unlike in the unmanaged case, erroneous key species identifications will not self-correct in this case. Thus, it is important to identify the key species in a managed fishery as the species that is most easily depleted to its target abundance by the fishery in question. This definition of the key species can be implemented with any type of population growth or species interactions, provided they allow relative depletability to be assessed if it differs from our measure of relative vulnerability.

1.3. Accounting for age structure.

Age structure is an important consideration in assessing the status of and threats to fish stocks (Hilborn & Walters 1992). Although we do not incorporate age structure in the presentation of our approach in section 1.1 above and in the main text, our approach can be easily adapted to consider age structure, by adjusting the way in which vulnerability is measured. Vulnerability, as defined in the main text, measures the fraction of the maximum per-capita population growth rate lost by each unit of effort. In principle, this concept could be measured in any type of age-structured model.

For example, suppose species i has A discrete age classes and time is also discrete. Let n_{ix}, t be the population size of species i of age class x in year t, N_i, t be the vector of these age-specific populations ($N_{i,t} = (n_{i1,t},. . ., n_{iA,t})$), and $\mathbf{N}_t$ be the matrix of populations of all species ($\mathbf{N}_t$'s dimension would be determined by species with the largest number of age classes). Individuals of species i give birth at rate b_{ix} in age class x and have probability $g_{ix}(\mathbf{N}_t) - \sum_j U_{ixj,t}$ of surviving from age class x to age class $x + 1$, where $U_{ixj,t}$ is the fraction of individuals of age class x (of species i) caught in fishery j in year t. By the

Euler–Lotka equation (Kot 2001), species i's population in year t has an overall population growth rate per time step approaching $\lambda_{i,t}$, which is the largest positive real solution of

$$\sum_{x=1}^{A}\left[\lambda_{i,t}^{-x}\left(\prod_{y=1}^{x-1}\left(g_{iy}(\mathbf{N}_t)-\sum_{j=1}^{M}U_{iyj,t}\right)\right)\right]=1 \quad (2.S.1.14a).$$

In other words, species i's population growth at time t is approaching $N_{i,t+1}=\lambda_{i,t}N_{i,t}$. Suppose further that species i's maximum intrinsic rate of population increase per discrete time step (e.g., yearly or monthly), $\lambda_{max,i}$, is known. Finally, let $\lambda_{-j,i,t}$ be the growth rate that would be approached at time t by species i if fishery j was absent, but all other fisheries and abundances of other species remained the same. $\lambda_{-j,i,t}$ would be the largest positive real solution of

$$\sum_{x=1}^{A}\left[\lambda_{-j,i,t}^{-x}\left(\prod_{y=1}^{x-1}\left(g_{iy}(\mathbf{N}_t)-\sum_{k\neq j}U_{iyk,t}\right)\right)\right]=1 \quad (2.S.1.14b).$$

Species i's vulnerability to fishery j at time t, $V_{ij,t}$ could be measured as

$$V_{ij,t=}\frac{\lambda_{-j,i,t}-\lambda_{i,t}}{E_{j,t}(\lambda_{max,i}-1)} \quad (2.S.1.15).$$

Vulnerability estimated in this way for an age-structured population may be used to generate V/V_{key} and T estimates, which would have similar interpretations to those in the non–age-structured models presented above. Similarly to the non–age-structured case, effort ($E_{j,t}$) can be ignored when estimating vulnerability ratios, as it will cancel out.

2. Data and Methods for Case Study.

2.1. General methodology and aims.

Our case study had two main aims: first, to test the accuracy of our approach to identifying threatened populations (commonly referred to as "stocks" in fisheries), using the parameter T (Figs. 2.2, 2.4, 2.S2); and second, to provide a rough approximation of how early our approach could have been used to identify threats to stocks that have recently been determined to be at risk and declining using conventional approaches (Fig. 2.4). This latter aim serves as a means to quantify any temporal advantage our approach may have over conventional methods of identifying threatened stocks. We chose the

Western and Central Pacific tuna and swordfish fisheries as a case study because several stocks in these fisheries have recently been identified as threatened and declining (Langley et al. 2006; Brodziak et al. 2009; Harley et al. 2010; Collette et al. 2011; IUCN 2011; Worm & Tittensor 2011) and because historical data on these fisheries and some of the threatened stocks are available for periods dating back several decades, some as early as 1950. For each stock, we estimated T in each year, following Eqs. 2.1 and 2.2, using the best currently available data on its population size (N) (measured as exploitable stock biomass, B), its catch rate in each fishery, and its maximum population growth rate (r). However, we replaced CPUE in each year with total catch in Eq. 2.1, as this is easier to measure, and effort cancels out when measuring the ratio of two stocks' vulnerabilities, leaving T in Eq. 2.2 unchanged. We used these estimates of T to test its accuracy against observed patterns of decline (Figs. 2.2 and 2.4). Data and sources on catch, effort, and intrinsic growth rate (r) are summarized below.

When approximating the earliest date at which threats to stocks could have been identified using our parameter T, we considered availability of data at the time in light of the data requirements of T. With some aquatic and most terrestrial species, it is possible to determine relative abundances (N) and catch rates (CPUE) with a single year of data, although this is less reliable in marine fisheries, as it is difficult to sample ocean stocks extensively. Modern stock assessments generally determine a stock's abundance by comparing observed total catch with inferred year-to-year trends in the abundance from survey or effort-standardized catch-per-unit-effort indexes of abundance within each age class (Cadima et al. 2003). We assumed that this type of analysis would have required at least 2 y of data when constructing Fig. 2.4, although stock assessments often use longer series to obtain more robust estimates (Hilborn & Walters 1992). Estimating T may not have been possible the first year in which we had catch and population data, but it would likely have been possible to estimate species' relative abundances not long after this first year of data, certainly still decades before threatened species' exploitation rates exceeded their MSY levels in the 1980s and 1990s. Estimating r empirically for fish stocks generally requires a stock size-recruitment time series of fairly significant length (Myers et al. 1999) and thus would not have been possible in the earliest years in which catch

data on each species were collected. To address this, we tested whether estimating T using r-values approximated using allometric scaling relationships would have affected the results (section 2.5).

2.2. Population data.

We used data from seven species, comprising nine distinctly recognized stocks in the Western and Central Pacific Ocean, namely albacore tuna (*Thunnus alalunga*), bigeye tuna (*Thunnus obesus*), blue marlin (*Makaira nigricans*), skipjack tuna (*Katsuwonus pelamis*), striped marlin (*Tetrapturus/Kajikia audax*), swordfish (*Xiphias gladius*), and yellowfin tuna (*Thunnus albacares*). Whereas the populations of bigeye tuna, blue marlin, skipjack tuna, and yellowfin tuna in the Western and Central Pacific Ocean are each considered to be and managed as a single stock (Kleiber et al. 2003; Langley & Hampton 2008; Langley et al. 2009; Harley et al. 2010), albacore tuna, striped marlin, and swordfish are each considered to have distinct stocks north and south of the equator (Langley et al. 2006; Brodziak & Piner 2010; Brodziak & Ishimura 2010; Hoyle 2011; ISC 2011). However, we were unable to obtain historical data on the southern stock of swordfish. The length of our population time series varied by stock [albacore tuna (north), 1966–2009; albacore tuna (south), 1959–2006; bigeye tuna, 1952– 2006; blue marlin, 1955–1997; skipjack tuna, 1972–2006; striped marlin (north), 1952–2004; striped marlin (south), 1950–2003; swordfish, 1951–2006; yellowfin tuna, 1952–2005]. Skipjack tuna is the key species in all of the fisheries in which there were available data and thus was not included in our main comparisons of T values and historical exploitation and abundance trends (Figs. 2.2, 2.3, 2.4).

We obtained yearly estimates for each stock of its exploitable population size (B) and its reproductive adult population size [termed spawning stock biomass (SSB) in fisheries] in mass units (tonnes) in each year and at MSY (B_{MSY}, SSB_{MSY}). For the southern stock of albacore tuna, bigeye tuna, skipjack tuna, the southern stock of striped marlin, and yellowfin tuna, these estimates came from the RAM Legacy Stock Assessment Database (Ricard et al. 2012), and for blue marlin, they came from a recent stock assessment (Kleiber et al. 2003). We obtained an estimate of B only for swordfish

from a recent stock assessment (Brodziak & Ishimura 2010) [we used biomass in subarea 1 from the two-stock scenario model (table 3.1 in Brodziak & Ishimura 2010)]. We were able to obtain estimates of *SSB* only for the northern populations of albacore tuna (ISC 2011) and striped marlin (Brodziak & Piner 2010). For these populations, we approximated *B* by assuming *SSB*/*B* for each population in each year was the same as in the southern population. We used the exploitable biomass (*B*) for each species as *N* when calculating vulnerability (*V*).

The population trajectories shown in Fig. 2.4 are generated using the *SSB* time series for all stocks except swordfish, for which we used *B*, with each value in each series divided by the largest value in the series, and the MSY value (as a fraction of the largest in the series) shown.

2.3. Catch and effort data and estimates of r, V, and $U_{Current}$/U_{MSY}.

We obtained public domain data on aggregate catch and effort in the Western and Central Pacific Ocean (WCPFC 2012), by year and 5° × 5° latitude and longitude, for each of longline, purse-seine, and pole-and-line fisheries, which together account for a large majority of tuna and swordfish catches in this region (92% in 2010) (WCPFC 2011). Because some 5° × 5° regions had very little or no catch in some years, we aggregated catches in each fishery within 15 regions defined by dividing the Western and Central Pacific Fisheries Commission (WCPFC) Convention area (WCPFC 2013) into four roughly equal latitudinal and longitudinal sections (rounded to the nearest 5°) (Fig. 2.S1). The size of these regions was chosen with the goal of being large enough to have significant catch in most regions, but small enough so that relative catch rates of the different species in each region were roughly uniform (WCPFC 2011). The length of the time series varied by gear (longline, 1950-2009; purse-seine, 1970–2009; pole-and-line, 1970-2008).

We distinguished within the purse-seine fishery between catch and effort from sets targeting schools associated with floating objects and those targeting free schools, as these are known to have different by-catch rates (SPC 2001). We also sought to distinguish within the longline fisheries between shallow sets, primarily targeting

swordfish, and deeper sets, primarily targeting tunas, as these are also known to have dramatically different catch rates (Crodwer & Myers 2001). However, although the WCPFC public domain data distinguish between purse-seine sets targeting free and associated schools, they do not distinguish between different types of longline sets (WCPFC 2012). We were able to find public longline catch and effort data disaggregated in this way only for the Hawaii-based fleet from 1991 to 2011 (National Oceanic and Atmospheric Administration (NOAA) 2012a), which composes only a fraction of the total effort and covers only a fraction of the study region.

In practice, fishery managers have access to confidential (non-publicly available) vessel-level data, which include the average number of hooks between floats used in longline sets (e.g., Kleiber et al. 2009). This information can be used to infer whether a vessel was using shallow or deep sets, as deeper sets have more hooks between floats (Kleiber et al. 2009). Thus, although we were unable to obtain the data necessary to directly distinguish between shallow- and deep-set longline effort, we assume that fishery scientists and managers within the institutions that collect such data can access the data and thus make this distinction. We disaggregated longline catch into shallow set and deep set in the following manner. We assumed that, although absolute catch rates for each species are certain to vary spatially and temporally, the catch rate of a species in the shallow-set fishery relative to its catch rate in the deep-set fishery is roughly constant across space and time and dependent on its habitat preferences with respect to the water column. In other words, for each species i, we assumed a constant ratio, c_i, of its average shallow-set ($\overline{CPUE}_{iSS\tau}$ in year τ) and deep-set ($\overline{CPUE}_{iDS\tau}$ in year τ) catches-per-unit-effort in all years and regions:

$$\frac{\overline{CPUE}_{iSS\tau}}{\overline{CPUE}_{iDS\tau}} = c_i \ (2.S2.1).$$

We estimated this ratio empirically, using the data from the Hawaiian fleet (NOAA 2012a) for each year they were available, and assumed the median of these values for each species as c_i (Fig. 2.S3). We obtained estimates of the total shallow- and deep-set effort in the North Pacific from 1971 to 2002 (Kleiber et al. 2009), where the two are distinguished as lines having >6.5 hooks between floats (deep set) and those having <6.5

hooks (shallow set) (Kleiber et al. 2009). Deep-set effort pre-1975 was close to 0 (Kleiber et al. 2009) and thus we assumed there to be a single shallow-set longline fishery before 1975. We used these data (Kleiber et al. 2009) to calculate the respective fractions of total longline effort in shallow and deep sets from 1971 to 2002 and assumed the fractions of total effort that were shallow set/deep set to be 0.12 and 0.88, respectively, from 2002 to 2009 (these are the mean fractions from 1999 to 2002) (Kleiber et al. 2009). We assumed these annual fractions, $p_{DS,\tau} \equiv E_{DS,\tau}/E_{T,\tau}$ and $p_{SS,\tau} \equiv E_{SS,\tau}/E_{T,\tau}$ [where $E_{SS,\tau}$, $E_{SS,\tau}$ and $E_{T,\tau}$ are respectively the cumulative efforts in year τ in the shallow-set, deep-set, and combined (shallow-set + deep-set) fisheries], were equal in the southern and northern fisheries. Using these assumptions, we calculated the total annual catch ($Catch = \overline{CPUE} *E$) for each species i in each year, τ, in the shallow- and deep-set fisheries, using Eqs. 2.S2.2b and 2.S2.2c, which are derived from [2.S2.2a]:

$$Catch_{iT,\tau} = \overline{CPUE}_{iT,\tau} E_{T,\tau} = \overline{CPUE}_{iSS,\tau} E_{SS,\tau} + \overline{CPUE}_{iDS,\tau} E_{DS,\tau} \quad (2.S2.2a),$$

$$Catch_{iDS,\tau} = \frac{\left(\dfrac{E_{DS,\tau}}{E_{T,\tau}}\right) Catch_{iT,\tau}}{\left(\dfrac{E_{DS,\tau}}{E_{T,\tau}}\right) + \left(\dfrac{E_{SS,\tau}}{E_{T,\tau}}\right)\left(\dfrac{\overline{CPUE}_{iSS,\tau}}{\overline{CPUE}_{iDS,\tau}}\right)} = \frac{p_{DS,\tau} Catch_{iT,\tau}}{p_{DS,\tau} + p_{SS,\tau} c_i} \quad (2.S2.2b),$$

$$Catch_{iSS,\tau} = \frac{p_{SS,\tau} Catch_{iT,\tau}}{p_{SS,\tau} + \dfrac{p_{DS,\tau}}{c_i}} \quad (2.S2.2c).$$

We also separately estimated each species' T value, assuming a single longline fishery for comparison (Fig. 2.S2). The results of each of these analyses were qualitatively similar for all species, highlighting the robustness of our approach to different delineations of fisheries.

For each population, we estimated the combined fishing mortality rate from all of the fisheries in our case study ($U_{Combined}$ in Fig. 2.2) in year τ as

$$U_{i,\tau} = \frac{\sum_j Catch_{ij,\tau}}{B_{i,\tau}} \quad (2.S2.3).$$

For South Pacific albacore and striped marlin, bigeye tuna, skipjack tuna, and yellowfin tuna, we calculated U_{MSY} as

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$$U_{MSY} = \frac{MSY}{B_{MSY}} \quad (2.S2.4),$$

where MSY (in tonnes) and B_{MSY} (stock biomass at MSY in tons) estimates were obtained from their respective stock assessments (Langley et al. 2006, 2009; Langley & Hampton 2008; Harley et al. 2010; Hoyle 2011). For North Pacific swordfish, an estimate of U_{MSY} was given directly in its stock assessment (Brodziak & Ishimura 2010). For North Pacific striped marlin, we used the relationship $F = -\ln(1 - U)$ (Ricard et al. 2012) to calculate U_{MSY} from an estimate of F_{MSY} given in its stock assessment (Brodziak & Piner 2010). Estimates of F_{MSY} and U_{MSY} were not given in the stock assessment of North Pacific albacore tuna (ISC 2011), so we assumed it had the same U_{MSY} as South Pacific albacore tuna.

For the blue marlin, estimates of F_{MSY} or U_{MSY} were not available (Kleiber et al. 2003). We estimated U_{MSY} from F_{MSY} as described above and estimated F_{MSY} by assuming it was equal to $2r$. We estimated r as follows, using a method developed by Myers et al. (1997). We obtained estimates, from its stock assessment (Kleiber et al. 2003) of its average age at maturity (T_m) and average natural (i.e., non-fishing-related) adult mortality rate (m), from which we calculated its average annual adult survival probability (Myers et al. 1997) (p_s) as $p_s = e^{-m}$. We then assumed blue marlin to have a maximum reproductive rate (number of recruits per spawner) (Myers et al.'s 1999), α, equal to that of swordfish, the most closely related species for which an estimate was available in Myers et al.'s (1999) recent meta-analysis of these values across species, and solved for r numerically from the following equation [from Myers et al. 1997]:

$$\left(e^r\right)^{T_m} - p_s\left(\left(e^r\right)^{T_m - 1}\right) - \alpha = 0 \quad (2.S2.5).$$

Because we were using catch and population data aggregated annually and across all size and age classes, it was appropriate to use a discrete-time version of the maximum per-capita growth rate, R, in place of r when estimating V for each population in each fishery. We assumed $R = 2U_{MSY}$ when estimating V, equivalent to an assumption of discrete-logistic growth (Costello et al. 2012).

To summarize, V_{ij} was estimated for population i (e.g., North Pacific striped marlin) in fishery j (e.g., shallow-set longline fishing in region BC) in year τ as

$$V_{ij\tau} = \frac{Catch_{ij\tau}}{R_i B_{i\tau}} \quad (2.S2.6).$$

T was estimated for each species in each year by inserting Eq. 2.S2.6 into Eq. 2.2.

2.4. Identifying the key species.

      To identify the key species in each fishery, we estimated the relative contributions made by catch of each stock to the total revenue of each fishery. In our main analysis, presented in Figs. 2.2–2.4, we identified the key species in a given fishery in a given year as the species generating the most revenue among those for which population data were available. Estimating relative revenue contributions required estimates of the price-per-unit mass paid to fishermen for all stocks relative to one another. We estimated these historical relative prices, using historical data on catch and landed values [in 2000 US dollars (USD)] from the Sea Around Us Project (2013). For all species in our analysis except blue marlin, these data were available for the period 1950–2006 within some or all of six regions in the Pacific: Northeast, Northwest, Southeast, Southwest, Eastern Central, and Western Central [note that the Western Central region in the Sea Around Us data is only a subset of the WCPFC Convention area (Sea Around Us Project 2013; WCPFC 2013)]. Missing historical price data for blue marlin were largely inconsequential, as the blue marlin would likely never have been identified as a key species. However, we nonetheless generated a point estimate of its price in 2000 USD by averaging annual price data from 2001 to 2008 from the Hawaii fleet (NOAA 2012b), adjusting for inflation. We used this point estimate as a proxy for its price in all years, to verify the assumption that it would never have been the key species.

      For each species and each region in which it was available, we generated an annual price estimate by dividing the total revenue (2000 USD) by the total catch (tons). Prices varied across regions, but data were not available for all regions for some species (Sea Around Us Project 2013). We filled in missing prices by fitting a linear model to the available price data for all species, with dummy variables for region and species and a continuous variable for year as predictors ($n = 1,125$, $R^2 = 0.5$, $P < 0.001$) (Fig. 2.S4). For northern populations (North Pacific striped marlin, swordfish, and albacore tuna), we

estimated their price in a given year by averaging their estimated (or predicted) prices in the Northwest and Western Central regions. For southern populations (South Pacific striped marlin and albacore tuna), we estimated their price in a given year by averaging their estimated (or predicted) prices in the Southwest and Western Central regions. For populations that were more equatorial (skipjack tuna, bigeye tuna, and yellowfin tuna), we estimated their price in a given year by averaging their estimated (or predicted) prices in the Northwest, Southwest, and Western Central regions.

2.5. Sensitivity.

In general, our estimates of T could have been affected by biases in our estimates of relative catch rates, abundances (B), and growth rates (R). Each component, $V_{ij}/V_{key,j}$, of $T_{i,\tau}$ will be biased by a factor equal to the factor by which each of ($Catch_{ij}/Catch_{key,jj}$), $B_i/B_{key,j}$, and $R_i/R_{key,j}$ are biased. For the case study presented here, we tested the sensitivity of T estimates for each population to several different assumptions (Fig. 2.S2). In the main analysis (Figs. 2.2, 2.3, and 2.4 and dark red T estimates in Fig. 2.S2), we made the following assumptions: (*i*) The key species in a given fishery in a given year was the stock generating the most revenue in that fishery in that year for which population data were available, (*ii*) estimates of r (or R) for each stock were available in all years, and (*iii*) shallow-set and deep-set longline catch were approximately disaggregated using the method shown in section 2.3 above. We found our T estimates to be largely robust to all three of these assumptions. To test the importance of assumption *i*, we tried two alternate methods for determining the key species: (1) We assumed the key species was the species contributing the most revenue in the majority of years where population data were available (Table 2.S1 and light red T estimates in Fig. 2.S2) and (2) we assumed that the species generating the second most revenue in each year was the key species of a given fishery (pink T estimates in Fig. 2.S2). In both cases, we held assumptions *ii* and *iii* constant. To test the importance of assumption *ii*, we re-estimated T values for all populations assuming R was unknown and was instead approximated using

the scaling relationship between body mass and population growth rate, $\dfrac{R_i}{R_{key,j}} \approx \left(\dfrac{M_i}{M_{key,j}}\right)^{-\frac{1}{4}}$

(Savage et al. 2004) (black *T* estimates in Fig. 2.S2), holding assumptions *i* and *iii* constant. We estimated Mi for each population by dividing the total catch in mass units by the total catch in individual units, both given for longline fisheries (WCPFC 2012), and averaging these values for each stock across all years. For skipjack tuna, catch in the longline fishery is not given (WCPFC 2012) (because its catch rate is very low), and we instead estimated Mi using estimates of its common length and length-weight relationship from FishBase (Froese & Pauly 2012). To test the importance of assumption *iii*, we re-estimated *T* for each population, holding estimates *i* and *ii* constant, but now treating the aggregate longline catch in each region as a single fishery (gray *T* estimates in Fig. 2.S2). In all cases, the threats predicted by T were similar.
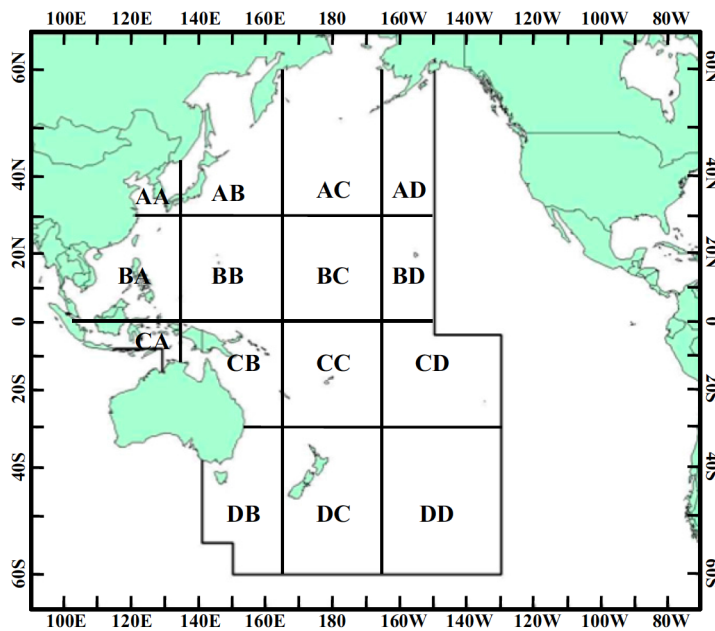
Figure 2.S1. Map of the regions used in the analysis. A map of the WCPFC Convention Area (WCPFC 2013), with the 15 regions used in our analysis shown. Regions were derived by dividing the Convention Area into 4 latitudinal and longitudinal sections of similar size.
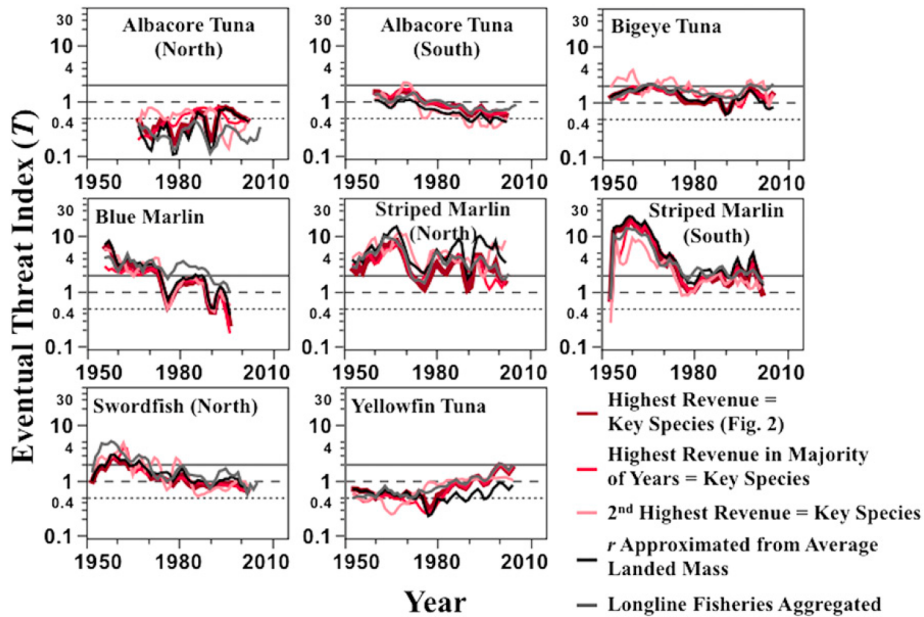
Figure 2.S2. Sensitivity of *T* estimates. A comparison of *T* values (3 year geometric mean) using base (dark red) and alternate estimation assumptions. In particular, estimates using: i) different assumptions guiding the identification of the key species (light red and pink); ii) approximations of relative growth rates, *r*, using relative body-mass (black); and iii) combining shallow-set/deep-set longline catch data (grey) are shown for each population. Grid lines are drawn for reference at *T* = 2 (solid), *T* = 1 (dashed), and *T* = 0.5 (dotted).
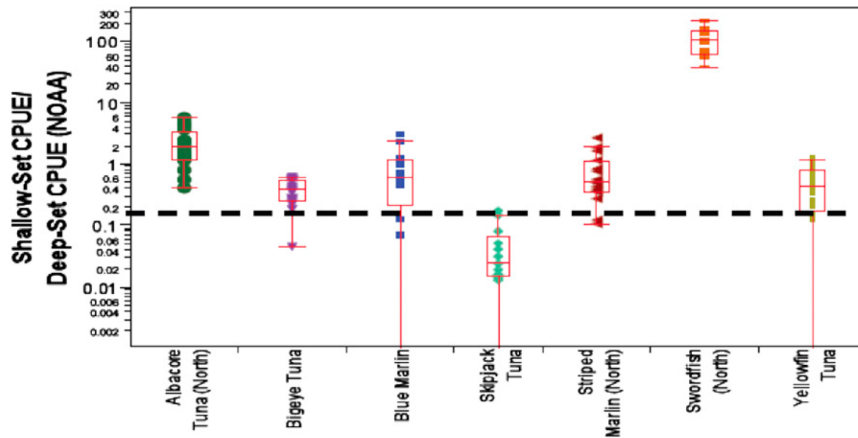
Figure 2.S3. The annual ratios of shallow-set to deep-set longline CPUE in the Hawaii-based fisheries are shown for each species, along with a box plot showing the median, inter-quartile ranges, and maximum and minimum. Yellowfin tuna, skipjack tuna and blue marlin each had a single year (2001) in which there was a reported shallow-set CPUE of 0 (NOAA 2012a). Notably, there was also very little total reported effort in the shallow-set fishery in that year (4 trips, 27 sets, 21380 hooks) (NOAA 2012a).
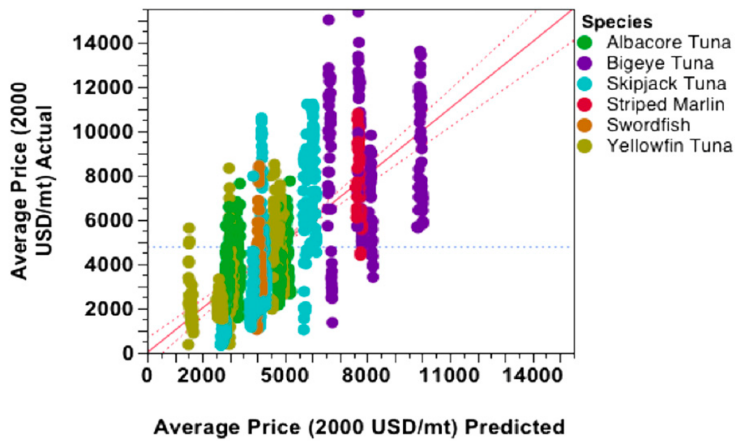
Figure 2.S4. Predicted vs. observed average prices from the model used to fill in missing regional prices ($n = 1125$, $R^2 = 0.5$, $p < 0.001$).

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Table 2.S1. Key species in majority of years.

Region/ fishery	Shallow-set longline pre-1975	Shallow-set longline post-1975	Deep-set longline	Purse seine, associated schools	Purse seine, unassociated schools	Pole and line
AA	Striped marlin, north	Albacore tuna, north	Albacore tuna, north	Skipjack tuna	Skipjack tuna	Skipjack Tuna
AB	Bigeye tuna	Swordfish, north	Bigeye tuna	Skipjack tuna	Skipjack tuna	Skipjack tuna
AC	Bigeye tuna	Swordfish, north	Bigeye tuna			Skipjack tuna
AD	Bigeye tuna	Swordfish, north	Albacore tuna, north			
BA	Yellowfin tuna	Swordfish, north	Yellowfin tuna	Skipjack tuna	Skipjack tuna	Skipjack tuna
BB	Bigeye tuna	Swordfish, north	Bigeye tuna	Skipjack tuna	Skipjack tuna	Skipjack tuna
BC	Bigeye tuna	Swordfish, north	Bigeye tuna	Skipjack tuna	Skipjack tuna	Skipjack tuna
BD	Bigeye tuna	Swordfish, north	Bigeye tuna	Skipjack tuna	Skipjack tuna	Skipjack tuna
CA	Yellowfin tuna	Yellowfin tuna	Yellowfin tuna	Skipjack tuna	Skipjack tuna	Skipjack tuna
CB	Yellowfin tuna	Albacore tuna, south	Yellowfin tuna	Skipjack tuna	Skipjack tuna	Skipjack tuna
CC	Albacore tuna, south	Albacore tuna, south	Bigeye tuna	Skipjack tuna	Skipjack tuna	Skipjack tuna
CD	Albacore tuna, south	Bigeye tuna	Bigeye tuna	Skipjack tuna	Skipjack tuna	Skipjack tuna
DB	Albacore Tuna, south	Albacore tuna, south	Albacore tuna, south	Skipjack tuna	Skipjack tuna	
DC	Albacore tuna, south	Albacore tuna, south	Albacore tuna, south	Skipjack tuna	Skipjack tuna	Skipjack tuna
DD	Albacore tuna, south	Albacore tuna, south	Albacore tuna, south			

Blank cells indicate gear–region combinations with no fishing.

Chapter 3

Harvested to extinction: Price flexibility vs. hyperstable catch rates

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Abstract.

The market values of harvested species rise as they become depleted due to falling supply, rarity value, or both. High price flexibility in response to the depletion of a harvested population can cause profits to be stable or increase even as the population declines toward extinction. Although recent empirical studies have focused on demonstrating rarity value-driven price flexibility in some species believed to be threatened by harvesting, extinction is predicted to occur only if the value of the harvest rises faster than the cost of obtaining harvest, which is also likely to increase as a population declines. Here, I present a simple mechanistic framework for assessing the likelihood that profits from harvesting a population would remain positive as abundance declines toward extinction. Drawing on empirical evidence from minke whales, caviar-producing sturgeons, bluefin tunas, and other marine species, I argue that threats of extinction from overharvesting are likely to be driven to a much greater extent by catch rates that are robust to abundance declines, termed 'hyperstable', resulting from aggregation behavior, advanced technology, or habitat destruction, than by price flexibility per se; though extinction does require some degree of price flexibility. My analysis provides a workable model for assessing threats of such extinctions, often called Anthropogenic Allee Effects, in both marine and terrestrial systems, and highlights a previously underappreciated interaction between threats of habitat destruction and overharvesting.

3.1 Introduction

Classic harvesting theory (Gordon 1954; Clark 1976) suggests that, when harvesting a single population, the rise in the cost of obtaining a unit of catch as the population declines can prevent its extinction, since harvesters would not make a profit once the population fell below a certain size. However, the prices of harvested commodities (e.g. meat, horns, tusks, pelts) tend to rise as the harvested population is depleted due to falling supply (Barten & Bettendorf 1989; Schrank & Roy 1991; Asche et al. 2007), an effect that can be magnified by 'rarity value' – elevated value placed on rare species by consumers (Dulvy et al. 2003; Courchamp et al. 2006). If prices are flexible (i.e. rise quickly) enough, in response to falling supply, to offset the rising costs of obtaining harvest as a population declines, it can be profitably harvested to extinction – a phenomenon proposed by Courchamp et al. (2006) and termed 'the Anthopogenic Allee Effect' (AAE). Moreover, even if prices do not increase significantly as abundance declines, a population can be driven to an abundance low enough to make it susceptible to extinction from stochastic or other forces if the value of its harvest is high enough, (Clark 1976; Courchamp et al. 1999; Lande et al. 2003; Branch et al. 2013).

There is concern that price-related threats may be driving a number of species harvested for luxury commodities towards extinction, including land mammals and insects hunted for trophies (Johnson et al. 2010; Palazy 2011; Palazy et al. 2012a; Biggs et al. 2013), collections (Courchamp et al. 2006; Tournant et al. 2012), or body parts regarded as having medicinal or aphrodisiac properties (Courchamp et al. 2006; Angulo & Courchamp 2009); and sources of luxury seafood including large whales (Clark 1973; Amundsen et al. 1995; see also Branch et al. 2013), caviar-producing sturgeon species (Acipenseriformes) (Pikitch et al. 2005; Lenhardt et al. 2006; Gault et al. 2008), bluefin and other high-value tunas (Collette et al. 2011), and some invertebrates (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).

Several recent studies have provided empirical evidence that prices have indeed risen as abundance declined, possibly due to rarity value, in sturgeons (Gault et al. 2008), mammals hunted for trophies (Palazy et al. 2011, 2012a,b), and collected beetles (Tournant et al. 2012) (see Angulo & Courchamp 2009; Angulo et al. 2009 for more general experiments); arguing for this as evidence of extinction threats to these species 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 alone are not a sufficient condition for extinction; ii) the AAE framework is built on an assumption of open-access, 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.

Though it has so far been challenging, empirically evaluating the susceptibility of a species or population to AAE and other value-related threats is important. Some broad correlates of extinction risk in harvested species are well known, including large body size, slow population growth rate, high market value, and low harvest cost due to high habitat accessibility (e.g. proximity to human population centers) (Roberts & Hawkins 1999; Purvis et al. 2000; Alroy 2001; Dulvy et al. 2003; Sethi et al. 2010; Collette et al. 2011; Branch et al. 2013; Purcell et al. 2014), though patterns of overharvesting in some systems run counter to these (e.g. Pinsky et al. 2011). However, mechanistic frameworks that identify biological and/or socioeconomic conditions likely to result in future extinction threats instead of identifying evidence for past declines could inform preventative conservation (e.g. Burgess et al. 2013).

Here, I present a framework for empirically assessing the susceptibility of a population to the Anthropogenic Allee Effect. Specifically, I show how combinations of bioeconomic conditions that would allow profits from harvesting a given population to remain positive as it is depleted to extinction can be identified empirically using a small set of measurable parameters, and often even when some are un-estimable. Drawing on

empirical evidence from caviar-producing sturgeons (Acipenseriformes), bluefin tunas (Atlantic bluefin tuna (ABF) (*Thunnus thynnus*), Pacific bluefin tuna (PBF) (*Thunnus orientalis*), and Southern bluefin tuna (SBT) (*Thunnus maccoyii*)), the Northeast Atlantic minke whale (*Balaenoptera acutorostrata*), and other marine species, I argue that prices, even of the most valued species, may rarely be responsive enough to declining abundance to cause deterministic extinction (AAE) unless catch rates are also highly robust to declines in abundance, or 'hyperstable' (Harley et al. 2001). Hyperstable catch rates can be caused by aggregation behavior (e.g. schooling or herding) (Winters & Wheeler 1985; Mackinson et al. 1997), technology or communication among harvesters (Hilborn & Walters 1987; Gaertner & Dreyfus-Leon 2004; Thorson & Berkson 2010; Torres-Irineo et al. 2014), and likely also by habitat destruction.

3.2 Identifying conditions conducive to AAE

General framework

The basic framework presented here considers the harvest of a single population with no discounting of future profits and constant cost per-unit-effort (e.g. hours of hunting or fishing), but possible extensions to consider opportunistic or multispecies harvesting, economies of scale, or discounting are discussed, along with possible extensions of the framework. The Anthropogenic Allee Effect (AAE) requires rising harvest values to allow harvesting a population to remain profitable even as it is driven to extinction (Courchamp et al. 2006). With constant per-unit-effort costs, AAE requires stable or increasing per-unit-effort revenue (RPUE) as abundance declines (Figure 3.1).

The RPUE from harvesting a population, i, RPUE_i, is equal to the catch-rate per-unit-effort (CPUE_i) multiplied by the price of each unit of catch (denoted p_i for population i), which are both functions of abundance (denoted N_i for population i):

$$\text{RPUE}_i(N_i) = p_i(N_i)\text{CPUE}_i(N_i) \quad (3.1).$$

CPUE generally falls as abundance (denoted N) decreases (Figure 3.1A) and, following Harley et al. (2001) and others, I assume the following relationship (Figure 3.1A):

$$\text{CPUE}_i(N_i) = q_i N_i^{\beta_i} \quad (3.2),$$

where q_i and β_i are constants. Here, β_i measures the percent change in CPUE_i resulting from a one percent change in abundance (N_i) – the elasticity of catch to abundance. When $\beta_i < 1$, catch is said to be 'hyperstable' because CPUE falls more slowly than abundance (Harley et al. 2001).

The price of catch of population i (p_i) generally increases as the supply of catch (denoted Q_{Si} for catch of population i) decreases (Figure 3.1B). The strength of this relationship is measured in economics, for harvested products, by the 'own-price flexibility of demand' (Houck 1965; Barten & Bettendorf 1989; Schrank & Roy 1991; Eales et al. 1997), denoted f_i for catch of population i. which measures the percentage increase in price that results from a one percent decrease in supply, all else equal:

$$\left(\frac{\partial p_i}{\partial Q_{Si}}\right)\left(\frac{Q_{Si}}{p_i}\right) = -f_i \quad (3.3a).$$

It should be noted that, though I define f_i using a negative sign so that f_i is positive when demand responds negatively to price, some studies do not (e.g. Eales et al. 1997). It is also worth briefly mentioning the more common measure of quantity-price relationships, own-price elasticity of demand (usually denoted ε), 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 ε, but not an exact reciprocal for most goods (i.e. $f \neq 1/\varepsilon$; see Houck et al 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 ε 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 better measure of quantity-price relationships in harvested species than demand elasticity.

Equation (3.3a) can be solved for p_i to give the following relationship between price (p_i) and supply of catch, when incomes and supplies of complement and substitute goods stay constant:

$$p_i\big(Q_{Si}(N_{i0})\big) = p_{i0}\left(\frac{Q_{Si}(N_i)}{Q_{Si}(N_{i0})}\right)^{-f_i} \quad (3.3b).$$

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Here, p_{i0} is the price at current abundance (N_{i0}), and the notation reflects the fact that the quantity of catch supplied (Q_{Si}) is a function of abundance (N_i). Specifically, at an equilibrium at abundance N_i, the quantity of harvest supplied ($Q_{Si}(N_i)$) is equal to the surplus production at that abundance (i.e. births – natural deaths), denoted $S_i(N_i)$ (Figure 3.1C).

I assume surplus production $S_i(N_i)$, has negative density-dependence (i.e. $S_i'(N_i) < 0$), which can be expressed as,

$$S_i(N_i) = Q_{Si}(N_i) = r_i N_i g_i(N_i) \quad (3.4),$$

where r_i is the maximum per-capita rate of population increase over a standard time-interval (e.g. years), and $g_i(.)$ ($g_i \leq 1$ by definition of r_i) is a function describing the density dependence of population i's growth. The assumption of strictly negative density-dependence implies that $g_i'(.) < 0$, with $g_i(0) = 1$, and $g_i(K_i) = 0$, where K_i is the un-harvested equilibrium abundance, or 'carrying capacity of population i (Figure 3.2A).

Putting equations (3.1), (3.2), (3.3), and (3.4) together, current economic and biological conditions, measured by β_i, f_i, and $g_i(N_i)$, give the following relationship between RPUE_i and abundance (N_i), all else equal:

$$\text{RPUE}_i(N_i) = \text{RPUE}_i(N_{i0}) \left(\frac{N_i}{N_{i0}} \right)^{(\beta_i - f_i)} \left(\frac{g_i(N_i)}{g_i(N_{i0})} \right)^{-f_i} \quad (3.5a),$$

where $\text{RPUE}_i(N_{i0}) = q_i N_{i0}^{\beta_i} p_i(N_{i0})$. Under the assumption of constant per-unit effort costs, it is empirically useful to rewrite equation (3.5a) as:

$$\left(\frac{R_i}{C_i} \right) = \left(\frac{R_{i0}}{C_{i0}} \right) \left(\frac{N_i}{N_{i0}} \right)^{(\beta_i - f_i)} \left(\frac{g_i(N_i)}{g_i(N_{i0})} \right)^{-f_i} \quad (3.5b),$$

where R/C is the ratio of revenues to costs, which can be measured at any effort scale. It can be shown, by taking the derivative of equation (3.5a) with respect to N_i, that per-unit-effort revenues (RPUE_i) increase as abundance (N_i) decreases (i.e. $\delta\text{RPUE}_i/\delta N_i < 0$) if:

$$f_i \left[1 + N_i \left(\frac{g_i'(N_i)}{g_i(N_i)} \right) \right] > \beta_i \quad (3.6).$$

The second term on the right-hand side of inequality (3.6) will be negative because $g_i'(.)$ < 0. The interpretation inequality (3.6) is that a one percent decrease in abundance (N_i) results in a β_i percent decrease in CPUE$_i$ and an increase in price of f_i percent or less. The price increase is dampened by the fact that the population's per-capita growth rate increases as its abundance decreases, as a result of negative density-dependence (i.e. $g_i'(.)$ < 0), which means that the supply of catch ($Q_{Si}(N_i) = r_iN_ig_i(N_i)$) decreases by less than one percent as a result of a one percent decrease in abundance.

In fact, the supply of catch (Q_{Si}) population i produces at equilibrium initially increases as abundance decreases from its carrying capacity (K_i) until it reaches its maximum sustainable yield- (MSY) producing abundance (denoted $N_{i,MSY}$ for population i), and then decreases (Figure 3.1C). Thus, when $N > N_{MSY}$, both CPUE and equilibrium price decrease as abundance decreases, implying that it is impossible for RPUE$_i$ to increase as abundance decreases when $N_i > N_{i,MSY}$. However, when $N_i < N_{i,MSY}$, equilibrium prices increase as the population decreases, and, as can be seen in inequality (3.6), the dampening effect of density-dependence on price responses to declining abundance approaches 0 as abundance (N_i) approaches 0. Thus, if $f_i > \beta_i$, RPUE$_i$ would be expected to initially decline as abundance declined, reaching a minimum at an abundance greater than 0 and smaller than $N_{i,MSY}$, and increasing at smaller abundances. Similarly, if $f_i = \beta_i$, RPUE$_i$ would be expected to monotonically decline as abundance (N_i) declined, but would approach a non-zero minimum as N_i approached 0 (Figure 3.1D). If this minimum RPUE is greater than opportunity costs (often measured as variable costs (Clark 1976; 1980)), the population faces deterministic extinction from AAE under open-access, starting from any initial size (Figure 3.1E). If costs are greater than this minimum, the population cannot be harvested deterministically to extinction if $f_i = \beta_i$, and has a critical size if $f_i > \beta_i$, above which it will be harvested to a stable non-zero equilibrium under open-access, and below which it will be harvested to extinction from AAE (Figure 3.1F) (see also Courchamp et al. 2006; Hall et al. 2008). All else equal, more flexible prices (i.e. larger f_i) will result in the minimum RPUE occurring at a larger abundance relative to N_{MSY} ($N_i/N_{i,MSY}$ for population i) (Figure 3.1D), and stronger density

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dependence (i.e. larger $|g_i'(.)|$) will result in the minimum RPUE occurring at a smaller $N_i/N_{i,MSY}$ (Figure 3.2B,C). If $f_i < \beta_i$, $RPUE_i$ would be expected to decline monotonically to 0 as abundance (N_i) declined, and the population would not be threatened by AAE (Figure 3.1D).

Empirical application

      The first step in empirically assessing whether current biological and economic conditions pose a threat of extinction by AAE to a population, *i*, is to estimate whether $f_i \geq \beta_i$. If not, then current conditions are unlikely to pose a threat of AAE (though the population may still be threatened by harvesting by other mechanisms). If price flexibility (f_i) is indeed estimated to be larger than or equal to catch elasticity (β_i), the next step is to determine whether $RPUE_i$ should be expected to increase or decrease as abundance declines from current abundance, by testing inequality (3.6). In addition to estimates of β_i and f_i, this requires estimates of the strength of density dependence (i.e. the shape of $g_i(N_i)$) and the current abundance relative to a reference point relevant to density-dependence (e.g. N_i/K_i or $N_i/N_{i,MSY}$). If $RPUE_i$ is estimated to be increasing as abundance declines, then current conditions pose a threat of extinction by AAE to the population, under open-access. If it is estimated that $f_i \geq \beta_i$, but that $RPUE_i$ is currently still decreasing as abundance declines (i.e. inequality (3.6) is determined to be false at current abundance), then an estimate of the current revenue/cost (R/C), in addition to the information collected above, can be used to determine, using equation (3.5b), if the minimum revenue would be expected to be greater than or less than costs. A projected minimum revenue greater than costs (i.e. a minimum $R/C > 1$) implies a threat of extinction by AAE under open-access. Even though some of these parameters, N/N_{MSY} and the strength of density-dependence in particular, may be difficult or impossible to estimate for some harvested populations, equations (3.5b) and (3.6) can be used to solve for the ranges of unknown parameters that would lead to a threat, as illustrated in Figure 3.3. Similarly, equations (3.5b) and (3.6) can be used to generate probabilistic assessments of AAE threats from uncertainty bounds on parameters. Informative

assessments of AAE threats are often possible even with very large uncertainty in one or more parameters.

Catch elasticity, β_i, can be estimated empirically from time series of CPUE and an independently estimated index of abundance ($I_i = c_i N_i$, where c_i is a constant) using linear regression on log-transformations of these data (Harley et al. 2001):

$$\log(\mathrm{CPUE}_{i,t}) = \alpha_i + \beta_i \log(I_{i,t}) \quad (3.7a),$$

where $\alpha_i = c_i q_i$ is the estimated intercept, and t is the time index (e.g. year, month, or day) of each observation. Harley et al. (2001) also discuss other methods for estimating β_i with this type of data to account for observation errors and other sources of potential bias. In some harvests (e.g. illegal poaching) effort, and consequently CPUE, may be difficult to estimate. In such cases, it may be possible to approximate β_i if fractional changes between two time periods in both the abundance ($\Delta N_i = (N_{i,2} - N_{i,1})/N_1$ or $(I_{i,2} - I_{i,1})/I_{i,1}$) and geographic range size, denoted A_i for population i, ($\Delta A_i = (A_{i,2} - A_{i,1})/A_1$) are known:

$$\beta_i = \frac{\% \text{ change in CPUE}}{\% \text{ change in abundance}} \approx \frac{\% \text{ change in density}}{\% \text{ change in abundance}} = \left. \left(\frac{1 + \Delta N_i}{1 + \Delta A_i} - 1 \right) \right/ \Delta N_i \quad (3.7b).$$

This estimation approach (equation (3.7b)) makes use of the fact that one of the main known drivers of hyperstability (i.e. $\beta < 1$) is range contraction in declining populations (Winters & Wheeler 1985; Mackinson et al. 1997), which leads to reductions in population density (one of the main determinants of CPUE) that are smaller than the 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). Other factors can cause hyperstability, 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); and aggregation among individuals in the harvested population (e.g. schooling, herding), as aggregations are generally easier for harvesters to locate than individuals and aggregating species often manifest declines to a greater extent as range contractions than density reductions (Mackinson et al. 1997).

However, equation (3.7b) may provide a useful baseline estimation method for β when reliable CPUE data is not available.

There are several ways to estimate f_i, (see Barten & Bettendorf 1989; Schrank & Roy 1991; Eales et al. 1997; Chiang et al. 2001 for examples). In general, estimating f_i requires time series data on consumer incomes or expenditures (denoted X), prices (p_i) and quantities supplied or traded (Q_{Si}) of the harvest or harvest product of population i, and quantities supplied or traded (when estimating f_i) of closely related complements or substitutes. The simplest possible estimation method uses a regression equation of the following form:

$$\log(p_{i,t}) = a_i - f_i \log(Q_{Si,t}) + \sum_j f_{ij} \log(Q_{Sj,t}) + f_{ix} \log(X_t) \text{ (3.8)}.$$

Here, t is again the time index of each observation, a_i is an estimated intercept, f_{ij} and f_{ix} are respectively the estimated 'cross-price flexibilities of demand' and 'income (or expenditure or scale) flexibility of demand', which respectively measure the effects of changes in the supply of related good j and changes in consumer incomes or expenditures on the price of harvest of population i (Houck 1965; Eales et al. 1997). I present this method for its simplicity and ease of interpretation (i.e. f is estimated directly by the regression) in light of the limited data for many rare harvested species. However, when time series of significant length (e.g. monthly for 10 or more years (e.g. Barten & Bettendorf 1989; Eales et al. 1997)) are available, modern demand studies have often used more complex estimation methods that allow for dynamic effects and are more firmly rooted in modern consumer theory (see Eales et al. 1997 for overview).

It is also important, for the purposes of both estimating f_i and more generally predicting extinction threats, to identify any other species or products that are perfect substitutes for harvest of population i, meaning that consumers do not distinguish between the two products. Perfect substitutes are defined, for the purpose of this 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

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between two products, 1 and 2, involves estimating the parameters in the following equation:

$$\log(p_{1,t}) = a + b\log(p_{2,t}) \quad (3.9),$$

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, j, is a perfect substitute for harvest of population i (i.e. the LOP holds), then treating them as separate products creates bias in estimating f_i, 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 Y), then the price responds to changes in the total supply of harvest of all populations in Y. In other words, all else equal, price would be given by (analogously to equation (3.3b)):

$$p_i\big(Q_{Si}(N_{i0})\big) = p_{i0}\left(\frac{\sum_{k\in Y} Q_{Sk}(N_k)}{\sum_{k\in Y} Q_{Sk}(N_{k0})}\right)^{-f_i} \quad (3.10).$$

This implies that the effect of a population's declining abundance on its harvest price ($\delta p_i/\delta N_i$) approaches 0 as its abundance approaches 0, eliminating the threat of AAE, if there are other more common populations or products which are perfect substitutes. Thus, with respect to threats of AAE, 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).

Estimating either the strength of density-dependence or the current population size relative to a reference point require time series estimates of an index of abundance, coupled with either catch data, recruitment data, or both (see Hilborn & Walters 1992 for canonical discussion on estimating abundance and reference points in fisheries; Myers et al. 1999 for methods of estimating the strength of density-dependence, as well as estimates for a wide range of fish taxa). It is also often required to assume a particular functional form of density-dependence. Two of the most common flexible forms (i.e. allowing for different strengths of density dependence) are the θ-logistic model (Gilpin & Ayala 1973), where $g_i(N_i) = 1 - (N_i/K_i)^{\theta_i}$, and the Beverton-Holt model (Beverton & Holt 1957), which, in the absence of age-structure, can be written in the form, $g_i(.)$, as (see Appendix A and Mangel et al. 2003):

$$g_i(N_i/K_i) = \frac{(1-h_i)(1-(N_i/K_i))}{(1-(N_i/K_i)+h_i(5(N_i/K_i)-1))} \quad (3.11a),$$

or equivalently,

$$g_i(N_i/N_{i,MSY}) = \frac{(1-h_i)\left(h_i(5-(N_i/N_{i,MSY}))+(N_i/N_{i,MSY})\left(1-2\sqrt{h_i(1-h_i)}\right)-1\right)}{(5h_i-1)\left(1+h_i((N_i/N_{i,MSY})-1)-(N_i/N_{i,MSY})\left(1-2\sqrt{h_i(1-h_i)}\right)\right)} \quad (3.11b),$$

where h is a measure of the strength of density-dependence termed 'steepness', which is defined as the fraction of the maximum recruitment that occurs at an abundance 20% the size of the carrying capacity (Mangel et al. 2013) (larger h implies stronger density-dependence) (Figure 3.1C, Figure 3.2). I assume this form of $g_i(.)$ (equation (3.11b)) in my discussion below of threats of AAE to commercial fish species, in light of published estimates of h and N/N_{MSY}.

3.3 Empirical examples in aquatic systems

The key parameters ($\beta, f, h, R/C$, and N/N_{MSY}) highlighted here for identifying conditions conducive to AAE, have been estimated for many aquatic exploited species, including some that are thought to be (or have recently been) facing possible value-related threats. For example, Ricard et al. (2012) and Costello et al. (2012) together

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provide estimates or approximations of N/N_{MSY} for most of the major harvested fish species worldwide; Lam et al. (2011) and Sumaila et al. (2007) recently estimated fishing costs and ex-vessel prices, from which R/C can be calculated; and Myers et al. (1999) estimate steepness (h) for a wide range of fish taxa. With the exception of groundfish, there have not yet, to my knowledge, been comparable compilation efforts for estimates of β or f for fish and other exploited aquatic species (see Schrank & Roy (1991) for overview of estimates of f and other components of the global groundfish demand system; Harley et al. (2001) for estimates of β from nearly 300 series from north Atlantic groundfish fisheries). However, numerous studies have estimated one or both of these parameters in specific systems.

Estimates of catch elasticity (β) in aquatic systems have varied widely among species and harvesting methods, but have tended to be less than or equal to 1 (indicating hyperstability). Estimates of β have been smallest among schooling species, often <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 1988; Mackinson et al. 1997), in addition to larger species, such as the minke whale (Amundsen et al. 1995), and likely Atlantic bluefin tuna (Pintassilgo & Duarte 2002). Other schooling tunas have (e.g. skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*)) have been estimated to have moderate hyperstability ($\beta \approx$ 0.3-0.7) in their surface fisheries (e.g. purse-seine, pole-and-line), which specifically target schools (Gaertner & Dreyfus-Leon 2004; Campbell et al. 2010), but low hyperstability ($\beta \approx 1$) in longline fisheries (Ward 2008; Campbell et al. 2010; Campbell & Kennedy 2010). Schooling populations are susceptible to hyperstable catches for two reasons: i) they tend to manifest population declines primarily as range contractions, maintaining school size and density (Winters & Wheeler 1985); and ii) schools are generally easier for fishers to locate than individual fish (Mackinson et al. 1997) and advances in fishing technology have greatly enhanced detection capabilities (Pintassilgo & Duarte 2002). A meta-

analysis of flatfish (megrim, plaice, sole) and gadiformes (cod, haddock, hake, pollock, whiting), mostly from trawl fisheries, estimated β values of 0.64-0.75 (Harley et al. 2001). There have been few estimates of β for commercial fisheries for diadromous species (e.g. salmonids, sturgeons), but recent estimates from anglers have ranged from ~ 0.6-1 for salmonids (Tsuboi & Endou 2008; Ward et al. 2013).

Estimates of f for fish products have varied among species, commodity types, and estimation methods, but have mostly been 0.5 or smaller (e.g. Schrank & Roy 1991; Eales et al. 1997; Jaffry et al. 1999; Chiang et al. 2001; Asche et al. 2007), suggesting an often small response of fish prices to falling supply. Of particular note, Eales et al. (1997) estimated f to be 0.46 for high value fresh fish in Japan, one of the main consumers of rare fish products. 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) – 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 (i.e. $f << 1$). The price flexibility, f, of fresh bluefin tuna (lumped ABF, PBF, and SBT) in Japan was estimated by Chiang et al. (2001) to be from 1984-1999 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 tunas. This is consistent with the relative historical stability observed in bluefin prices (Figure 3.4A,B compare annual catches (data from Ricard et al. 2012) with average Japanese import prices (data from FAO 2014), where SBT (Figure 3.4A) is distinguished from ABF and PBF (Figure 3.4B)). Historical caviar prices (Figure 3.4C) have risen more than those of bluefin tunas, but are still consistent with the consensus among price flexibility estimates in fish that harvest prices tend to rise by half of the percentage by which harvest supplies decline, or less. To my knowledge, there have been no studies estimating price flexibility for caviars, likely due in part to a lack of widely available data to which modern estimation methods (see Eales et al. 1997) can be applied. To

preliminarily address this gap for caviars, I use historical (1980-2011) country-level price and quantity data from FAO (2014) on exports of caviar and caviar substitutes (defined by FAO (2014) as roe products from species other than sturgeons and paddlefishes) to estimate price flexibility (f) using equation (3.8), with per-capita real GDP (in units of purchasing-power parity), averaged over importing countries weighted by their fraction of total imports over the time period, as a proxy for expenditure. This analysis estimates a price flexibility (f) of 0.48 (Table 3.S1). Though publicly available data with which to estimate price flexibilities of hunted whales are sparse, one series from the Norwegian harvest of Northeastern minke whale (Amundsen et al. 1995) suggests a price flexibility possibly in the neighborhood of 0.65 (i.e. prices have historically risen by roughly 0.65% on average for every 1% decline in catch) (Figure 3.4D).

The pervasive observation of low price flexibility ($f << 1$, most often < 0.5), even in highly valued aquatic species, suggests that threats of AAE may be very unlikely except among species that have both few substitutes and very high hyperstability ($\beta < 0.5$). Even species that do meet both of these criteria are unlikely to have RPUE currently increasing as abundance decreases unless ($\beta << 0.5$) and/or they are already nearly extinct (Figure 3.3A). However, if they are caught in fisheries with substantial profit margins ($R/C > 1.5$, e.g. tuna purse-seine and pole-and-line fisheries, which have $R/C > 2.5$ on average (Lam et al. 2011)), even moderate depletion and $\beta \approx f$ can allow minimum revenues to remain above costs (Figure 3.3B,C).

Severe hyperstability in the Northeastern minke whale ($\beta \approx$ 0-0.15) (Amundsen et al. 1995) may have allowed its profitable harvest to extinction, had the international moratorium on whaling not been imposed during the 1980s ($R_{MIN}/C > 1$; Figure 3.3B). It should be noted that Amundsen et al. (1995) reached the opposite conclusion in a simulation of open-access Norwegian whaling, though this relied on an assumption of constant prices, which seems to have been violated (Figure 3.4D). There have not been, to my knowledge, many past studies directly estimating β for sturgeons or bluefin tunas. However, β is thought to be very low (~0.2) in the ABF fishery, which mostly uses purse-seine and other gears which target schools (Pintassilgo & Duarte 2002). Catch

elasticity (β) is thought to be larger in SBT fisheries, with recent studies assuming moderate β for Australian purse-seine fisheries, which target younger fish in schools (e.g. Kennedy 1999 assumes $\beta = 0.6$); and assuming β close to 1 in Japanese longline fisheries (Kennedy 1999; Campbell & Kennedy 2010). Though there is little information with which to estimate β for sturgeons, there may be reason to believe that catches are quite hyperstable (i.e. $\beta \ll 1$), because many of the most severely depleted caviar-producing sturgeons (e.g. Beluga sturgeon (*Huso huso*), Russian sturgeon (Osetr) (*Acipenser gueldenstaedtii*)) have faced suffered significant habitat destruction caused by pollution, hydroelectric dams, and other forms of encroachment (IUCN 2013), which has undoubtedly led to range contraction.

To test the approximation method for β from range data I present here (equation (3.7b)), I use this method to approximate average (i.e. across all gears) β values for tunas by combining the average 1960-1999 range contraction across 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 decline in each population (in units of total biomass) over the same period (Figure 3.4E). Multiple populations of the same species in the same ocean were aggregated to be compatible with Worm & Tittensor's (2011) range contraction estimates, and estimated range contractions of SBT were averaged across all 3 oceans (Atlantic, Pacific, Indian). Estimates of β using this approach are quite consistent with existing hypotheses (Figure 3.4E). Species caught mostly in longline fisheries (albacore (*Thunnus alalunga*), bigeye, SBT) had average β 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 β estimates. Estimates of average β 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 highly unlikely that the true βs for these species is negative (this would mean CPUE increases as abundance decreases), but likely that they are indeed very low.

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Based on these analyses, open-access harvesting would likely pose an AAE extinction threat to Northeastern minke whale ($f > \beta$, $R_{MIN}/C > 1$; Figure 3.3B), could (depending on the degree of catch hyperstability, β) pose a threat to ABF, PBF, and caviar-producing sturgeons such as the severely depleted Beluga and Russian sturgeons (f may be greater β, R_{MIN}/C may be greater than 1; Figure 3.3A,C), but would not likely pose a deterministic extinction threat to SBT ($f < \beta$). These analyses also suggest that range contraction may indeed be a key driver of catch hyperstability, and may provide a useful tool for empirically estimating catch elasticities (β) when CPUE data is difficult to obtain.

3.4 Discussion

Since Courchamp et al. (2006) first hypothesized that the rising value of a population's harvest as it was depleted might cause deterministic extinction - the Anthropogenic Allee Effect (AAE) - several studies have empirically demonstrated that harvest prices of rare species indeed rise in response to falling supply, partly due to rarity value (Courchamp et al. 2006; Gault et al. 2008; Angulo et al. 2009; Palazy et al. 2011, 2012a,b; Tournant et al. 2012). However, empirically assessing whether rarity value or other factors could drive prices up fast enough to maintain harvest profits as a population was depleted has remained elusive (Harris et al. 2013). This study presents an intuitive approach to empirically predicting extinction threats from AAE under open-access. First, it provides a basic and readily estimable indicator of the possibility of an AAE: AAE can only occur if the own-price flexibility of demand of a population's harvest is larger than or equal to the elasticity of its catch to its abundance (i.e. $f \geq \beta$). To my knowledge, this fundamental requisite of price-driven extinction has not been previously highlighted. This study also illustrates how other factors such as the strength of density-dependence and the current level of depletion can affect the threat of AAE to a population, but that informative assessments are possible even with large uncertainties in these factors.

To date, the literature on AAE has mostly focused on price flexibility – the idea that, as a harvested population is depleted, both scarcity (moving along the demand curve) and increases in demand driven by preferences for rarity (shifts in the demand

curve) (Courchamp et al. 2006; Hall et al. 2008) can lead to price increases large enough to allow profitable harvesting to extinction. However, the evidence presented and reviewed in this study suggests that, at least in fish and whales, AAE threats are likely to be driven to a far greater extent by hyperstable catch rates than rising prices, as prices generally rise proportionally more slowly than catches decrease – with estimated own-price flexibilities generally 0.5 or lower (e.g. Barten & Bettendorf; Schrank & Roy 1991; Eales et al. 1997; Chiang et al. 2001). Conceptually, this may be related to the fact that most harvest products, even the most highly valued luxuries such as caviar and bluefin tuna sashimi, have partial substitutes. If consumers devote a constant share of their budgets to a particular good, irrespective of the supplies and prices of other goods, then (assuming constant incomes) the own-price flexibility (f) of this good should be 1, because a one percent decrease in supply would be exactly offset by a one percent increase in price, allowing consumers to maintain their expenditure. However, the existence of substitutes causes consumers to prefer to shift some of their demand away from a product whose supply has fallen, rather than accepting a price increase that fully offsets the lost supply (Mas-Collel et al. 1995). Moreover, my analysis demonstrates that populations whose harvests have perfect substitutes are very unlikely to be threatened by AAE, unless all perfect substitutes are also threatened, as perfect substitutability causes the impact of declines in a population's abundance on its price to diminish as it approaches extinction.

In contrast, catch-rates should generally be expected to be hyperstable – declining at a slower rate than abundance ($\beta < 1$) – as a result of range contraction, technology, information-sharing among harvesters, aggregation behavior (e.g. herding, schooling), or other factors (Winters & Wheeler 1985; Hilborn & Walters 1987; Mackinson et al. 1997; Harley et al. 2001; Gaertner & Dreyfus-Leon 2004; Thorson & Berkson 2010; Torres-Irineo et al. 2014). The fact that price flexibilities are generally smaller than 0.5, it is likely that populations must have catch elasticities (β) of 0.5 or smaller to be threatened by AAE. Among harvested fish populations, those with catch elasticities this small have been predominantly schooling species, which manifest population declines as range contractions, maintaining population density (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 (referred to as 'catchability-led stock collapse (Pitcher 1995)).

Though seldom studied, it is likely that many terrestrial harvested species have hyperstable catch rates as well, particularly those that aggregate. Estimating β in terrestrial harvests has likely been hindered by difficulty in obtaining catch-per-unit-effort (CPUE) data in many terrestrial harvests, particularly poaching. However, in this study I introduce a novel approach (equation (3.7b)) to approximating β from range data, and provide preliminary validation for this approach. Additionally, because range contraction is an important driver of hyperstable catch rates, it is likely that habitat destruction could exacerbate harvesting threats of extinction by overharvesting, 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 is an important area of future research. The extinction of the passenger pigeon (*Ectopistes migratorius*), which has been attributed to both habitat destruction and overharvesting (e.g. Bucher 1992), is one potentially interesting historical case study. Climate change could possibly also lead to range contraction-related overharvesting threats to some species.

This study largely focuses on open-access mechanisms of extinction by overharvesting, which has been a source of criticism for some empirical studies of AAE, as there are property rights in many harvests, including some poaching (Harris et al. 2013), and certainly many fisheries (Worm et al. 2009), including most whales (International Whaling Commission (IWC 2014)) and all 3 bluefin tuna species (CCSBT 2011a,b; IATTC 2012; ISC 2012). There is some management of trade in sturgeons under the Convention on International Trade in Endangered Species (CITES 2014).

While it is true that some types of cooperation, governance, or management can prevent extinction of a harvested population under most circumstances, it is nonetheless important to understand open-access incentives, as there is rarely perfect enforcement or access restriction, particularly in the oceans. There is significant illegal and unreported fishing of SBT, for example (Polachek 2012), despite a very strong recent tradition of management, led by the Commission for the Conservation of Southern Bluefin Tuna (CCSBT). For populations that are not yet managed, understanding open-access threats can inform management priorities. Moreover, in populations for which $f > \beta$, there may be profit maximizing incentives to deplete the population, though the strengths of such incentives likely depend on the type of cooperation or property rights, the discount rate, and other factors. This merits further study. Nonetheless, it is important to note that finding $f > \beta$ or that the projected minimum revenue-to-cost ratio (R/C) is greater than 1 implies that deterministic extinction is possible under current biological and economic conditions and open-access incentives, not that extinction will happen necessarily. It is important to consider other incentive structures that may exist, and to re-estimate β and f on a regular basis as technologies and demand conditions can change. Estimating f at regular intervals may be particularly important because this could allow detection of shifts in demand associated with preferences for rarity (Hall et al. 2008), rather than sensitivities of prices to scarcity.

The assumption of constant per-unit-effort costs in this study is also worthy of mention. Though this is frequently assumed in bioeconomic harvesting models (Clark 1976, 1985), it is unlikely to be the case in reality, as costs can be highly influenced by variable fuel prices, economies of scale, or technological advances, for example (see Lam et al. 2011 for recent global analysis of fishing costs). Economies of scale, which would cause per-unit effort costs to decrease as effort increased, might increase threats of AAE. The framework presented here could be extended to include changing costs. However, the utility of this added complexity is strongly dependent on the predictability of future cost variations. If such predictability is absent, then constant costs may be a good baseline assumption.

This study presents an approach to assessing direct deterministic extinction threats to harvested populations from high and increasing value of targeted harvests, but does not consider indirect threats from ecological interactions with other populations (e.g. Estes et al. 2009), 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 approach presented here with other approaches considering these other factors is a fruitful area of future research. For example, Burgess et al. (2013) develop a mechanistic approach to predicting extinction threats from multispecies harvesting which relies on estimating the relative depletion rates of species relative to those of highest economic or management importance. Burgess et al.'s (2013) approach could be easily combined with the approach presented here to allow predictions of the threat posed by a target species' high and rising value to other species caught along with it. Similarly, the approach presented here for estimating the profit-abundance relationship of a population's harvest could be combined with estimates of its minimum stochastically viable population size (Lande et al. 2003; Brook et al. 2006) to evaluate threats of extinction from stochastic forces.

Overharvesting is a significant threat to many populations and 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), and highly valued tunas (Collette et al. 2011), are rapidly declining and are thought to be threatened with extinction by the AAE as a result of their rarity-value (Courchamp et al. 2006). This study demonstrates how this threat can be predicted from data readily available for many of these species; and provides evidence suggesting that hyperstable catch rates resulting from aggregation, range contraction, and possibly habitat destruction, are more likely drivers of AAE than rising prices, at least in minke whales, bluefin tunas, sturgeons, and other fish. More research is needed to evaluate the possible threat of hyperstable catch to hunted land-mammals (e.g. rhinos, elephants, ungulates, large cats), and this study illustrates one possible method that does not require catch data. Combining simple mechanistic theories with low-data assessment approaches

likely offers many fruitful avenues for predicting extinction threats from harvesting and other human activities before consequences become severe and irreversible (Burgess et al. 2013; Gaines & Costello 2013).
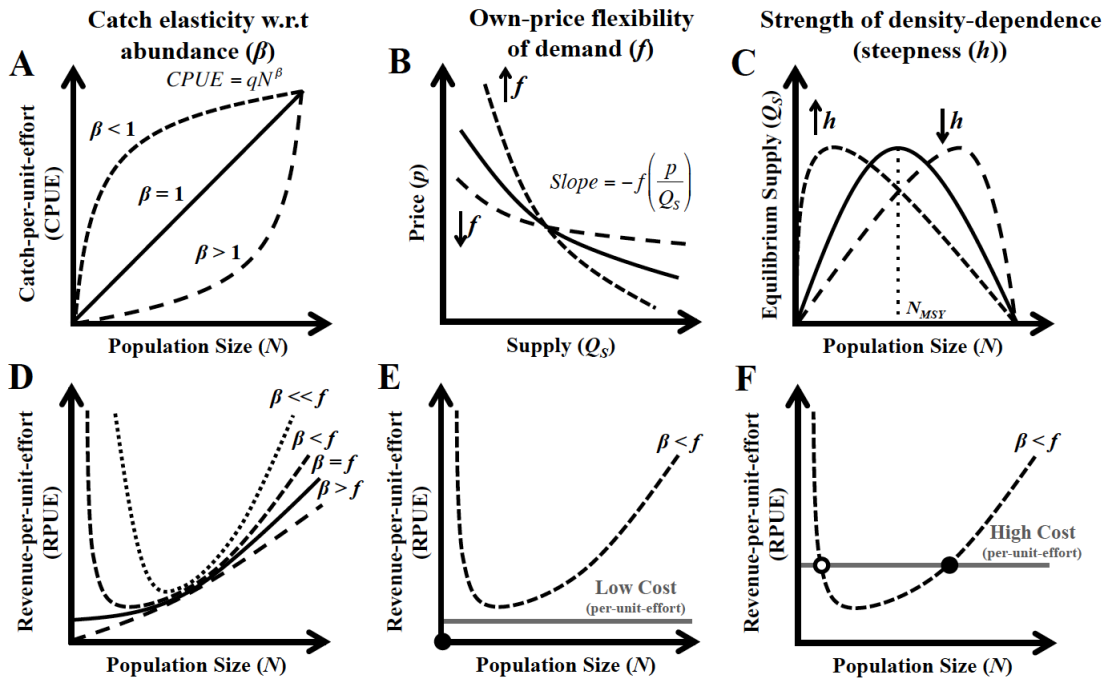
Figure 3.1. Factors determining the relationship between revenue and abundance of a harvested population: (**A**) Catch elasticity with respect to abundance (β) measures the shape of the catch-per-unit-effort (CPUE)-abundance (N) relationship. (**B**) Own-price flexibility of demand (f) measures the strength of the response of prices (p) to changes in harvest supply (Q_S). (**C**) Harvest supplied at a particular abundance at equilibrium is determined by strength of density-dependence, which can be measured by steepness (h), the fraction of maximum recruitment occurring at an abundance 20% carrying capacity. (**D**) shows the shape of the relationship between revenue-per-unit-effort ($RPUE$) and population size (N) with different values of β and f. When $f > \beta$, low costs result in deterministic extinction (**E**), while high costs result in alternative stable states (extinction, and filled circle), and an unstable tipping point (open circle) (**F**).

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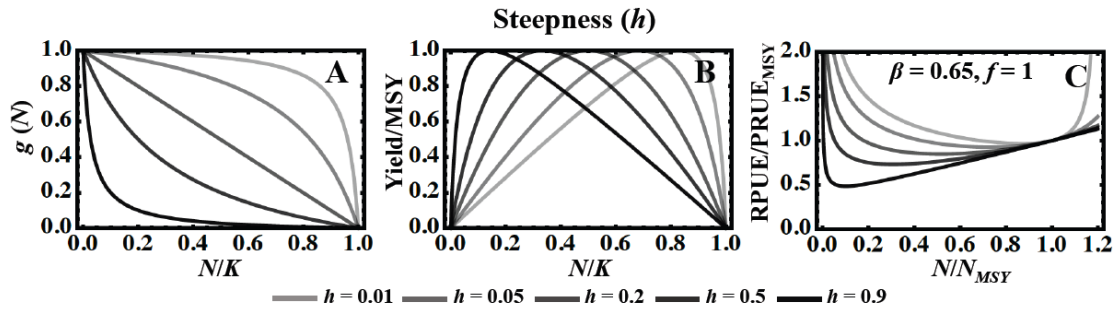
Figure 3.2. The importance of the strength of density dependence (steepness). (**A**) and (**B**) respectively illustrate effects of varying steepness on the relationships between abundance (N) and per-capita growth rate (**A**) and sustainable yield (**B**). (**C**) illustrates the impact of varying steepness on the relationship between RPUE and abundance.
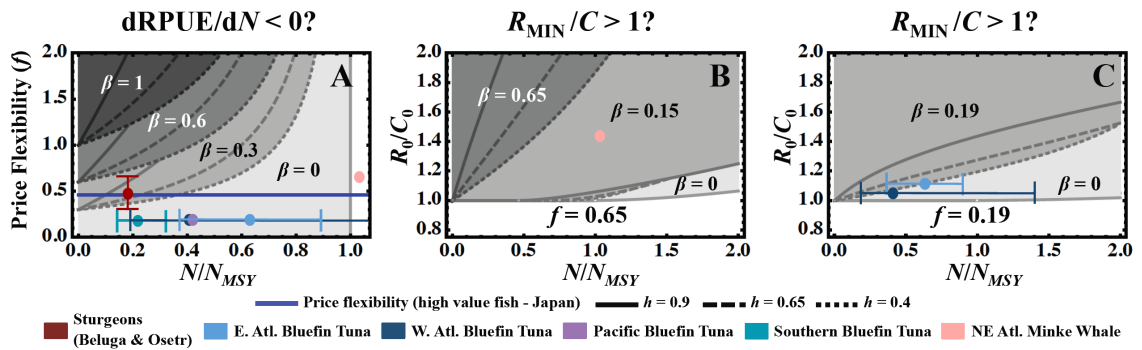
Figure 3.3. Assessing threats under parameter uncertainties. In each panel, shaded regions corresponding to each set of β and h values indicate ranges in the other parameters for which there is a threat of AAE: in (**A**), because parameters in this range imply RPUE is currently inversely related to abundance (i.e. dRPUE/dN < 0); and in (**B**) and (**C**), because parameters in this range imply that the minimum revenue-to-cost-ratio (R_{MIN}/C) as abundance declines to extinction from its current level is greater than 1. Estimates with uncertainty bounds (where applicable) are shown for sturgeons (N/N_{MSY} from Costello et al. 2012 for Beluga (*Huso huso*) and Osetr (*Acipenser gueldenstaedtii*)), East and West Atlantic bluefin tuna (N/N_{MSY} estimate and bounds from ICCAT 2012), Pacific bluefin tuna (N/N_{MSY} estimate from ISC 2012), Southern bluefin tuna (N/N_{MSY} estimate and bounds from CCSBT 2013), and Northeast Atlantic minke whale (N/N_{MSY} and R/C values shown are pre-moratorium (geometric mean of 1983-1985) from Amundsen et al. 1995). The Northeast Atlantic minke whale ($\beta \approx$ 0-0.15, $f \approx$ 0.65) would likely be threatened by open-access harvesting (**B**: $R_{MIN}/C > 1$). Atlantic bluefin tuna ($\beta \approx$ 0.2, $f = 0.19$) could be threatened with low steepness (**C**) ($h \approx$ 0.3-0.7 (Myers et al. 1999)).

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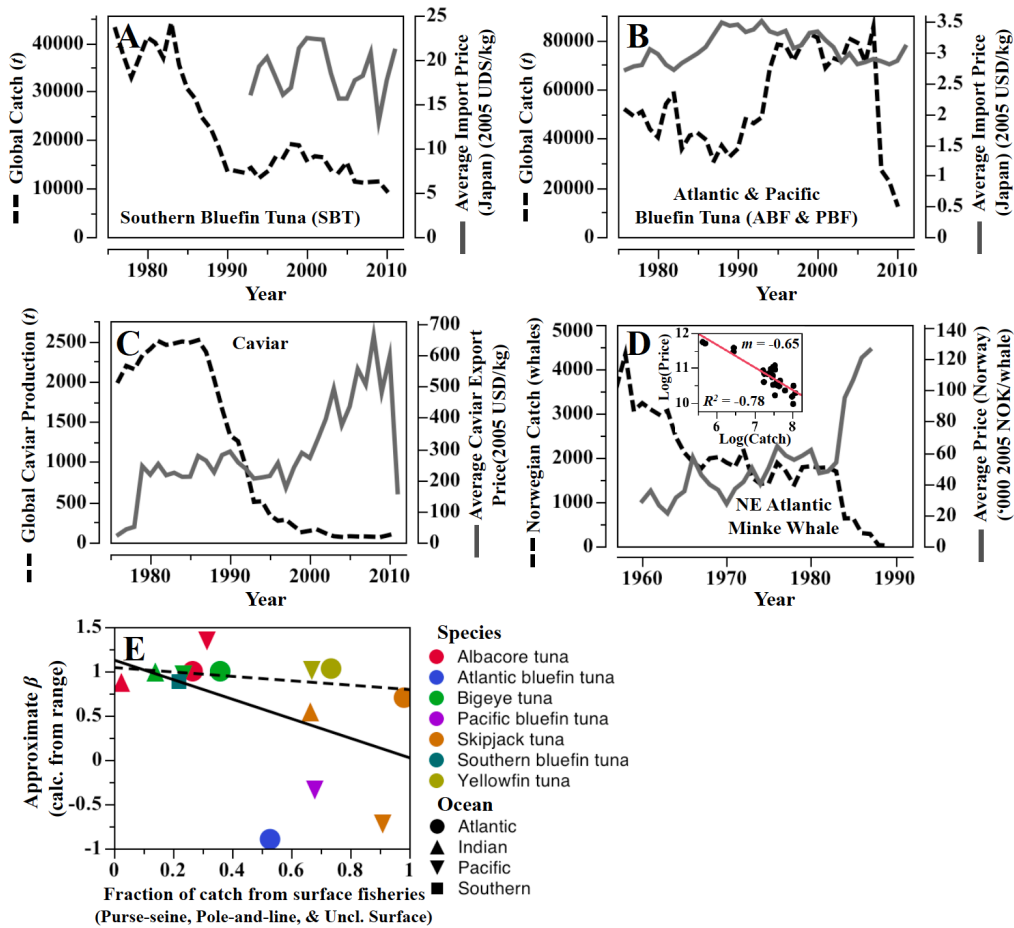
Figure 3.4. Price trends in highly valued species and estimates of catch elasticity from range in tunas.
(A)-(D) illustrate trends in supplies and prices of (A) SBT, (B) ABF and PBF, (C) caviar (data from FAO 2014), and (D) the Northeast Atlantic minke whale (data from Amundsen et al. 1995). All prices were converted from nominal to real value using data on annual inflation in the relevant currency (US Dollar (USD) or Norwegian Kroner (NOK)) from the World Bank (2014). (E) shows estimates of average β for tuna species calculated from observed changes 1960-1999 in geographic range (data from Worm & Tittensor 2011) and abundance (data from Ricard et al. 2012), 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 β of 1.13 in tunas with no catch in surface fisheries, and an average β of 0.03 in tunas caught exclusively in surface fisheries. The dashed line is fit excluding negative β estimates, and suggests average βs of 1.04 and 0.79 with no surface fisheries and exclusively surface fisheries, respectively.

3.5 Supplementary Material

Appendix A. Transforming the Beverton-Holt Model

With a single age-class, a Beverton-Holt population growth model for a population, i, can be written as:

$$\frac{dN_i}{dt} = \frac{x_i N_i}{1 + y_i N_i} - M_i N_i \quad (3.S1),$$

where the first term is the Beverton-Holt (1957) stock-recruitment relationship (x_i and y_i are positive constants), and M_i is a positive constant representing natural mortality. The steepness (h_i), defined as the fraction of maximum recruitment occurring at an abundance 20% of natural equilibrium abundance, or carrying capacity ($K_i = (1/y_i)((x_i/M_i) - 1)$), can be shown to be equal to (Mangel et al. 2013):

$$h_i = \frac{(x_i/M_i)}{4 + (x_i/M_i)} \quad (3.S2a).$$

Equation (3.S2a) can be re-arranged to express x_i in terms of h_i and M_i:

$$x_i = \frac{4 h_i M_i}{1 - h_i} \quad (3.S2b).$$

The maximum per-capita growth-rate in this model is $r_i = x_i - m_i$, implying that $g_i(.)$ is given by:

$$g_i(N_i) = \frac{1}{x_i - M_i}\left[\frac{x_i}{(1 + y_i N_i)} - M_i\right] \quad (3.S3).$$

Substituting (3.S2b) into equation (3.S3) gives:

$$g_i(N_i) = \frac{h_i(5 + y_i N_i) - y_i N_i - 1}{(5 h_i - 1)(1 + y_i N_i)} \quad (3.S4).$$

The right-hand side of equation (3.S4) can be set equal to 0 to solve for K_i in terms of h_i and y_i:

$$K_i = \frac{5 h_i - 1}{y_i(1 - h_i)} \quad (3.S5).$$

Finally, N_i in equation (S4), can be rescaled in terms of K_i by multiplying each N_i by

multiplying each N_i in equation (S4) by $\left(\left[\dfrac{5h_i-1}{y_i(1-h_i)}\right]\Big/K_i\right)$ (which is equal to 1), which

gives equation (3.11a):

$$g_i(N_i/K_i) = \frac{(1-h_i)(1-(N_i/K_i))}{(1-(N_i/K_i)+h(5(N_i/K_i)-1))} \quad (3.11a).$$

$N_{i,MSY}$ as a fraction of K_i is given by (Mangel et al. 2013):

$$\frac{N_{i,MSY}}{K_i} = \frac{\sqrt{\dfrac{4h_i}{1-h_i}}-1}{\dfrac{4h_i}{1-h_i}-1} \quad (3.S6a),$$

which implies that:

$$N_{i,MSY} = \left(\frac{\sqrt{\dfrac{4h_i}{1-h_i}}-1}{\dfrac{4h_i}{1-h_i}-1}\right)\left(\frac{5h_i-1}{y_i(1-h_i)}\right) \quad (3.S6b).$$

Equation (3.S6b) can be used to rescale N_i in equation (3.S4), giving equation (3.11b):

$$g_i(N_i/N_{i,MSY}) = \frac{(1-h_i)\left(h_i\left(5-(N_i/N_{i,MSY})\right)+(N_i/N_{i,MSY})\left(1-2\sqrt{h_i(1-h_i)}\right)-1\right)}{(5h_i-1)\left(1+h((N_i/N_{i,MSY})-1)-(N_i/N_{i,MSY})\left(1-2\sqrt{h_i(1-h_i)}\right)\right)} \quad (3.11b).$$

Table 3.S1. Estimates of aggregate price flexibilities (*f*) for exported caviar (data from FAO 2014).

Model Effect	Estimate (S.E.)
Intercept	4.38 (6.51)
Own-price flexibility (*f*) - caviar	-0.48 (0.082)***
Cross-price flexibility - caviar exports	-0.035 (0.18)
Income flexibility	0.42 (0.78)
Number of obs.	32
R^2	0.75
Model *p*	<0.0001

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

Chapter 4

Competition-driven assessment failures in multispecies fisheries and solutions

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Abstract.

Multispecies fisheries catch numerous species simultaneously, and are particularly likely to catch species that compete ecologically with one another, as non-random spatial and temporal targeting patterns, bait, size selective nets, and other niche-relevant technologies are typically used.   It is also common for sustainable harvest levels to be estimated for target and by-catch populations using single-species population models. Here, I present theoretical evidence suggesting that assessments using single-species population models are likely to significantly overestimate the sustainable harvests of competitors with lowest susceptibility to overfishing (strong stocks), which can lead to management that causes unexpected collapses. In contrast, single species models can often provide reliable estimates of sustainable harvests of the competitors with highest susceptibility to overfishing (weak stocks) in a multispecies harvest. This finding is of potential concern because assessment and management efforts in many fisheries focus on strong stocks, which often produce much of a fishery's revenue. I offer two solutions to these problems. First, I show how conditions under which biased estimates of sustainable harvests may occur, and bounds on the magnitude of such biases, can be identified using conventional single-species assessment models. Second, I discuss how recent advances in the management of weak stocks and by-catch species can effectively eliminate this threat.

4.1. Introduction

Since the rise of industrial fishing in the mid twentieth century, fisheries have had profound impacts on many marine ecosystems (Jackson et al. 2001, Worm et al. 2006), severely depleting many target populations (Worm et al. 2009, Costello et al. 2012, Ricard et al. 2012). However, the assessment and management of marine fisheries has also seen considerable advances in recent decades, with encouraging signs that overfishing is on the decline in many places, and many once depleted stocks have begun to rebuild (Costello et al. 2008, Worm et al. 2009, Hilborn & Ovando 2014). However, multispecies fisheries, in which multiple species are caught simultaneously, still pose significant threats (Gaines & Costello 2013) because fully exploiting a target stock (population) may result in overexploitation of more easily depleted (weaker) stocks and species caught unintentionally as by-catch (e.g. Hall 2000; Lewison et al. 2004a,b).

Harvested fish populations exist within diverse and complex ecosystems, but their sustainable harvests are mostly estimated using single species population models (Hilborn & Walters 1992). Some have called for a transition away from single-species assessment and management approaches and toward 'ecosystem-based fishery management' (EBFM) (Pikitch et al. 2004), while others have argued that such a transition is not necessarily pressing, citing the many recent examples of success in traditional fisheries management (Hilborn & Ovando 2014). There is conceptual merit to both of these perspectives. Clearly, single species approaches may fail to capture critical fishery-relevant ecosystem properties; but fisheries science is also highly data-limited. The majority of fisheries do not even have sufficient data with which to perform traditional single-species assessments (Costello et al. 2012), and those for which whole ecosystem models can be applied empirically (e.g. Link et al. 2002; Christensen & Walters 2004; Hilborn 2011) are an even smaller minority.

A possibility that has not yet been widely explored in fisheries science is that single species population models may, under some conditions, be able to effectively abstract multispecies reality, and thus provide accurate estimates of maximum sustainable yield (MSY) and other reference points for a population despite their simplicity. Such abstraction would occur if the dynamics of a population being assessed were qualitatively

similar to the dynamics predicted by a single-species model, and the effects of interactions with other species were thus captured implicitly by the parameter estimates in the assumed single-species model (Schaffer 1981); allowing the relationship between yield and effort to be correctly predicted. In such cases, single-species assessment models would not only be adequate, they would be ideal, as their simplicity in comparison to multispecies models would be statistically advantageous. One might imagine that multispecies realities indeed often do create yield-effort relationships for stocks that resemble a single-species model, as yield is certain to be zero at zero effort and efforts beyond a certain level, with some sort of peak in between (Figure 4.1). However, a few theoretical studies have provided counterexamples in predator-prey models (Abrams 2009a,b,c) and models of either predation or competition with switching or other dynamic interactions (Abrams 2009b,c; Tschirhart 2012) – finding yield-effort relationships to sometimes be not strictly concave (e.g. having multiple local maxima) or sharply-peaked (i.e. locally non-differentiable). Such studies have not yet considered simultaneous species and gear interactions, as would occur in a multispecies fishery, but the analogous situation of shared predation among species has been shown to have important ecological implications (e.g. Holt 1977; Holt et al. 1994).

Here, I theoretically assess the reliability of estimates of MSY and other stock reference points from single-species assessment models in stocks being harvested along with their ecological competitors in multispecies fisheries. I focus on competitive interactions because these are the most likely among species caught in modern multispecies fisheries, which, as a result of targeting specific spatial and temporal habitats typically using size-selective nets and/or bait, are likely to be catching species occupying similar ecological niches. I show that estimates of reference points using flexible single-species models such as the Beverton-Holt model (Beverton & Holt 1957) may often be reliable for weak stocks – those most susceptible to overfishing – but will sometimes significantly overestimate the productivity of strong stocks, with potentially dangerous consequences for management. I discuss possible methods of empirically predicting when this bias will occur and estimating bounds on its magnitude within traditional stock assessment frameworks, as well as some management solutions.

4.2. Methods & Results

(a) Two stocks and a single fishing type

Assessments of the status and health of a fish stock (population) involve estimating its abundance (denoted N_i for stock i) and harvest rate (denoted F_i for stock i), and how these compare to the abundance and harvest rate that would produce MSY (respectively denoted $N_{i,MSY}$ and $F_{i,MSY}$ for stock i) or some other reference point, along with the yield (i.e. total catch) produced at the reference point in question (Hilborn & Walters 1992; Cadima et al. 2003). For brevity, I focus my analysis on MSY, but the basic results can be applied to any other reference point. Data inputs typically include catch data (including age-structure if applicable (e.g. length-frequency data)), effort data, and an index of abundance, either calculated from catch-per-unit-effort (CPUE) or independent research surveys (Hilborn & Walters 1992; Harley et al. 2001; Cadima et al. 2003). In the case of single-species assessments, a single-species population growth model is assumed, whose parameters are estimated using the data; and the fitted model is used to predict MSY, N_{MSY}, F_{MSY}, N/N_{MSY}, F/F_{MSY}, etc. (Hilborn & Walters 1992; Cadima et al. 2003).

The parameters of the assumed single-species population growth model determine how fast the abundance of the stock (N) is predicted to fall with increasing fishing effort (denoted E), and how fast the per-capita production rate (birth rate – natural death rate), denoted $g_i(N_i)$ for stock i, is predicted to increase as abundance (N_i) decreases (assuming negative density-dependence in population growth) (Figure 4.1A,B). Both of these relationships are observed or inferred from the data, which allows the parameters in the model to be estimated. For example, suppose a stock, i, caught by a single type of fishing, with effort, $E(t)$, at time t, is assumed to have a constant catchability (per-capita-per-unit-effort catch rate), denoted q_i, and logistic population growth (Schaefer 1954) in the absence of harvesting, $(g_i(N_i) = r_iN_i(1 - N_i/K_i))$, where r_i is the maximum per-capita growth rate, and K_i is the natural equilibrium abundance, or carrying capacity - assumed to be equal to the pre-harvest abundance, denoted N_{i0} ($N_{i0} = K_i$)). These assumptions

result in the following predicted instantaneous population rate of change relative to pre-harvest levels, $dn_i(t)/dt$ (where $n_i(t) = N_i(t)/N_{i0}$) at time t:

$$\frac{dn_i(t)}{dt} = n_i(t)\big(g_i(n_i(t)) - q_i E(t)\big) \quad (4.1a),$$

where,

$$g_i(n_i(t)) = r_i(1 - n_i(t)) \quad (4.1b).$$

Additionally, yield (or total catch), denoted $Y_i(t)$ for stock i at time t, would be given by:

$$Y_i(t) = q_i N_{i0} n_i(t) E(t) \quad (4.1c).$$

Observations of $dn_i(t)/dt$ (or a discrete time equivalent), $n_i(t)$, $E(t)$ and $Y_i(t)$ allow estimation (e.g. using maximum likelihood) of q_i (estimate denoted $\hat{q}_i$), r_i (estimate denoted $\hat{r}_i$), and N_{i0} (estimate denoted $\hat{N}_{i0}$) using equations (4.1a,b,c). The predicted relationship between fishing effort (E) and yield (predicted yield from stock i is denoted $\hat{Y}_i$) at the corresponding equilibrium abundance, denoted $n_i^*(E)$, (i.e. where $dn_i(t)/dt = 0$) would be:

$$\hat{Y}_i(E) = \hat{N}_{i0} n_i^*(E) g_i\big[n_i^*(E)\big] = \hat{N}_{i0} \hat{q}_i \left(E - \left(\frac{\hat{q}_i}{\hat{r}_i}\right) E^2 \right) \quad (4.2).$$

The predicted MSY$_i$, $N_{i,MSY}$, $F_{i,MSY}$, and effort at MSY (denoted E_{MSYi}) would be given by: $\left\{ \hat{MSY}_i = \dfrac{\hat{r}_i \hat{N}_{i0}}{4}, \hat{N}_{i,MSY} = \dfrac{\hat{N}_{i0}}{2}, \hat{F}_{i,MSY} = \dfrac{\hat{r}_i}{2}, \hat{E}_{MSYi} = \dfrac{\hat{r}_i}{2\hat{q}_i} \right\}$.

Suppose now that there is a multispecies fishery catching two competing stocks, denoted s and w, whereby the 'weak' stock, w, is more greatly impacted by the fishing effort than the 'strong' stock, s. For the weak stock, fishing effort has the direct negative consequence of mortality and the indirect negative consequence of creating an unfavourable competitive imbalance – by putting greater pressure on its population than on the population of its stronger competitor. Thus, for the weak stock, competition magnifies the population impact of fishing mortality, which reduces its productivity (achievable yields (Y_w) and per-capita production rate $g_w(.)$) relative to non-competitive conditions (Figure 4.1A,C). However, the shape of its density-dependence ($g_w(.)$ vs. n_w) yield-effort (Y_w vs. E) relationships still often resemble those of a single-species model

(Figure 4.1A,C). Thus, it is often possible to accurately estimate MSY and other fishery reference points (e.g. F/F_{MSY}) for the weak stock using a single-species assessment model (Figure 4.1A,C).

In contrast, fishing effort has the direct negative consequence of mortality for the strong stock, but the indirect benefit of creating a favourable competitive imbalance – by putting greater pressure on the population of its weaker competitor than on its own population. If the direct population cost of effort is less than the indirect benefit, the shape of the yield-effort relationship may still resemble that of a single species model (Figure 4.1B,D, Figure 4.2A,B,D); but if the indirect benefit is larger, the stock may seem infinitely productive, as increasing effort will actually increase the equilibrium stock size – a 'hydra effect' (Figure 4.2C), named (and discussed in more detail) by Abrams (2009d) after the mythological creature that grows two heads in place of one that is cut off. In either case, the strong stock will switch from a high-productivity regime to a lower-productivity regime at the effort level at which the weak stock is driven extinct (or functionally extinct), because maintaining the high productivity regime would require the abundance of the weak stock to continue declining into the negative range to maintain the indirect benefit of harvesting for the strong stock (Figure 4.1B,D, Figure 2).

Thus, the productivity of the strong stock may be accurately predicted by fitting a single-species model over the range of efforts at which the weak stock is extant, but MSY is likely to be overestimated if the weak stock is driven extinct at a lower effort (denoted $E_{wExtinct}$) than the effort at which the strong stock would be predicted to reach its MSY under its productivity regime in the presence of the weak stock (denoted $\hat{E}_{MSYs}$) (Figure 4.1B,D, Figure 4.2A,B,C vs. D). If the overestimate of MSY is large enough, attempts to achieve the MSY could cause both stocks to collapse (e.g. as is the case Figure 4.1B,D). The same logic can be applied to any other reference point.

Assuming constant q_s and q_w, the condition for overestimation of strong stock MSY and F_{MSY}, $E_{wExtinct} < \hat{E}_{MSYs}$, is equivalent to $\left(\hat{F}_s / \hat{F}_{s,MSY}\right) < \left(F_w / F_{w,Extinct}\right)$ because $F_i = q_i E$ and current effort (E) is the same for both stocks. This will hold for any type of density-dependence or assessment model, $g_i(.)$, not only the logistic. Moreover, if the

productivity (Y_i, $g_i(.)$) of the weak stock is reliably estimated, the condition for overestimation can be evaluated from the single-species assessments themselves as: $\left(\hat{F}_s/\hat{F}_{s,MSY}\right) < \left(\hat{F}_w/\hat{F}_{w,Extinct}\right)$ (where $\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)$ is assumed to be an unbiased estimate of $\left(F_w/F_{w,Extinct}\right)$). If it is indeed estimated that $\left(\hat{F}_s/\hat{F}_{s,MSY}\right) < \left(\hat{F}_w/\hat{F}_{w,Extinct}\right)$, then the potential bias in $\hat{MSY}_s$ and $\hat{F}_{s,MSY}$, are bounded by the fact that the true MSY_s and $F_{s,MSY}$ can be no smaller than yield and fishing mortality predicted at $E_{wExtinct}$ ($\hat{Y}_s\left(\hat{E}_{wExtinct}\right)$) and $\hat{F}_s\left(\hat{E}_{wExtinct}\right)$). This implies that:

$$\frac{\hat{MSY}_s}{MSY_s} \leq \frac{\hat{MSY}_s}{\hat{Y}_s\left(\hat{E}_{wExtinct}\right)} \quad (4.3a),$$

$$\frac{\left(F_s/F_{s,MSY}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)} \leq \frac{\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)} \quad (4.3b).$$

In other words, the difference between true MSY (MSY_s) and predicted MSY ($\hat{MSY}_s$) for the strong stock will be no greater than the difference between predicted MSY and predicted yield at the effort at which the weak stock is predicted to be driven extinct ($\hat{Y}_s\left(\hat{E}_{wExtinct}\right)$) (equation (4.3a)) (e.g. Figure 4.2A vs. B), and similarly for effort (equation (4.3b)). Equations (4.3) imply that bounds on biases in predicted MSY ($\hat{MSY}_s$) and F_{MSY} ($\hat{F}_{s,MSY}$) for the strong stock can be empirically identified using only single-species assessments. These equations (4.3) both depend on the assumption that the single species population models used in assessing both the strong stock and the weak stock accurately predict their equilibrium statics (Y_i vs. E, and $g_i(.)$ vs. $n_i^*(E)$), but do not assume a specific population model (e.g. logistic).

To provide a concrete example, I return to the logistic growth assessment model (equations (4.1a,b,c)), but now assume that the true population growth in the absence of harvesting is described by a Lotka-Volterra competition model for both stocks, whereby $g_i(N_i,N_j) = 1 - (N_i/K_i) - c_{ij}(N_j/K_j)$, for $i,j = s,w$; $i \neq j$, where $c_{ij} = c_{ji}$ is a positive constant defining the strength of competition, which is assumed to correlate with niche similarity (sensu MacArthur & Levins 1967). In other words, $0 \leq c_{ij} \leq 1$, where $c_{ij} = 1$ would imply

that stocks i and j were ecologically identical, $c_{ij} = 0$ would imply no niche overlap (nor interaction). This assumption provides a concrete interpretation of c_{ij} and guarantees that stocks co-exist stably in the absence of harvesting (MacArthur & Levins 1967). The weak stock, w, has a higher 'vulnerability' to fishing, denoted V_i and defined as $V_i = q_i/r_i$ for stock i (Burgess et al. 2013; see also Clark 1976; Holt 1977), than the strong stock, s (i.e. $V_w > V_s$) (q_s, q_w, r_s, r_w are still assumed to be constant). Without harvesting, the equilibrium abundance of stock i (i.e. N_{i0}) is given by:

$$N_{i0} = \frac{K_i}{1 + c_{ij}} \quad \text{(4.4a)}.$$

Over the range of fishing efforts where both stocks are extant (i.e. N_s, $N_w > 0$, $E < E_{wExtinct}$), the equilibrium abundance of stock i (as a fraction of N_{i0}), $n_i^*(E)$, with fishing effort E is given by:

$$n_i^*(E) = 1 - V_i \left(\frac{1 - c_{ij}\left(V_j/V_i\right)}{1 - c_{ij}} \right) E \quad \text{(4.4b)},$$

the relationship between equilibrium abundance ($n_i^*(E)$) and per-capita production rate ($g_i(.)$) is given by:

$$g_i\left[n_i^*(E), n_j^*(E)\right] = r_i \left(\frac{1 - c_{ij}}{1 - c_{ij}\left(V_j/V_i\right)} \right)\left(1 - n_i^*(E)\right) \quad \text{(4.4c)},$$

and the equilibrium yield with fishing effort E, $Y_i(E)$, is given by:

$$Y_i(E) = N_{i0}q_i \left(E - V_i \left(\frac{1 - c_{ij}\left(V_j/V_i\right)}{1 - c_{ij}} \right) E^2 \right) \quad \text{(4.4d)}.$$

At fishing efforts larger than $E_{wExtinct}$, the equilibrium abundance-effort ($n_s^*(E)$ vs. E) density-dependence ($g_s(.)$ vs. $n_s^*(E)$) and yield-effort (Y_s vs. E) relationships for the strong stock are given by:

$$n_s^*(E) = \left(1 + c_{sw}\right)\left(1 - V_s E\right) \quad \text{(4.5a)},$$

$$g_s\left[n_s^*(E)\right] = r_s\left(1 - \left(\frac{N_s^*(E)}{K_s}\right)\right) = r_s\left(1 - \left(\frac{n_s^*(E)}{1 + c_{sw}}\right)\right) \quad \text{(4.5b)},$$

$$Y_s(E) = \left(1 + c_{sw}\right)N_{s0}q_s\left(E - V_s E^2\right) \quad \text{(4.5c)}.$$

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As can be seen from equation (4.4b), hydra effects (i.e $dn_i^*(E)/dE > 0$) occur for the strong stock when $V_s < c_{sw}V_w$. While the weak stock is extant, as can be seen from comparing equations (4.4c) and (4.1b), and (4.4d) and (4.2a), the equilibrium density-dependence ($g_i(.)$ vs. n_i) and yield-effort (Y_i vs. E) relationships of both the weak stock and the strong stock (if there is no hydra effect) are perfectly abstracted by a logistic equation; specifically one where:

$$\hat{r}_i = r_i \left(\frac{1 - c_{ij}}{1 - c_{ij}\left(V_j/V_i\right)} \right) \quad (4.6),$$

$\hat{q}_i = q_i$, and $\hat{N}_{i0} = N_{i0} = K_i\left(1 + c_{ij}\right)$. As can be seen from equation (4.6), competition indeed makes the weak stock less productive ($\hat{r}_w < r_w$) (Figure 4.1A) and the strong stock more productive ($\hat{r}_s > r_s$) (Figure 4.1B), with the productivity of the strong stock reverting ($\hat{r}_s = r_s$) once the weak stock is driven extinct (Figure 4.1B,D).

If r_s and r_w are indeed estimated as $\hat{r}_s$ and $\hat{r}_w$ according to equation (4.6), the bias in predicted MSY (or any other reference point) for the strong stock ($M\hat{S}Y_s$) can be solved for analytically (Appendix A). As illustrated in Figure 4.3A, though the bias in $M\hat{S}Y_s$ depends on the strength of competition (c_{sw}), which is difficult to measure, it is approximately equal to the estimable upper bound defined by equation (4.3a) over a large range of c_{sw} (~$c_{sw} > 0.5$). In the logistic model, this upper bound on $M\hat{S}Y_s$ bias is given by (Appendix A):

$$\frac{M\hat{S}Y_s}{MSY_s} \leq \frac{\left(\frac{\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)} \right)^2}{\left(\frac{2\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)} - 1 \right)} \quad (4.7),$$

It should be noted however that mean estimates of r_s and r_w will be similar but not exactly equal to $\hat{r}_s$ and $\hat{r}_w$ in equation (4.6) in practice because the logistic model would be fit to transient (i.e. non-equilibrium) data. Unlike in a single-species case (equation (4.1b)), the transient density-dependence relationship ($g_i(n_i(t),n_j(t))$ vs. $n_i(t)$) will not be

identical to the equilibrium relationship $(g_i(n_i^*(E), n_j^*(E)))$ vs. $n_i^*(E)$, given by equation 4.4c). Specifically, mean estimates of r_s will be slightly smaller than $\hat{r}_s$ in equation (4.6), and mean estimates of r_w slightly larger than $\hat{r}_w$ in equation (4.6), to a degree positively related the rate at which the fishery develops (i.e. how quickly $E(t)$ increases) relative to population dynamics (see Figure 4.S1). In other words, rapid fishery expansion introduces an additional, albeit small, source of bias into predictions of competing stocks' responses to fishing, which makes strong stocks appear less productive and weak stocks more productive. In the case of the strong stock, this bias may actually partially counteract the larger bias that is the primary focus of this study.

(b) Three or more stocks

With more than two stocks, yield-effort and density-dependence relationships can still often be well abstracted by single-species models over the range of efforts where all stocks are extant. For example, suppose now that there are J competing stocks, with Lotka-Volterra competition (MacArthur & Levins 1967) as above, such that the rate of change of the abundance of stock i, $dN_i(t)/dt$, is given by:

$$\frac{dN_i(t)}{dt} = N_i(t)\left(r_i\left[1 - \left(N_i(t)/K_i\right) - \sum\nolimits_{j=1, j\neq i}^{J} c_{ij}\left(N_i(t)/K_i\right)\right] - q_i E(t)\right) \quad (4.8),$$

where $c_{ij} < 1$ for all i,j. The pre-harvest equilibrium abundance, N_{i0}, of stock i, is given by:

$$N_{i0} = K_i \sum\nolimits_{j=1}^{J} \left(\mathbf{C}^{-1}\right)_{ij} \quad (4.9a),$$

where,

$$\mathbf{C} = \begin{bmatrix} 1 & c_{12} & \dots & c_{1J} \\ c_{21} & 1 & \dots & c_{2J} \\ \dots & \dots & \dots & \dots \\ c_{J1} & c_{J2} & \dots & 1 \end{bmatrix} \quad (4.9b),$$

$\mathbf{C}^{-1}$ is the inverse of $\mathbf{C}$, and $(\mathbf{C}^{-1})_{ij}$ is the element in the ith row and jth column of $\mathbf{C}^{-1}$. Over the range of efforts at which all stocks are extant, the equilibrium abundance of stock i, scaled to N_{i0}, $n_i^*(E)$, is given by:

$$n_i^*(E) = 1 - \left(\frac{V_i}{X}\right)E \quad (4.9c),$$

where

$$X = \left(\frac{\sum_{j=1}^{J}\left(\mathbf{C}^{-1}\right)_{ij}}{\sum_{j=1}^{J}\left(\mathbf{C}^{-1}\right)_{ij}\left(V_j/V_i\right)}\right) \quad (4.9d);$$

the relationship between equilibrium abundance ($n_i^*(E)$) and per-capita production rate ($g_i(.)$) is given by:

$$g_i\left[\mathbf{n}^*(E)\right] = r_i X\left(1 - n_i^*(E)\right) \quad (4.9e),$$

where $\mathbf{n}^*(E) = \left\{n_1^*(E),...,n_J^*(E)\right\}$, and the equilibrium yield with fishing effort E, $Y_i(E)$, is given by:

$$Y_i(E) = N_{i0}q_i\left(E - \left(\frac{V_i}{X}\right)E^2\right) \quad (4.9f).$$

Similarly to the two stock case, these relationships are perfectly abstracted by a logistic growth model with $\hat{r}_i = r_i X$ for any stock for which $X > 0$ ($X < 0$ would result in a hydra effect).

However, the key difference is that, with 3 or more stocks, shifts in the productivity of stronger stocks following extinction of the weakest stock can be either positive or negative, implying that it is possible to have either positive or negative bias in estimation of MSY or other reference points. Nonetheless, the empirically estimable upper bounds on positive bias given by equations (4.3) and (4.7) still apply because the equilibrium statics are well abstracted over the range of efforts at which all stocks are extant. An illustrative example of this is provided in Figure 4.3B,C using the above model with 3 stocks. The strongest stocks are most likely to have positive MSY estimation bias, but can also have negative bias (Figure 4.3B). Bias is particularly likely to be positive if a strong stock is much stronger than all others (Figure 4.3B). The upper bound on bias defined by equation (4.7) (Figure 4.3A) is clearly visible in both Figure 4B,C. Similarly to the two-stock case, there are likely to be small biases in estimating the

abstracted yield-effort and density-dependence relationships as a result of transient dynamics.

(c) Multiple fishing types

All results presented thus far are general to multiple fishing types under the assumption of constant relative efforts among them (i.e. when $E_k(t)/\sum_l E_l(t)$, where $E_k(t)$ is the effort of fishing type k at time t, is constant for all k). Constant relative effort implies that,

$$F_i = \sum_k q_{ik} E_k = \sum_k E_k \left(\sum_k q_{ik} \left(\frac{E_k}{\sum_k E_k} \right) \right) = \bar{q}_i E \ (4.10),$$

where $\bar{q}_i$ is a constant, and $E = \sum_k E_k(t)$. Thus, with constant relative efforts, all fishing types together behave identically to a single fishing type with vulnerability, $\bar{q}_i$, for stock i and effort E.

Multiple fishing types with changing relative efforts would impact the results similarly to changing catchabilities, q, which both result in changing per-unit-effort mortality rates (i.e. average catchability, $\bar{q}_i$). In both cases, the parameter estimates of single-species assessment models should not be affected if underlying population growth is truly a single-species process (i.e. there are no species interactions), assuming observations or estimates of indices of abundance (i.e. n_i) and per-capita production ($g_i(.)$) are unaffected by changing $\bar{q}_i$. For example, if both the underlying population growth and assessment models are logistic, then estimation of r_i using equation (4.1b) would be unaffected by changing $\bar{q}_i$; and observations of CPUE and n_i would allow the changes in $\bar{q}_i$ to be inferred. Though abundance indices estimated from fishery-independent surveys may be largely unaffected by changes in fishery q, it is possible for CPUE-based abundance indices to be affected (see Maunder & Punt (2004) for review of CPUE-based abundance indices).

However, changes in $\bar{q}$ would impact estimates, using single-species models, of the productivity of stocks that competed with one another (or interacted otherwise), because changes in relative $\bar{q}$ among different stocks would impact the indirect effects of

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fishing effort on population growth via competition (or other ecological interactions). Though beyond the scope of this study, it is likely that temporal dynamics in $\bar{q}$ would have widely varied and strongly context-dependent impacts on the estimation and competition-related estimation bias in stock reference points using single-species assessment models. Moreover, because dynamic $\bar{q}$ should impact productivity estimates of stocks interacting with others in the fishery, but should not impact productivity estimates of stocks without species interactions, significant changes in estimated productivity of a stock, in the absence of exogenous explanations (e.g. climate change), may be a sign of important ecological interactions worth considering in the assessment process.

(d) Flexible population models (Beverton-Holt) and steepness

The logistic model has been a central focus of this study thus far due to its tractability, but it is also important to briefly consider more flexible population models, such as the Beverton-Holt model (Beverton & Holt 1957), which are much more commonly used in fisheries research (Hilborn & Walters 1992), and are also much more likely to be able to accurately abstract most pre-collapse yield-effort relationships. The Beverton-Holt model with a single age class can be written in the form of equation (4.1b), with $g_i(n_i(t))$ given by (see Appendix A in Chapter 3)); Mangel et al. 2013):

$$g_i\big(n_i(t)\big) = r_i \left[\frac{\big(1-h_i\big)\big(1-n_i(t)\big)}{\big(1-n_i(t)+h_i\big(5n_i(t)-1\big)\big)} \right] \quad (4.11),$$

Here, h_i is the 'steepness' of population growth of stock i, defined as the fraction of maximum recruitment produced at an abundance 20% the size of carrying capacity (Mangel et al. 2013), and is a measure of the strength of density-dependence (high steepness implies strong density-dependence). This transformed Beverton-Holt model (equation (4.11)) is identical to the logistic model (equation (4.1b)) when $h_i = 0.2$ (for all i).

Steepness impacts the bias in estimating MSY and other reference points. For example, suppose MSY is predicted for a strong stock, s, (MŜY$_s$) using a fitted Beverton-

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Holt model, where steepness is estimated as $\hat{h}_s$, the current fishing effort is estimated to be a fraction, $\hat{F}_s/\hat{F}_{s,MSY}$, of E_{MSYs}, and a fraction, $\hat{F}_w/\hat{F}_{w,Extinct}$, of the effort needed to drive the weakest stock extinct, $E_{wExtinct}$. If $\left(\hat{F}_s/\hat{F}_{s,MSY}\right) < \left(\hat{F}_w/\hat{F}_{w,Extinct}\right)$, the predicted upper bound on bias in $M\hat{S}Y_s$, assuming constant relative effort among different fishing types (from equation (4.3a), see Appendix B for full derivation), is given by:

$$\frac{M\hat{S}Y_s}{MSY_s} \leq \frac{\left(\sqrt{\hat{h}_s\left(1-\hat{h}_s\right)}-2\hat{h}_s\right)\left(\left(1-\hat{h}_s\right)(1-u)-2\sqrt{\hat{h}_s\left(1-\hat{h}_s\right)}\right)u}{\sqrt{\hat{h}_s\left(1-\hat{h}_s\right)}\left(1-\hat{h}_s+\left(5\hat{h}_s-1\right)u-2\sqrt{\hat{h}_s\left(1-\hat{h}_s\right)}\right)} \quad (4.12a),$$

$$u = \frac{\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)} \quad (4.12b).$$

As illustrated in Figure 4.4A, strong apparent density-dependence (i.e. high $\hat{h}_s$) results in smaller potential biases in MSY estimation. The upper bound on bias in $\hat{F}_s/\hat{F}_{s,MSY}$ is still given by equation (4.3b).

Additionally, unlike in the case of logistic growth, even flexible single-species models do not perfectly abstract a stock's density-dependence and yield-effort relationship when competing stocks differ in the strength of true (i.e. not estimated) density-dependence (true steepness, h_i, in this model). They often provide good approximations, but there are exceptions. For example, Figure 4.4B-F compare true and abstracted equilibrium yield-effort ($Y_i(E)$ vs. E) relationships in two-stock fisheries, in which the true population dynamics are assumed to be described by a Beverton-Holt model modified to include competition by defining per-capita production as:

$$g_i\left(x_i(t)\right) = r_i\left[\frac{\left(1-h_i\right)\left(1-x_i(t)\right)}{\left(1-x_i(t)+h_i\left(5x_i(t)-1\right)\right)}\right] \quad (4.13),$$

$$x_i(t) = \left(N_i(t)/K_i\right)+c_{ij}\left(N_j(t)/K_j\right) \quad (4.13b),$$

where $x_i(t)$ is the sum of abundances of all stocks in the fishery, scaled to their carrying capacities, and weighted by their competition coefficients. Though true yield-effort relationships often strongly resemble relationships predicted by a single-species model,

strong (true) density-dependence in strong stocks (i.e. high h_s), coupled with weaker (true) density-dependence in weak stocks, (i.e. low h_w) can lead to two-peaked yield-effort relationships for the strong stock (Figure 4.4E,F), which can make abstraction unreliable, but does not necessarily systematically bias MSY and F/F_{MSY} estimates in the same way as weak stock collapses (Figure 4.4E). The two-peaked yield-effort relationship for the strong stock with $h_s > h_w$ occurs because the stronger density-dependence of the strong stock (i.e. $h_s > h_w$) compensates for its lower vulnerability ($V_s < V_w$) at high combined abundances (i.e. large x_i), making the strong stock actually more easily depleted (i.e. weaker) at low efforts, but less easily depleted (stronger) at high efforts. In fact, two-peaked yield-effort relationships could cause strong stocks to be estimated to be weak if the observations only cover a low range of efforts (Figure 4.4F), thereby reducing the threat of overestimation of references points (but increasing the likelihood of underestimation).

4.3. Discussion

Using relatively simple models, this study demonstrates an important pitfall of single-species stock assessment frameworks that is caused by ecological competition in multispecies fisheries. Though flexible single-species models, such as the Beverton-Holt (Beverton & Holt 1957) model can often provide reasonably accurate predictions of yield-effort relationships with any set of extant competing populations, estimates of achievable and sustainable yields at efforts beyond those that cause the collapse (i.e. extinction or functional extinction) of the weakest stock are highly unreliable. Significant overestimation of reference point yields (e.g. MSY) and mortality rates (e.g. $F_{MSY}/F_{Current}$) is particularly likely in the strongest stocks as a result of this bias. Such overestimation can lead to unintended overfishing and possibly even unexpected collapses of these strong stocks and other weaker stocks caught along with them (e.g. Figure 4.1B). This finding might be cause for concern in some fisheries, as strong stocks are often the main contributors to multispecies fishery profits, and are consequently often the central focus of assessment and management.

However, there are several possible solutions that can effectively eliminate this threat of overestimation and consequent overfishing that do not necessarily require abandoning single-species assessment frameworks. First, as I illustrate here, single-species assessment models can often reliably identify conditions under which bias in reference point estimates are likely. In particular, if it is estimated, within a single-species assessment framework, that $\left(\hat{F}_w/\hat{F}_{w,Extinct}\right) > \left(\hat{F}_s/\hat{F}_{s,\text{Reference Point}}\right)$ (where s denotes a strong stock and w denotes the stock estimated to be weakest – depleted at the lowest effort; where each is assessed separately using a single-species model), it is likely that $\left(\hat{F}_s/\hat{F}_{s,\text{Reference Point}}\right)$ is biased by a factor of up to $\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)/\left(\hat{F}_s/\hat{F}_{s,\text{Reference Point}}\right)$ (equation (4.3b)). The upper bound on bias in the reference point yield (e.g. MSY) can be calculated from the single-species assessment model used (e.g. equation (4.7a) for the logistic model, equations (4.12) for the Beverton-Holt model). More precise estimates of biases may be possible if competition strengths can be measured, though this is likely to be difficult in practice.

Systematic reference point estimation bias arises when some stocks are much more susceptible to overfishing from current practices than others, which is also the well-known weak stock problem (Hall et al. 2000; Gaines & Costello 2013). The condition for estimation bias demonstrated here, $\left(\hat{F}_w/\hat{F}_{w,Extinct}\right) > \left(\hat{F}_s/\hat{F}_{s,\text{Reference Point}}\right)$, implies that any solution that effectively addresses the weak stock problem (i.e. leads to balance in the exploitation rates of different stocks) also eliminates the potential for systematic overestimation of reference points in strong stocks. There have been several examples of recent success in reducing disproportionate depletion of weak stocks and by-catch species, using technological innovations (e.g. turtle excluder devices (Crowder et al. 1994)), and incentives (e.g. multispecies catch quotas) encouraging fishers to avoid spatial or temporal targeting behaviours that are associated with high catch of weak stocks and by-catch (Hall 2000; Cox et al. 2007; Branch & Hilborn 2008; Moore et al. 2009). My results suggest that such management successes, in addition to reducing threats of overfishing to weak stocks, are likely to have the added benefit of allowing for more reliable MSY estimation from strong stocks. There is also evidence that catch

balancing may lead to higher fishery yields and profits (Garcia et al. 2012; see also Chapter 5). Further research and advances in mitigating exploitation imbalances in multispecies fisheries is thus critical.

My results also add important insights to the small but growing literature on when single-species assessment models can reliably estimate yield-effort relationships, or more generally, the shape of realized density-dependence (Abrams 2009a), by abstracting multispecies reality. Both Abrams (2009b) and Tschirhart (2012) showed that switching and other dynamic behaviours, in models of either predation or competition, can lead to non-differentiable portions (i.e. sharp peaks or valleys) in yield-effort relationships, whereby the harvested population switches abruptly from one productivity regime to another. My analysis highlights the potential of weak stock collapses to create similar regime shifts for strong stocks with which they compete. The potential for such shifts in different harvests is important to understand, as they can lead to unexpected collapse if they occur at efforts beyond the range of historical observations. It is likely that weak stock collapses cause shifts in productivity regimes in many if not most types of ecosystems, but this has not yet been widely studied, and is an important area of future research.

Abrams (2009a,b,c) also showed that predators often have realized density-dependence relationships that have both concave and convex segments, leading to yield-effort relationships with multiple peaks (similar to Figure 4.4E,F) as a result of predator satiation and prey-density-dependence (Abrams 2009a), adaptive changes in prey behaviour (Abrams 2009b), or changes in apparent competition between multiple prey-types in response to increasing predator mortality-rates (Abrams 2009c). My analysis shows that opposing asymmetries in vulnerability (catch-rate/growth rate) and the strength of density dependence (i.e. strong stocks, with lowest vulnerability, have strongest density dependence) can produce similar patterns in less vulnerable competing species (strong stocks) (Figure 4.4E,F). This occurs because the 'strong' stock is in fact more easily depleted (i.e. weaker) at low efforts due to its stronger density-dependence. In effect, the two-peaked yield-effort relationship is caused by a reversal in which stock is stronger and which is weaker. Consequently, any other factor that could lead to

reversals in relative depletability among stocks along an effort gradient may also result in two-peaked yield-effort relationships in strong stocks. For example, if stocks with higher growth rates (r) also had more hyperstable catches (which would cause q to rise more quickly as abundance (N) declined), the stocks with lower growth rates and lower hyperstbility might be more easily depleted at low efforts (i.e. weaker) but less easily depleted at high efforts (i.e. stronger), leading to a two-peaked yield-effort relationship.

This study focuses on biases in single-species assessments driven by inter-specific interactions (competition in particular), but there may be other sources of bias. One that may be of particular concern is fishery-induced evolution, whereby fisheries impose selection pressures on the life histories of stocks, often towards smaller body size and earlier age at maturity (Hutchings & Fraser 2008). Fishery-induced evolution is thought to cause overestimation of the recovery potential of many depleted stocks (e.g. see Hutchings 1999; Olsen et al. 2004 for evidence in northwest Atlantic cod (*Gadus morhua*)).

Imbalances in exploitation rates of different species in multispecies fisheries pose threats to weak stocks and by-catch species by creating economic incentives to deplete them in order to obtain profits from stronger stocks (Burgess et al. 2013; Gaines & Costello 2013). This study illustrates how such imbalances also can lead to overestimation of the sustainable yields of strong stocks as a result of ecological competition. Together, these principles imply that misuse of single-species assessment models in multispecies fisheries could exacerbate the weak stock problem by creating misleading incentives to overfish in pursuit of phantom catches that evaporate when a weak stock collapses. Fortunately, as illustrated and discussed here, the potential for bias in single-species assessments in multispecies fisheries is both quantifiable and correctable within existing assessment and management frameworks.
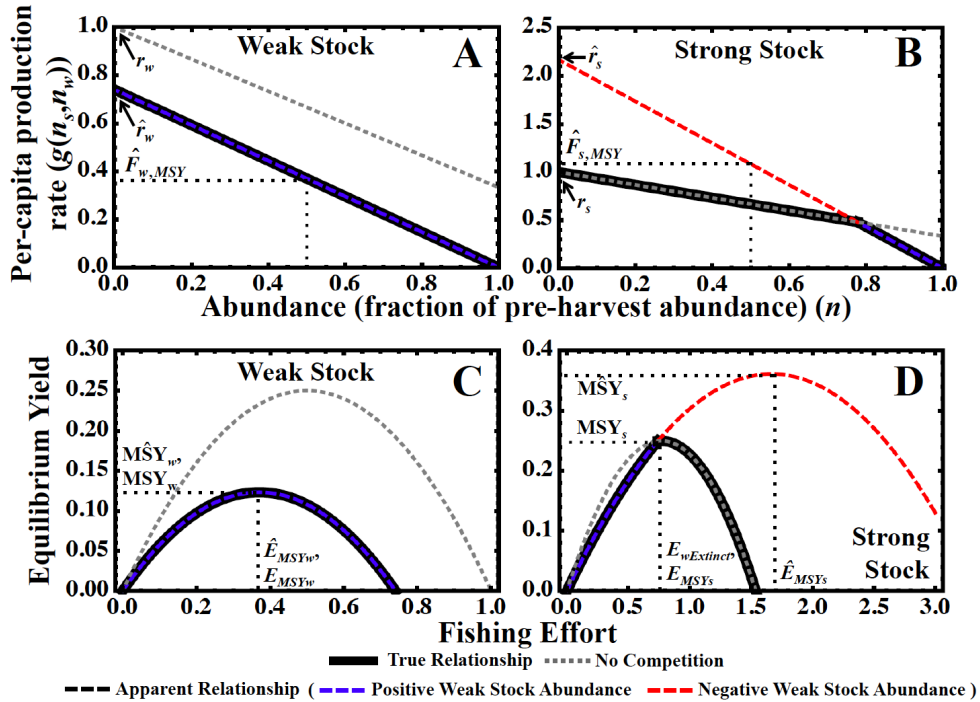
Figure 4.1. Apparent (red and blue dashed curves) and actual (black solid curves) (**A**, **B**) density-dependence (per-capita production vs. abundance) and (**C**, **D**) yield-effort relationships with competition, as well as yield-effort relationships, that would occur without competition (grey dotted curves), are shown in models with logistic growth, Lotka-Volterra competition, two stocks and one type of fishing. Blue sections of the apparent relationships indicate portions where the weak stock is extant; red sections indicate portions where the weak stock would have to have negative abundance for the predicted yields or per-capita production from the strong stock to be achieved. (**A**, **C**) and (**B**, **D**) show these relationships respectively for the weak and strong stock with parameter values: $\{r_w = r_s = q_w = 1, q_s = 0.65, c_{sw} = 0.5\}$. Under these parameter values, both the strong and weak stocks are driven extinct at lower fishing efforts than the effort that would be predicted, by fitting a single-species model, to produce MSY for the strong stock ($\hat{E}_{MSYs}$) (**B**, **D**).
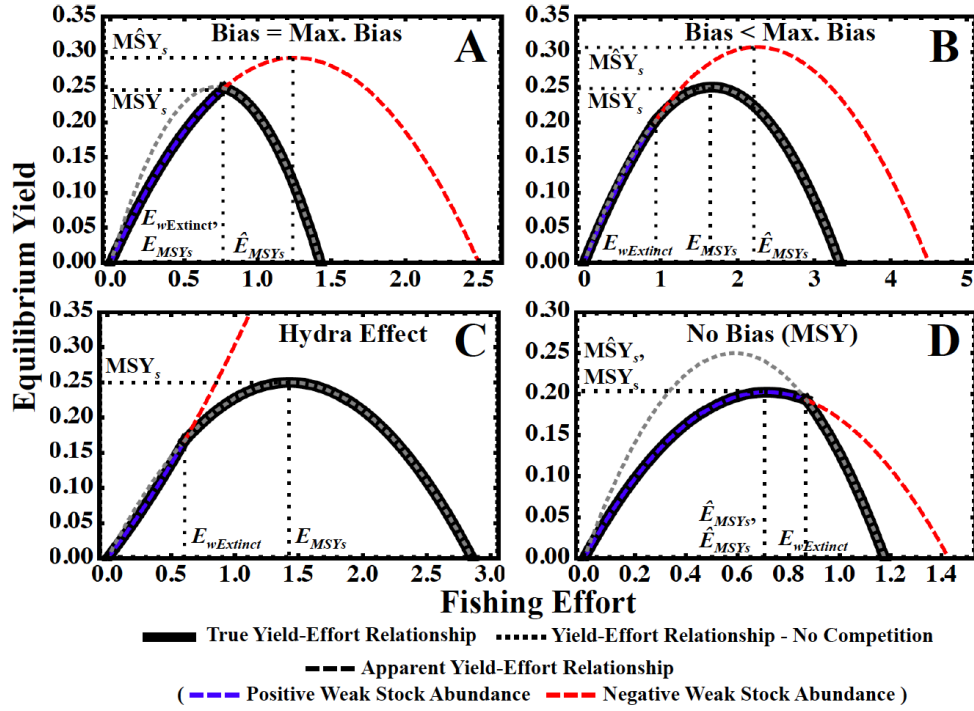
Figure 4.2. Apparent (red and blue dashed curves) and actual (black solid curves) yield-effort relationships with competition, as well as yield-effort relationships, that would occur without competition (grey dotted curves), are shown for the strong stock in two-stock models with logistic growth, and Lotka-Volterra competition. Blue sections of the apparent yield-effort relationship indicate portions where the weak stock is extant; red sections indicate portions where the weak stock would have to have negative abundance for the predicted yields to be achieved. The panels illustrate how the magnitude of biases in MSY estimates for the strong stock ($\hat{\text{MSY}}_s$) depend on the relative values of efforts causing extinction of the weak stock ($E_{wExtinct}$), true MSY for the strong stock (E_{MSYs}), and the effort predicted to produce MSY for the strong stock under the productivity regime in which the weak stock is extant ($\hat{E}_{MSYs}$). The maximum possible biases (given by equation 4.3) occur when true MSY occurs at the extinction effort of the weak stock (i.e. $E_{MSYs} = E_{wExtinct}$) (**A**), whereas biases are smaller than this maximum when $E_{MSYs} > E_{wExtinct}$ (**B, C**). (**C**) shows a hydra effect, whereby fishing effort increases the abundance of the strong stock while the weak stock is extant. MSY_s is estimated without bias (i.e. $\text{MSY}_s = \hat{\text{MSY}}_s$) (**D**) when the predicted MSY effort for the strong stock ($\hat{E}_{MSYs}$) is smaller than $E_{wExtinct}$. Parameter values are: $\{r_w = r_s = q_w = 1\}$ in all panels; (**A**): $\{q_s = 0.7, c_{sw} = 0.5\}$; (**B**): $\{q_s = 0.3, c_{sw} = 0.1\}$; (**C**): $\{q_s = 0.35, c_{sw} = 0.5\}$; (**D**): $\{q_s = 0.85, c_{sw} = 0.5\}$.
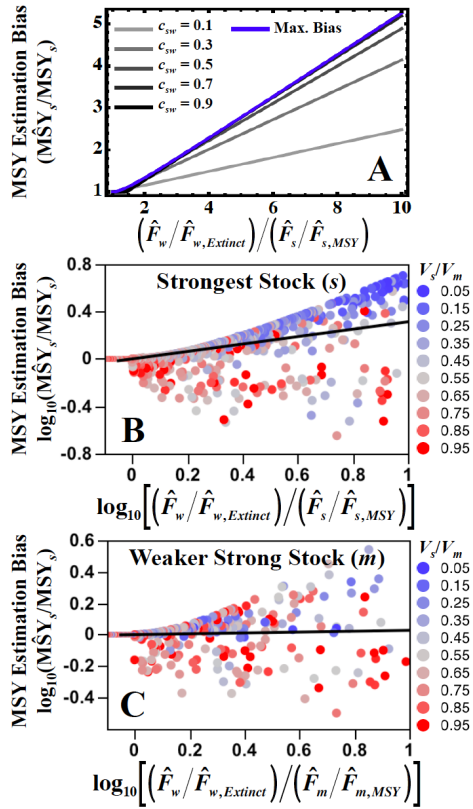
Figure 4.3. Panel (**A**) shows the exact (black and grey curves) and maximum (blue curve) biases in estimated strong stock MSY (M$\hat{S}$Y$_s$) in a two-stock model with logistic growth, Lotka-Volterra competition and a single type of fishing. With more than two stocks, single-species assessment models can either over- or underestimate strong stock MSY. Panels (**B**) and (**C**) show MSY estimation biases for (**C**) the strongest stock (*s*) and (**D**) the weaker strong stock, or medium stock (*m*) from 2000 randomly selected parameter sets ({$r_i = 1$, $q_i \sim U[0.3,1]$, $c_{ik} \sim U[0,0.9]$ for $i = 1,2,3$}, identities of strong, weak and medium stocks were determined by ranking apparent vulnerabilities, $\hat{V}_i$). Parameter sets with hydra effects are not shown as apparent MSY does not exist.

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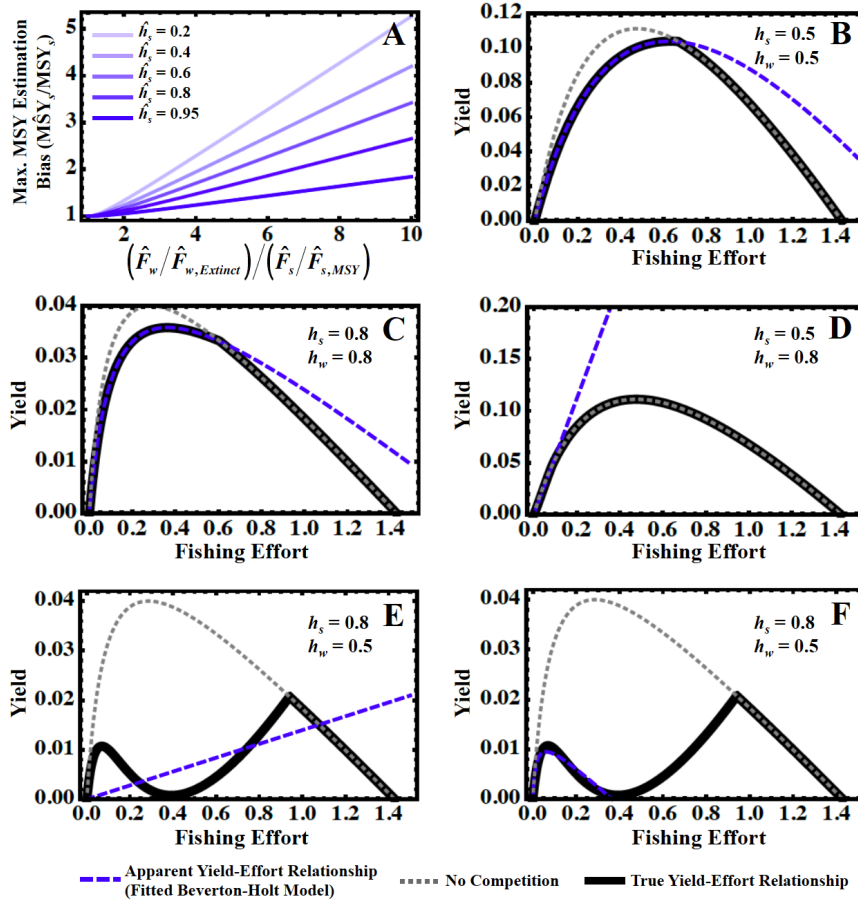
Figure 4.4. (**A**) shows predicted maximum biases in estimating strong stock MSY, MSY_s, using a Beverton-Holt model (from equations (4.12a)) at different levels of apparent steepness, $\hat{h}_i$. (**B**)-(**E**) show true (solid black curves), apparent (dashed blue curves), and no-competition (dotted grey curves) yield-effort relationships in 2-stock models with a single type of fishing and modified Beverton-Holt growth (equations (4.13)). The apparent relationships (blue dashed curves) shown are obtained from fitting the yield-effort relationship predicted by a single species Beverton-Holt model to the true yield effort relationships (solid black curves) over the range of at which the weak stock is extant, in all panels except (**F**), where the fit is performed over the range $E = \{0, 0.4\}$. Parameter values are: $\{r_w = r_s = q_w = 1, q_s = 0.7, c_{sw} = c_{ws} = 0.5\}$ for all panels, with steepness (h) values shown in the panels.

4.4 Supplementary Material

Appendix A – Analytical derivation of MSY estimation bias with Lotka-Volterra competition and assumed logistic growth (Figure 4.3A)

In a two-stock, single fishing type system, in which the true dynamics are governed by Lotka-Volterra competition (equation (4.8)), and MSY for each stock is estimated using a logistic growth model (equations (4.1)), the relationship between true MSY for the strong stock, MSY_s, and estimated MSY, $M\hat{S}Y_s$ (as illustrated by the black and grey curves in Figure 4.3A), is given by:

$$\frac{M\hat{S}Y_s}{MSY_s} = \begin{cases} 1, & \dfrac{\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)} \leq 1 \\[3em] \dfrac{\left(\dfrac{\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)}\right)^2}{\left(\dfrac{2\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)}-1\right)}, & 1 < \dfrac{\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)} \leq \dfrac{1}{1-c_{sw}} \\[3em] \dfrac{1+2c_{sw}\left(\dfrac{\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)}\right)}{\left(1+c_{sw}\right)^2}, & \dfrac{\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)} > \dfrac{1}{1-c_{sw}} \end{cases} \quad (4.S1)$$

The proof of this is as follows:

The yield effort relationship for the strong stock, when the weak stock is extant, is given by (from equation (4.2):

$$Y_s(E) = \hat{N}_{s0}\hat{q}_s\left(E - \hat{V}_s E^2\right) \quad (4.S2a),$$

where,

$$\hat{q}_s = q_s \quad (4.S2b),$$

$$\hat{r}_s = r_s\left[\frac{1-c_{sw}}{1-c_{sw}\left(V_w/V_s\right)}\right] \quad (4.S2c),$$

$$\hat{V}_s = \frac{\hat{q}_s}{\hat{r}_s} = V_s \left[\frac{1 - c_{sw}(V_w/V_s)}{1 - c_{sw}} \right] \quad (4.S2d),$$

$$\hat{N}_{s0} = \frac{K_s}{1 + c_{sw}} \quad (4.S2e).$$

The weak stock goes extinct at an effort, $E_{wExtinct}$ where,

$$F_{w,Extinct} = \hat{q}_w E_{wExtinct} = \hat{r}_w \quad (4.S3a),$$

and thus,

$$E_{wExtinct} = \frac{1}{\hat{V}_w} \quad (4.S3b).$$

Using similar logic, it can be shown that the predicted MSY effort for the strong stock (assuming no hydra effects), $\hat{E}_{sMSY}$ is given by:

$$\hat{E}_{MSYs} = \frac{1}{2\hat{V}_s} \quad (4.S4).$$

Similarly, the MSY effort if the weak stock is not present is $1/(2V_s)$, which is smaller than $\hat{E}_{MSYs}$ because $V_s < V_w$, which implies that $\hat{V}_s < V_s$. Because of this, if $E_{wExtinct} \geq \hat{E}_{MSYs}$, it must be the case that yield is a decreasing function of effort at higher efforts; and thus $\text{MSY}_s = \text{M}\hat{\text{S}}\text{Y}_s$ if $\left(\hat{V}_w/2\hat{V}_s\right) \leq 1$. Because fishing mortality, F, is proportional to fishing effort for both stocks, $\dfrac{\hat{V}_w}{2\hat{V}_s} = \dfrac{\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)}$ at any given effort level. Thus, $\text{MSY}_s =$

$\text{M}\hat{\text{S}}\text{Y}_s$ if $\dfrac{\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)} \leq 1$. If $\dfrac{\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)} > 1$, MSY_s will either be equal to the yield at

the effort level where the weak stock goes extinct (if $\dfrac{1}{\hat{V}_w} \geq \dfrac{1}{2V_s}$) or it will be equal to the

MSY that would be realized if the weak stock never existed (if $\dfrac{1}{\hat{V}_w} \leq \dfrac{1}{2V_s}$).

From equations (4.S2a) and (4.S3), the yield of the strong stock at the extinction effort of the weak stock is:

$$Y_s\left(E_{wExtinct}\right) = \left(\frac{K_s}{1+c_{sw}}\right)\left(\frac{\hat{q}_s}{\hat{V}_w}\right)\left(1-\frac{\hat{V}_s}{\hat{V}_w}\right) \quad (4.S5).$$

Substituting $\mathrm{M\hat{S}Y}_s = \hat{N}_{s0}\left(\frac{\hat{r}_s}{4}\right) = \left(\frac{K_s}{1+c_{sw}}\right)\frac{\hat{q}_s}{4\hat{V}_s}$ into equation (4.S5) gives:

$$Y_s\left(E_{wExtinct}\right) = 4\mathrm{M\hat{S}Y}_s\left(\frac{\hat{V}_s}{\hat{V}_w}\right)\left(1-\frac{\hat{V}_s}{\hat{V}_w}\right) \quad (4.S6).$$

Substituting $\dfrac{\hat{V}_w}{2\hat{V}_s} = \dfrac{\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)}$ in equation (4.S6) gives:

$$Y_s\left(E_{wExtinct}\right) = \mathrm{M\hat{S}Y}_s\left[\frac{\left[\dfrac{2\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)}-1\right]}{\left(\dfrac{\left(\hat{F}_w/\hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s/\hat{F}_{s,MSY}\right)}\right)^2}\right] \quad (4.S7).$$

The yield of the strong stock at the MSY it would reach without the presence of the weak stock, denoted $\mathrm{MSY}_{s,w\text{-}}$, is equal to $(r_sK_s/4)$, which, by equations (4.S2b,c), is equal to:

$$\mathrm{MSY}_{s,w-} = K_s\left(\frac{\hat{q}_s}{4\hat{V}_s}\right)\left[\frac{1-c_{sw}\left(V_w/V_s\right)}{1-c_{sw}}\right] \quad (4.S8).$$

From equations (4.S2b,c), it can be shown that:

$$\left(\frac{V_w}{V_s}\right) = \left[\frac{c_{sw}+\left(\hat{V}_w/\hat{V}_s\right)}{1+c_{sw}\left(\hat{V}_w/\hat{V}_s\right)}\right] \quad (4.S9).$$

Substituting equation (4.S9) into equation (4.S8) gives:

$$\mathrm{MSY}_{s,w-} = \mathrm{M\hat{S}Y}_s\left[\frac{\left(1+c_{sw}\right)^2}{1+c_{sw}\left(\hat{V}_w/\hat{V}_s\right)}\right] \quad (4.S10),$$

which is equivalent to:

$$MSY_{s,w-} = M\hat{S}Y_s \left[\frac{(1+c_{sw})^2}{1 + 2c_{sw}\dfrac{(\hat{F}_w/\hat{F}_{w,Extinct})}{(\hat{F}_s/\hat{F}_{s,MSY})}} \right] \quad (4.S11),$$

Thus, the true MSY, MSY_s, will be given by equation (4.S7) if $\dfrac{1}{\hat{V}_w} \geq \dfrac{1}{2V_s}$, and equation

(4.S11) if $\dfrac{1}{\hat{V}_w} \leq \dfrac{1}{2V_s}$. Equations (4.S2b,c) can also be used to show that the condition,

$\dfrac{1}{\hat{V}_w} \geq \dfrac{1}{2V_s}$, is equivalent to:

$$\frac{(\hat{F}_w/\hat{F}_{w,Extinct})}{(\hat{F}_s/\hat{F}_{s,MSY})} \leq \frac{1}{1-c_{sw}} \quad (4.S12).$$

Thus, the true strong stock MSY, MSY_s, is given by:

$$MSY_s = \begin{cases} M\hat{S}Y_s, & \dfrac{(\hat{F}_w/\hat{F}_{w,Extinct})}{(\hat{F}_s/\hat{F}_{s,MSY})} \leq 1 \\[4ex] M\hat{S}Y_s \left[\dfrac{\left[\dfrac{2(\hat{F}_w/\hat{F}_{w,Extinct})}{(\hat{F}_s/\hat{F}_{s,MSY})} - 1 \right]}{\left(\dfrac{(\hat{F}_w/\hat{F}_{w,Extinct})}{(\hat{F}_s/\hat{F}_{s,MSY})} \right)^2} \right], & 1 < \dfrac{(\hat{F}_w/\hat{F}_{w,Extinct})}{(\hat{F}_s/\hat{F}_{s,MSY})} \leq \dfrac{1}{1-c_{sw}} \\[6ex] M\hat{S}Y_s \left[\dfrac{(1+c_{sw})^2}{1 + 2c_{sw}\left(\dfrac{(\hat{F}_w/\hat{F}_{w,Extinct})}{(\hat{F}_s/\hat{F}_{s,MSY})} \right)} \right], & \dfrac{(\hat{F}_w/\hat{F}_{w,Extinct})}{(\hat{F}_s/\hat{F}_{s,MSY})} > \dfrac{1}{1-c_{sw}} \end{cases} \quad (4.S13),$$

from which equation (4.S1) follows.

Appendix B – Derivation of equation (4.12)

With a single age class, the predicted density-dependence of strong stock s, $\hat{g}_s(n_s)$, using a Beverton-Holt assessment model, is given by:

$$\hat{g}_s(n_s) = \frac{\left(1 - \hat{h}_s\right)\left(1 - n_s\right)}{\left(1 - n_s + \hat{h}_s\left(5n_s - 1\right)\right)} \quad (4.S14),$$

where $\hat{h}_s$ is the estimated steepness of strong stock s. The predicted maximum bias in $M\hat{S}Y_s$ is determined by the difference between $M\hat{S}Y_s$ and the predicted yield at an effort a fraction $\dfrac{\left(\hat{F}_s / \hat{F}_{s,MSY}\right)}{\left(\hat{F}_w / \hat{F}_{w,Extinct}\right)}$ of the estimated MSY effort, denoted $1/u$ below for ease of notation, where $u = \dfrac{\left(\hat{F}_w / \hat{F}_{w,Extinct}\right)}{\left(\hat{F}_s / \hat{F}_{s,MSY}\right)}$. The predicted yield as a function of effort is given by:

$$\hat{Y}_s\left(\hat{n}_s(E)\right) = \hat{N}_{s0} \bar{\hat{q}}_s \hat{n}_s(E) E \quad (4.S15),$$

where $\bar{\hat{q}}_s$ is the average estimated qs, weighted by relative efforts, and $\hat{n}_s(E)$ is the predicted equilibrium abundance at with total effort, E, found by solving the equation:

$$\hat{g}_s\left(\hat{n}_s(E)\right) = \bar{\hat{q}}_s E \quad (4.S16),$$

which defines equilibrium at effort E. Inserting the solution of equation (4.S16) into (4.S15) gives:

$$\hat{Y}_s(E) = \frac{\hat{N}_{s0} \hat{r}_s E \bar{\hat{V}}_s \left(1 - \hat{h}_s\right)\left(1 - E\bar{\hat{V}}_s\right)}{1 - E\bar{\hat{V}}_s + \hat{h}_s\left(5E\bar{\hat{V}}_s - 1\right)} \quad (4.S17),$$

where $\bar{\hat{V}}_s = \left(\dfrac{\bar{\hat{q}}_s}{\hat{r}_s}\right)$.

The predicted total effort, E, at MSY, $\hat{E}_{MSYs}$, can be calculated from equation (4.S17) to be:

$$\hat{E}_{MSYs} = \frac{\left(1 - \hat{h}_s\right) + 2\sqrt{\hat{h}_s\left(1 - \hat{h}_s\right)}}{\bar{\hat{V}}_s\left(5\hat{h}_s - 1\right)} \quad (4.S18).$$

Inserting equation (4.S18) into (4.S17) gives the predicted MSY:

$$\hat{MSY}_s = \frac{\hat{N}_{s0}\hat{r}_s\left(1-\hat{h}_s\right)\left(\sqrt{\hat{h}_s\left(1-\hat{h}_s\right)}-2\hat{h}_s\right)\left(\left(1-\hat{h}_s\right)-2\sqrt{\hat{h}_s\left(1-\hat{h}_s\right)}\right)}{\left(5\hat{h}_s-1\right)^2\sqrt{\hat{h}_s\left(1-\hat{h}_s\right)}}$$ (4.S19).

The actual MSY will be no smaller than the predicted yield at an effort $\hat{E}_{\mathrm{MSYs}}/u$, which is equivalent to:

$$\mathrm{MSY}_s \geq \frac{\hat{N}_{s0}\hat{r}_s\left(1-\hat{h}_s\right)\left(1-\hat{h}_s-2\sqrt{\hat{h}_s\left(1-\hat{h}_s\right)}\right)\left(1-u+\hat{h}_s(5u-1)-2\sqrt{\hat{h}_s\left(1-\hat{h}_s\right)}\right)}{u\left(5\hat{h}_s-1\right)^2\left(\left(1-u\right)\left(1-\hat{h}_s\right)-2\sqrt{\hat{h}_s\left(1-\hat{h}_s\right)}\right)}$$ (4.S20).

Dividing equations (4.S19) and (4.S20) gives equation (4.12a):

$$\frac{\mathrm{M\hat{S}Y}_s}{\mathrm{MSY}_s} \leq \frac{\left(\sqrt{\hat{h}_s\left(1-\hat{h}_s\right)}-2\hat{h}_s\right)\left(\left(1-\hat{h}_s\right)(1-u)-2\sqrt{\hat{h}_s\left(1-\hat{h}_s\right)}\right)u}{\sqrt{\hat{h}_s\left(1-\hat{h}_s\right)}\left(1-\hat{h}_s+\left(5\hat{h}_s-1\right)u-2\sqrt{\hat{h}_s\left(1-\hat{h}_s\right)}\right)}$$ (4.12a).
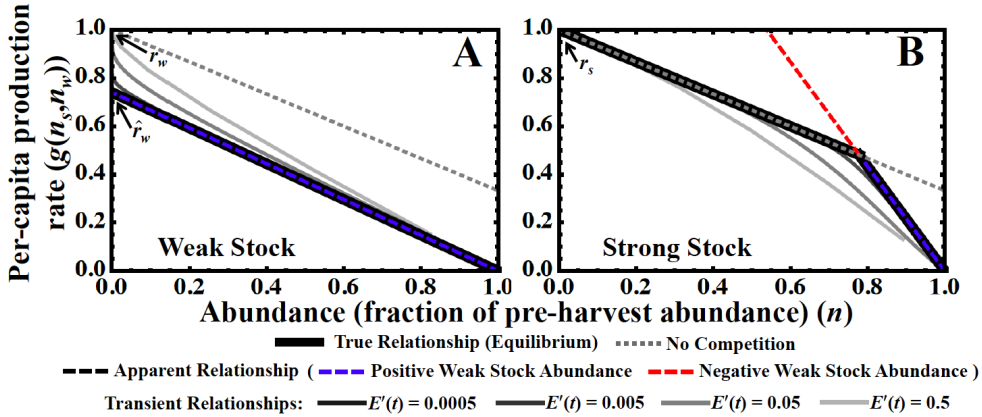
Figure 4.S1. A comparison of equilibrium (solid black curves) and transient (solid grey curves) density dependence relationships ($g_i(.)$ vs. n_i) in a weak stock (**A**) and a strong stock (**B**) having Lotka-Volterra competition and caught by a single fishing type with no other competitors. Parameter values are the same as in Figure 4.1 ({$r_w = r_s = q_w = 1$, $q_s = 0.65$, $c_{sw} = 0.5$}). Blue and red dashed curves illustrate apparent equilibrium density dependence in the presence of the weak stock (blue regions indicate the range of equilibrium abundances at which the weak stock is extant, red regions indicate strong stock productivities that would require negative weak stock abundance). Rapid fishery development (i.e. large $E'(t)$) results in more balanced transient depletion of the two stocks than would occur at successive equilibria, which results in weaker indirect competitive effects, and thus a strong stock that seems less productive (**B**) and a weak stock that seems more productive (**A**).

Chapter 5

Consequences of fleet diversification in managed and unmanaged fisheries

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Abstract.

Biological diversity is known to play an important role in generating and maintaining ecosystem productivity and other functions, and has consequently become a central focus of many efforts to preserve ecosystem services. Theoretical parallels suggest the diversity of fishing fleets may have a similarly important role in determining the productivity and ecological impacts of fisheries, but this possibility has rarely been explored. Here I present theoretical analyses showing that the diversity of métiers – combinations of technology and fishing grounds – and technical efficiencies in a fishing fleet can be important determinants of the productivity, profitability, and ecological impacts of fisheries, particularly mixed-stock or multispecies fisheries. Diversification of métiers can increase yields and reduce adverse ecological impacts in both managed and open-access multispecies fisheries. Diversification of technical efficiencies creates opportunities for larger profits in well-managed fisheries, but often decreases yields and worsens ecological impacts in open-access fisheries. These results suggest that the potential impact of management may be highest in fisheries with diverse fleets, highlighting the importance of managing large, international fisheries such as those targeting tunas.

5.1 Introduction

Biological diversity is widely considered to be an important driver of the productivity and stability of ecosystems and the services that they provide (McCann 2000; Loreau et al. 2001; Balvanera et al. 2006; Cardinale et al. 2006; 2011; Tilman et al. 2006, 2012; Worm et al. 2006; Palumbi et al. 2009; Isbell et al. 2011, 2013; Reich et al. 2012). In ecological communities of consumers, diversity leads to high productivity through complementarity effects, whereby species with different resource requirements are able to partition resources more efficiently (Tilman et al. 1997; Lehman and Tilman 2000; Loreau and Hector 2001; Thébault and Loreau 2003); and sampling effects, whereby more diverse communities are more likely to contain highly productive species by chance (Lehman and Tilman 2000; Loreau and Hector 2001; Thébault and Loreau 2003). Both of these effects cause consumer diversity to impact resource availabilities (Tilman et al. 1997). Diversity increases the stability of ecosystems' productivities and services through 'portfolio effects', whereby functional redundancies between species allow sudden perturbations affecting one species to be compensated by other similar species; and 'negative covariance effects', whereby sudden collapses in the abundance of a species lead to compensatory increases in the abundances of its competitors (Lehman and Tilman 2000; McCann 2000).

The role of biological diversity in promoting high and stable yields in fisheries has been well studied, with similar conclusions: Diverse aquatic ecosystems are generally thought to lead to more productive and stable fisheries (e.g. Worm et al. 2006; Schindler et al. 2010). The diversity of fishing fleets is also likely to play an important role in determining the productivity, stability, and ecological impacts of fisheries, but this has not been widely or systematically explored. Though there are strong theoretical parallels between fishers and ecological consumers, there are also some important differences. Fishers' behaviours and incentives can be complex and plastic, and can be influenced by management (Branch et al. 2006). Fisheries management can also have varying goals including profits, employment, food production, subsistence, recreation, and cultural value (Branch et al. 2006; Beddington et al. 2007; Worm et al. 2009; Chan et al. 2012). Fishers can vary widely in their technical efficiencies, and thus may not be bound to the

same types of tradeoff surfaces as many other organisms are hypothesized to be – where it has been suggested that differences among species in overall resource-use efficiency are minor compared to differences in resource specialization (Tilman 2011).

Fishing fleets can be diverse in a variety of ways. Fishers within a particular fishery may differ from one another in terms of their choice of fishing grounds, vessel sizes and gear-types, and target species; as well as their objectives, expert knowledge, behavioural plasticity, risk aversion, and other differences (Branch et al. 2005; 2006). Recent evidence from some fisheries suggests that certain types of fleet diversity create important opportunities for progress toward management objectives in certain situations. For example, in mixed-stock or multispecies fisheries, in which any particular gear-type is likely to catch multiple species or stocks (populations), management often faces the challenge of navigating tradeoffs between overexploiting slow-growing populations and under-exploiting more rapidly reproducing populations (Hilborn 1976; Boyce 1996; Hilborn et al. 2004; Burgess et al. 2013; Gaines & Costello 2013). Recent studies on multispecies trawl and groundfish fisheries in the E.U. (Marchal et al. 2011; Ulrich et al. 2011), United States (Dougherty et al. 2013), Canada and New Zealand (Sanchirico et al. 2006), and tuna fisheries in the Pacific (Sibert et al. 2012) have each found that management can overcome some of these tradeoffs at large spatial scales through management schemes that govern the allocation of fishing rights among fishers having different fishing grounds, gears or target species. In fisheries with diversity in economic efficiency, management using individual transferable quotas (ITQs) can increase fishery profits by encouraging the trading of fishing rights from low-efficiency fishers to high-efficiency fishers (Grafton et al. 2000; Marchal et al. 2011; Grainger and Costello 2012; Schnier and Felthoven 2013). Balancing exploitation across species in a marine ecosystem is generally thought lead to the highest combined yields and least adverse ecological impacts (Garcia et al. 2012). Fleet diversity is likely to have significant influence on exploitation balancing.

Here, I use a combination of general theoretical models and stochastic simulations to illustrate some important opportunities and pitfalls presented by fleet diversity to the yields, profits, and ecological objectives of managed and open-access fisheries.

Following recent bioeconomic literature, I consider fleet diversity in terms of two concepts: 1) 'métiers' (ICES 2003; Marchal et al. 2013) (also called 'fishing opportunities' (Branch et al. 2005)) – unique combinations of fishing gear and geographic targeting that have roughly uniform relative catch-rates of different stocks in a multispecies or multi-stock fishery; and 2) technical efficiency (Hilborn 1985b; Marchal et al. 2013) – which determines the costs at which fishers obtain particular catches at particular abundances.

Specifically, I provide theoretical evidence suggesting that: i) diversifying métiers in multispecies fisheries should often lead to higher yields and less overfishing in both managed and open-access fisheries – by creating opportunities to reduce tradeoffs between management objectives for different stocks and encouraging balanced exploitation under open-access via competition; and ii) diversifying technical efficiency should create opportunities for greater profits in managed fisheries, but lead to more severe depletions (and thus lower yields) in open-access fisheries also via competition. For brevity, my analysis focuses on equilibrium statics, and thus effects of fleet diversity on the temporal stability of yields, profits, stocks, and ecosystems, as well as other possible dynamic effects are not considered explicitly, but are discussed and deserve future study.

5.2 Defining fleet diversity

The analyses presented here use a 'fishing unit', defined as a group of fishers from a particular métier having a particular efficiency, as the base unit of fleet diversity. Métiers are defined in this analysis by their relative catch-rates of different stocks. Efficiency is defined by the costs of obtaining a particular set of catches at a particular set of stock abundances. Thus, a particular fishing unit's métier is defined by relative catchabilities (per-capita-per-unit-effort catch rates) for different stocks, while its efficiency is determined in combination by the magnitudes of stocks' catchabilities and the per-unit-effort costs of fishing.

Defining fishing effort in terms of unit costs (i.e. measuring effort in dollars instead of hooks, days, etc.) allows for a simple mathematical representation of métiers

and efficiency as components of catchability that are directly comparable across gear-types. Suppose S different fish stocks are caught in a fishery, and each stock has population size, $N_i(t)$ for stock i at time t, and a per-capita growth rate, $g_i(\mathbf{N}(t))$ for stock i, in the absence of fishing, where $\mathbf{N}(t) = (N_1(t), N_2(t), ..., N_S(t))$ (i.e. stocks may interact with one another). Suppose fishers in a particular fishing unit, j, are spending $E_j(t)$ (in dollars or some other monetary unit) on fishing effort and catch a fraction, q_{ij}, of individuals of stock i with each dollar spent (q_{ij} is the catchability of stock i in fishing unit j). Because relative catch-rates are the key distinguishing features of fishing units for the purposes of this analysis, it is instructive to consider q_{ij} constant for all stocks (i) and fishing units (j), and to consider changes in q_{ij} for any particular fisher – resulting from catch hyperstability (Harley et al. 2001), economies of scale (e.g. Squires and Kirkley 1991), or changing behaviour, for example – as transitions between fishing units. Thus, stock i, if only targeted by fishing unit, j, has a rate of change, $dN_i(t)/dt$ at time t, given by:

$$\frac{dN_i(t)}{dt} = N_i(t)\big(g_i(\mathbf{N}(t)) - q_{ij}E_j(t)\big) \quad (5.1a).$$

Stock i's price-per-individual caught is denoted, p_i, and I assume throughout this analysis that it is either constant or increasing as its harvest falls, $p_i = p_i(N_i(t))$ (i.e. $p_i'(.) \leq 0$ because harvest falls as population size (N) falls) (see Clark 1976, 1985; Courchamp et al. 2006), but does not increase enough to result in rising per-unit-effort revenues with decreasing abundance (i.e. $d[p_i(N_i)N_i]/dN_i > 0$ for all N_i, i is assumed) (see Appendix A in the Supplementary Material; Courchamp et al. 2006). The total profits of fishers in fishing unit j at time t, $\pi_j(t)$, are thus given by,

$$\pi_j(t) = E_j(t)\left(\sum_{i=1}^{S} p_i(N_i(t))q_{ij}N_i(t) - 1\right) \quad (5.1b).$$

Métiers and efficiency are defined mathematically by partitioning q_{ij} into two components: m_{ij} (where $\sum_i m_{ij} = 1$), a fraction representing the métier's catch rate of stock i relative to other stocks, and e_j, another constant representing fishing unit j's efficiency, such that $q_{ij} = m_{ij}e_j$. With this substitution, equations (5.1a) and (5.1b) become:

$$\frac{dN_i(t)}{dt} = N_i(t)\left(g_i(\mathbf{N}(t)) - m_{ij}e_jE_j(t)\right) \quad (5.2a)$$

$$\pi_j(t) = E_j(t)\left(e_j\sum_{i=1}^{S}p_i(N_i(t))m_{ij}N_i(t) - 1\right) \quad (5.2b).$$

It can be seen from equations (5.2a) and (5.2b) that $\{m_{ij}\}_{\forall j}$ captures the relative catch rates of different stocks by fishers in fishing unit j (i.e. its métier), and e_j captures the cost efficiency of catch in fishing unit j, controlling for relative catch rates and stock abundances (i.e. its technical efficiency).

5.3 Fleet diversity in managed fisheries

In managed fisheries, fleet diversity creates opportunities to increase yields and profits while also minimizing adverse ecological impacts. Diversity in efficiency creates opportunities for management to increase fishery-wide profits by implementing a policy that causes the most efficient fishers to take larger shares of the catch. Diversity in métiers in multispecies fisheries creates opportunities for management to reconcile profit- and yield-maximization with prevention of overfishing and other ecological objectives by increasing the available degrees of freedom in the relative aggregate catch rates of different stocks (Figure 5.1, Figure 5.S2).

With few different métiers in a multispecies fishery, profits, yields, and management goals for different stocks often tradeoff with one another as a result of fishers' lack of control over the relative catch-rates of different stocks in the fishery (Boyce 1996; Squires et al. 1998) (Figure 5.1a,b). As a result, it is often impossible to set a target catch or effort-quota that does not either over-exploit some stocks or under-exploit others (Figure 5.1b). However, a multispecies fishery with multiple métiers that are diverse in their relative catch rates can achieve a much wider range of combinations of exploitation rates and equilibrium abundances of its stocks. This is accomplished by influencing both total fishing effort and relative fishing efforts among métiers through management (Figure 5.1c).

To be precise, in a multispecies fishery with only a single métier, j, the set of possible equilibrium abundances of different stocks is constrained to a one-dimensional

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surface whose shape is largely determined by the stocks' relative catch rates in the métier and their relative population growth rates (Figure 5.1a,b; Burgess et al. 2013). I hereafter refer to this as the 'vulnerability constraint' of métier j, because the relative catch rates and population growth rates of stocks determine their relative 'vulnerabilities' to depletion by métier j (Burgess et al. 2013). For example, if all stocks have logistic population growth ($g_i(.) = r_i(1 - (N_i/K_i))$ for all i, where r_i is the maximum per-capita growth rate and K_i is the carrying capacity of stock i (Schaefer 1954)), then the equilibrium abundances, N_x^* and N_y^*, of any two non-extinct stocks, x and y, must satisfy:

$$\frac{\left(1 - \dfrac{N_x^*}{K_x}\right)}{\left(1 - \dfrac{N_y^*}{K_y}\right)} = \frac{\left(m_{xj}\middle/r_x\right)}{\left(m_{yj}\middle/r_y\right)} \quad (5.3).$$

Equation (5.3) defines the vulnerability constraint of métier j in this model, which is linear with a slope determined by the relative values of m_{ij}/r_i (normalized catchability/maximum growth rate) for different stocks (see also Holt 1977; Clark 1985). The shapes of vulnerability constraints under some other types of ecological assumptions are discussed in Appendix A, and illustrated in Figure 5.S1a-e.

In a multispecies fishery with multiple métiers, any desired combination of stocks' equilibrium abundances that lies in the region in population space bounded by the vulnerability constraints of the different métiers could be achieved by implementing a policy that influences both the total effort fishery-wide and relative efforts in different métiers (Figure 5.1c). This is illustrated mathematically in Appendix B. The space of possible sets of equilibrium stock abundances in a fishery has a dimensionality determined by the number of different métiers. Thus, it is highly unlikely that a particular target set of stock abundances in a managed fishery will be achievable if there are fewer métiers than stocks to be managed. This is also shown mathematically in Appendix B, and illustrated graphically in Figure 5.S2. Additionally, because the relative impacts of a métier on different stocks are determined by the relative vulnerabilities of stocks to the métier (m_{ij}/r_i in the logistic model) rather than simply their relative catch

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rates (m_{ij}), it is the diversity in relative vulnerabilities of stocks among métiers (i.e. differences in $\{(m_{ij}/r_i)\}_{\vee j}$ rather than $\{m_{ij}\}_{\vee j}$) that is particularly important in providing opportunities for yield and profit gains in managed fisheries.

   Figure 5.2a,b shows the results of stochastic simulations of a 5-stock fishery illustrating the opportunities that fleet diversity offers managed fisheries for increases in yields and profits, and reduction in weak stock collapses by avoiding the inter-stock tradeoffs common in multispecies fisheries. For simplicity, each stock is assumed to have logistic population growth and constant prices, though the qualitative results generalize to more complex models. Each simulation fixes the number of fishing units and randomly generates 500 parameter sets, $\{r_i, m_{ij}, e_j, K_i\}$ for all i and j (r_i, $(m_{ij}/r_i) \sim$ U[0,1] (m_{ij}'s are normalized after each draw to sum to 1); $e_j \sim$ U[1,10]; $K_i \sim$ U[10,100]; for simplicity, p_i is fixed at 1 for all stocks, as K_i already provides a randomly selected determinant of the relative values of the same per-capita catch rate from different stocks), and sets equilibrium fishing efforts, E_j^* for all j, in order to maximize either yield (Figure 4a) or profit (Figure 5.4b) from all 5 stocks combined. The maximum achievable yield (MAY) or profit (MAP) from the fishery as a whole, with each parameter, set is compared to the theoretical maximum yield (MTY; the sum of maximum sustainable yields (MSY) for all stocks) or profit (MTP) from the fishery given the stocks' ecological parameters and the bounds on efficiency placed on the random selection of fishing units. The average number of stocks persisting at the achievable maximum (MAY or MAP) is also reported. This procedure was repeated for both yield- (Figure 5.2a) and profit-maximization (Figure 5.2b), allowing métiers only, efficiencies only, or both to vary among fishing units within each random draw.

   As the theory predicts, diversifying métiers increased the average fishery-wide maximum achievable yields (Figure 5.2a) and profits (Figure 5.2b). Diversifying métiers also reduced the average frequency of stock extinctions required for yield- or profit-maximization (Figure 5.2a,b) by creating opportunities for management to avoid tradeoffs between overexploiting some stocks and under-exploiting others by influencing relative effort allocations among métiers. Diversifying efficiency increased fishery-wide achievable profits (Figure 5.2b), but had no effect on the achievability of yields (Figure

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5.2a) or stock extinction frequencies at the optima (Figure 5.2a,b). Results are qualitatively similar with m_{ij} and r_i drawn independently, but yields and profits increase more slowly with diversity of métiers, and saturate at higher diversities.

5.4 Fleet diversity in unmanaged fisheries

In an unmanaged, or 'open-access' fishery, effort levels are driven by profits and eventually determined by the conditions that make further effort unprofitable (Clark 1976) (Figure 5.3a). The impacts of fleet diversity on yields, profits, and stocks (Figure 5.4) are mediated by competition between fishers (Figure 5.3b,c,d). Competition tends to favour the most efficient fishers in the fishery (Figure 5.3b), and the likelihood of having high efficiency extremes in a fishing fleet increases with its diversity via a sampling effect (see Loreau & Hector 2001 for discussion of an analogous sampling effect contributing to the positive effect of biodiversity on ecosystem productivity). As a result, fleet diversification tends to lead to greater aggregate efficiency (Figure 5.4a), which allows profits at lower stock abundances and thereby tends to lead to decreases in long-term yields and increases in the frequency and severity of stock collapses (Figure 5.4b). Competition among fishers in different métiers tends to either favour métiers with more balanced exploitation rates (Figure 5.3c) or result in co-existence (Figure 5.3d), both of which lead to more balanced aggregate exploitation rates (Figure 5.4a), often resulting in higher yields and fewer stock collapses (Figure 5.4b). I illustrate these points mathematically below, graphically in Figure 5.3, and in stochastic simulations in Figure 5.4. Fleet diversity has little to no effect on long-term profits, because profits tend towards zero at any diversity of fishing units, provided that there is no monopoly or oligopoly in the fleet's ownership (Clark 1976).

To illustrate these points graphically and mathematically, I assume (following Clark (1976; 1985)) that fishing effort within an individual fishing unit increases when profits are positive, decreases when they are negative, and stays constant when profits are 0 (i.e. revenues are exactly equal to opportunity costs). In other words, I assume, for fishing unit j, that $dE_j(t)/dt < 0$ if $\pi_j(t) < 0$, $dE_j(t)/dt > 0$ if $\pi_j(t) > 0$, and $dE_j(t)/dt = 0$ if $\pi_j(t) = 0$. I do not make specific assumptions about the rate or manner in which effort

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adjusts to profit conditions. Thus, in a fishery catching S stocks with only a single fishing unit, j, equilibrium would occur at a set of stock abundances, $\mathbf{N}^{*j} = \{N_1{}^{*j}, \ldots, N_S{}^{*j}\}$, satisfying:

$$e_j \sum_{i=1}^{S} p_i\left(N_i^{*j}\right) m_{ij} N_i^{*j} = 1 \quad (5.4).$$

Equation (5.4) defines an $S - 1$ dimensional surface on which $\mathbf{N}^{*j}$ must lie, which I hereafter refer to as the 'profitability constraint' of fishing unit j. It is illustrated in Figure 5.3 under the assumption of constant prices (where it is linear) and in Figure 5.S1f under the assumption of increasing prices with decreasing abundance (where it is generally convex, see Appendix A). Its slope is determined by the métier (Figure 5.3c,d) and its position relative to the origin is determined by efficiency (Figure 5.3b). Equilibrium with a single fishing unit occurs at the intersection of its vulnerability and profitability constraints (Figure 5.3a).

Competition between fishing units for fish has strong parallels with ecological communities of consumers competing for resources, which have been extensively studied. One of the seminal results in ecological competition theory is that outcomes of competition depend largely on species' abilities to invade communities of their competitors – meaning that they have positive growth rates when they are rare and competitors are at equilibrium (MacArthur and Levins 1964; Levin 1970; Tilman 1980). As Tilman (1980) illustrates graphically and mathematically, if two species are competing and: i) each can invade the other's equilibrium, they co-exist; ii) one can invade the other's equilibrium, but not vice versa, the successful invader will competitively exclude the other; iii) neither can invade the other's equilibrium, one species will exclude the other, but which wins will depend on which establishes first or increases in abundance faster (called a 'priority effect'). The same principles apply to competing fishing units, except that it turns out that priority effects require fishers from different fishing units to receive different prices for the same catch, and are thus unlikely (see Appendix C, Figure 5.S3). There are some additional complexities when equilibria are not stable (e.g. see McGehee and Armstrong 1977; Armstrong and McGehee 1980), which I do not consider explicitly here for brevity. However, these complexities do not

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affect the general principle that outcomes of competition are driven by species' (or analogously, fishing units') abilities to invade each other's established populations (Armstrong and McGehee 1980), and thus should also not affect the qualitative results I present concerning the effects of diversity of métiers and efficiency on yields and ecological outcomes.

As illustrated in Figure 5.3b, competition favours efficiency because more efficient fishers can still make profits at stock abundances resulting in zero profits for less efficient fishers within the same métier. This can be easily shown by substituting e_k ($e_k >$ e_j) into equation (5.4) for e_j, which would transform the equation to an inequality (i.e. $\pi_k(\mathbf{N}^{*j}) > 0$). Similarly, less efficient fishers make negative profits at the equilibria of more efficient fishers of the same métier ($\pi_j(\mathbf{N}^{*k}) < 0$), which would eventually force them to exit the fishery. Because competition favours efficiency, and because increasing diversity increases the likelihood of sampling high efficiency extremes, increasing fleet diversity should increase the aggregate efficiency of open-access exploitation, on average, though the diversity of active vessels would eventually decline as inefficient vessels exited the fishery.

A high diversity of métiers is more likely to lead to balanced exploitation of the stocks in a fishery than a low diversity of métiers for two reasons: 1) competition among fishers with equal efficiency tends to favour those in métiers with more balanced exploitation of the different stocks (Figure 5.3c); and 2) competitive co-existence between fishers in two different métiers leads to aggregate relative exploitation rates among stocks that are intermediate to those that would be produced by each métier individually (Figure 5.3d). Specifically, in a fishery in which all fishing units have the same efficiency and all m_{ij} between 0 and 1 are technologically feasible for any stock, i, (i.e. all possible métiers are feasible) competition among infinitely diverse métiers results in relative equilibrium abundances, N_x* and N_y*, of any two extant stocks, x and y, satisfying:

$$p_x\left(N_x^{\,*}\right)N_x^{\,*} = p_y\left(N_y^{\,*}\right)N_y^{\,*} \quad (5.5),$$

In other words, all extant stocks have relative equilibrium abundances equal to the inverse of their equilibrium price-ratios (i.e. $(p_x^*/p_y^*) = (N_y^*/N_x^*)$, where $p_i^* = p_i(N_i^*)$).

This occurs because: i) in a fishery in which all fishers are equally efficient, there exists a métier that can invade any equilibrium point not satisfying equation (5.5) (e.g. métier 2 in Figure 5.3c); and ii) co-existence among multiple fishing units occurs at equilibrium stock sizes at the intersection of their profitability constraints (Figure 5.3d), and all possible profitability constraints with a particular efficiency intersect at a single point, at which equation (5.5) is satisfied (Figure 5.3c,d). Point ii) follows from equation (5.4). To illustrate point i), suppose a fishery in which all fishers have the same efficiency is at an equilibrium, $\mathbf{N}^* = \{N_1^*,\ldots, N_S^*\}$, not satisfying equation (5.5). This implies that there is at least one pair of stocks, x and y, with the property $p_x(N_x^*)N_x^* > p_y(N_y^*)N_y^*$. Given this fact, any new fishing unit, k, with the property relative to any established fishing unit, j, that $m_{xk} > m_{xj}$, $m_{yk} < m_{yj}$, and $m_{ik} = m_{ij}$ for all $i \neq x,y$, will have positive profits at this equilibrium, and thus be able to invade the fishery. Moreover, the invasion of fishing unit k would increase the overall mortality rate of stock x relative to stock y, which would reduce N_x^* relative to N_y^*. Assuming that $d[p_i(N_i^*)N_i^*]/dN_i^* > 0$ ($i = x, y$) (i.e. revenues from any stock are positively related to its abundance), this would decrease the difference between $p_x(N_x^*)N_x^*$ and $p_y(N_y^*)N_y^*$, which would iteratively lead to equation (5.5) being satisfied at infinite diversity.

Putting the results concerning efficiency and balanced exploitation together: In an open-access fishery where all métiers are feasible for any efficiency up to a maximum efficiency, e_{MAX}, and métiers are independent of efficiencies, infinite fleet diversity results in an equilibrium, denoted $\mathbf{N}^{**e_{MAX}}$, at which equation (5.5) holds for all extant stocks, and all are exploited with efficiency e_{MAX}. To be precise, $\mathbf{N}^{**e_{MAX}} = \left\{N_1^{**e_{MAX}},\ldots,N_S^{**e_{MAX}}\right\}$ solves (from equations (5.4) and (5.5)),

$$p_i\left(N_i^{**e_{MAX}}\right)N_i^{**e_{MAX}} = \frac{1}{e_{MAX}} \quad (5.6),$$

for all extant stocks. This is illustrated in a stochastic simulation of a fishery targeting two stocks having logistic growth and constant prices in Figure 5.4a (see caption for

parameter values/distributions). As fleet diversity increases, the distribution of equilibria converges toward $\mathbf{N}^{**e_{MAX}}$ (Figure 5.4a).

Of course, the convergence of stock sizes, as a result of fleet diversification, to the equilibrium, $\mathbf{N}^{**e_{MAX}}$, described by equation (5.6), depends on the assumption that efficiencies are distributed independently from métiers (i.e. e_{MAX} is the same for all métiers). In reality, however, this is not likely to be the case. For example, if some stocks are generally easier or cheaper to catch than others due to their range or ecology, métiers with higher relative catch rates of these stocks are likely to be more efficient. One simple way to consider this in the modeling framework presented here is to let $q_{ij} = e_j a_i m_{ij}$, where e_j measures the overall efficiency of fishing unit j that is independent of its target stock, and a_i ($a_i > 0$) measures how easy stock i is to catch relative to other stocks. With this definition of q_{ij}, increasing fleet diversity in a fishery with maximum efficiency, e_{MAX}, will drive equilibrium stock abundances towards an equilibrium, $\mathbf{N}^{**e_{MAX}}$, described by:

$$p_i\left(N_i^{**e_{MAX}}\right)a_i N_i^{**e_{MAX}} = \frac{1}{e_{MAX}} \quad (5.7),$$

where $p_x\left(N_x^{**e_{MAX}}\right)a_x N_x^{**e_{MAX}} = p_y\left(N_y^{**e_{MAX}}\right)a_y N_y^{**e_{MAX}}$ for any two stocks, x and y. Thus, the general results are that a diversification of métiers will tend to drive stocks to be exploited to relative abundances at which they generate equal marginal revenue for equally efficient classes of technology, and diversification in efficiency will tend to broadly decrease stocks' abundances.

By promoting balanced exploitation, diversification of métiers typically leads to higher yields and reduces the likelihood of weak stock collapses. In contrast, diversification of efficiency typically reduces yields and increases the likelihood of weak stock collapses by promoting high aggregate efficiency. These points are illustrated in Figure 5.4b in a stochastic simulation of the same 2-stock fishery as in Figure 5.4a (see caption for parameter values/distributions).

Provided efficiency is finite, $\mathbf{N}^{**e_{MAX}}$ will occur at a positive abundance (equation (5.6)/(5.7), Figure 5.4a). Thus, the effect diversifying métiers reducing the likelihood of weak stock collapses will typically dominate the opposite effect of diversifying

efficiency, meaning that broad increases in fleet diversity should generally reduce the threat of weak stock collapses, as is the case in the simulated example in Figure 5.4b. However, whether the positive effect of diversifying métiers on equilibrium yield dominates the negative effect of diversifying efficiency will be context-dependent – driven largely by the maximum feasible efficiency, e_{MAX}. If e_{MAX} is sufficiently large, as in the simulated example in Figure 5.4b, the effect of métier diversification increasing yield dominates at very low fleet diversity, but the efficiency effect dominates at higher diversity as the métier effect saturates. However, the effect of diversifying métiers can dominate at high fleet diversity if e_{MAX} is sufficiently small.

While these results should generalize to most types of fleets and fished stocks, there are some important exceptions. In particular, as discussed in Appendix D and illustrated in Figure 5.S4, diversification in either métiers or efficiency often leads to the collapse of stocks whose non-substitutable prey or mutualists are also caught in the fishery; and diversifying métiers can sometimes increase the likelihood of stock collapses in fisheries where technological limitations make some relative catch-rates infeasible. Additionally, any stock whose price can rise fast enough to increase the revenues it generates as its abundance falls (i.e. $\mathrm{d}[p_i(N_i)N_i]/\mathrm{d}N_i < 0$ for stock i) is likely to be fished to extinction in general (Courchamp et al. 2006), but diversifying métiers or efficiency can also increase the chances of this (see Appendix A).

For by-catch populations, having little or no commercial value, the effect of diversifying métiers on the likelihood of collapse depends on the range of feasible relative catch rates and the way in which by-catch rates impact the efficiency of catching commercially valued stocks. If by-catch comes at an efficiency cost, then diversifying métiers would be expected to reduce impacts on by-catch species, as low-by-catch métiers would be favoured by competition. In contrast, if by-catch mitigation comes at an efficiency cost, then diversifying métiers in an open-access fishery would have the opposite effect, increasing the impacts on by-catch species. Diversifying métiers could similarly increase impacts on by-catch species if low-by-catch technologies were infeasible.

5.5 Discussion

This study presents two broad theoretical results: I) Diversifying métiers in multispecies fisheries often leads to higher yields and less overfishing in both managed and open-access fisheries – by creating opportunities to reduce tradeoffs between management objectives for different stocks and encouraging balanced exploitation under open-access. II) Diversifying technical efficiency creates opportunities for greater profits in managed fisheries, but tends to lead to more severe depletions (and thus lower yields) in open-access fisheries. Together, these results suggest that the potential value of transitioning from open-access to management in a fishery often increases with the diversity of its fleet.

The results concerning managed fisheries follow directly from the principle that more diverse fleets give managers more possible combinations of relative catch rates and costs (i.e. more degrees of freedom), with which they can more effectively balance objectives for different stocks and minimize costs, through controls influencing both total fishery-wide effort and relative efforts among different types of fishers. The results concerning open-access fisheries follow from the following principles of competition among fishers: i) All else equal, fishers with high technical efficiency (i.e. they obtain catches at low costs relative to other fishers, with stock abundances being equal) will tend to outcompete less efficient fishers, and high efficiency extremes are more likely to be sampled in a diverse fishery. ii) If a particular fishing fleet is exploiting commercially valued stocks highly asymmetrically relative to their prices and abundances, and technology exists to adopt an alternate fishing practice that better targets a currently underexploited stock, someone will eventually adopt this practice and profitably enter the fishery, increasing the overall fishing pressure on the previously underexploited stock relative to others (i.e. balancing exploitation) as a result. Greater diversity in fishing technology increases the likelihood, again because of a sampling effect, that technology will exist to exploit such economic opportunities. iii) Métiers with highly different catch profiles (relative catch-rates among stocks) compete less, and are likely to coexist in a fishery, resulting in relative aggregate catch rates among stocks that are intermediate to those each métier would produce on its own (e.g. Figure 5.3d). Greater diversity in

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métiers increases the likelihood of sampling catch profiles across the full range, thus more likely resulting in balanced aggregate exploitation.

Though these principles, and the results (I) and II)) that they imply, are illustrated mathematically in this paper using simplifying assumptions that may be unrealistic – notably: a) that fleet diversity can be partitioned into discrete fishing units, each with uniform relative catch rates and efficiency; and b) that open-access equilibria are stable enough for basic equilibrium-based competition results in theoretical ecology (Tilman 1980; see Armstrong and McGehee 1980) to hold – they are likely to be far more general. Similar theoretical simplifications have been used, for example, to conceptually illustrate some of the mechanisms underlying positive relationships between biodiversity and ecosystem productivity (e.g. Tilman et al. 1997), which have proven to be highly robust both theoretically and empirically to added complexities (see Cardinale et al. 2006, 2011 respectively for recent meta-analysis and review).

Thus, these model simplifications (a) and b) above) should be thought of as conceptual tools for understanding broad results, rather than accurate descriptions of reality. It is likely that many open-access fisheries have unstable or cyclic dynamics. Relative catch rates – the defining characteristic of métiers – and technical efficiency are likely to vary continuously, such that no two fishers are identical. However, there is empirical evidence that métiers can be grouped somewhat discretely into groups of vessels with highly similar relative catch rates (Branch et al. 2005), and it is possible that the same is true for efficiency. For example, vessels of similar size with similar distances between ports of origin and fishing grounds may have similar fuel and labour costs. Thus, the fleet diversity that is important in practice is likely to be the number of these different semi-discrete vessel 'types', and more importantly, how different they are from one another in their efficiency and relative catch rates.

Recent studies provide some empirical support for the benefits of diversity in métiers in managed and open-access fisheries. For example, Dougherty et al. (2013) showed, theoretically and in simulations of western U.S. groundfish fisheries, that setting multispecies harvest quotas at a local scale to achieve coast-wide goals could increase overall fishery yields without increasing the likelihood of collapsing any of the stocks. If

métiers vary spatially due to the varying juxtapositions of species' ranges on different fishing grounds, the type of management Dougherty et al. (2013) propose is equivalent to regulating the relative efforts in different métiers. Similar results have also been found for other multispecies fisheries in the E.U. (Marchal et al. 2011; Ulrich et al. 2011), Canada and New Zealand (Sanchirico et al. 2006), and Western and Central Pacific tuna fisheries (Sibert et al. 2012). Burgess et al. (2013) provide evidence suggesting that the diversification of métiers in Western and Central Pacific tuna fisheries resulting from the expansion of industrial deep-set longline, purse-seine and pole-and-line fishing methods reduced the long-term threat of collapse posed by these fisheries to many tuna and billfish populations by tending to increase the balance in their exploitation rates. Garcia et al. (2012) provided evidence for the benefits of catch balancing to yields, profits, and the ecological impacts of fisheries in simulations of several marine ecosystems.

There is also some empirical support for the ideas that fishers with high technical efficiencies can competitively dominate diverse fleets and increase overfishing, and that management can exploit differences among fishers' technical efficiencies to increase fishery-wide profits. For example, Schnier and Felthoven (2013) found that the introduction of individual transferable quotas (ITQ) in the Bering Sea and Aleutian Island crab fishery increased the likelihood of inefficient fishers exiting the fishery. This is consistent with theory suggesting that rights-based fishery management leads to fishery-wide efficiency by incentivizing the redistribution of fishing effort to more efficient fishers (Grafton et al. 2000). Similar results have been seen in other fisheries (e.g. Weninger 1998; 2008; Brandt 2007; Costello et al. 2010; Grainger and Costello 2012). In open-access fisheries, the rise of industrial fishing in the mid-20th century and subsequent wide-spread fishery collapses (e.g. Myers and Worm 2003; Pauly et al. 2005; Worm et al. 2006; 2009) is evidence of the ability of efficient fishers to competitively dominate fisheries, and the increases in ecological risk associated with efficiency gains.

Though the results presented here suggest that management is likely to face fewer tradeoffs between yield- or profit-maximization and species conservation in diverse fleets, it is important to note that the structures of some food webs may make such tradeoffs difficult or impossible to overcome, regardless of fleet diversity. For example,

if a fishery targets both a predator and its prey, maximizing yield or profit across the whole fishery might require the elimination of the predator to increase prey catches. Matsuda and Abrams (2006) explore such tradeoffs in detail and outline several instructive examples. Similarly, as discussed in Appendix D, diversification of either métiers or efficiency in open-access fisheries may exacerbate indirect threats from fisheries to some specialist predators and mutualists. The vulnerability of top predators and other marine species to fishing-induced trophic cascades has been extensively documented both empirically (e.g. Estes et al. 1998; Pauly et al. 1998; Jackson et al. 2001; Frank et al. 2005; Essington et al. 2006; Myers et al. 2007) and theoretically (e.g. May et al. 1979). In addition, the introduction to a fishery of gears that have adverse impacts on the ecosystem in addition to the harvest itself (e.g. habitat destruction by trawls) may in some cases have negative impacts on the productivity of the fishery that outweigh the benefits of additional fleet diversity. Ecosystem-based fishery management (Pikitch et al. 2004) or other holistic approaches to fishery management may be particularly important in large fisheries with diverse fleets.

The focus of my analysis of open-access fisheries on equilibrium statics rather than dynamics did not allow the analysis to consider the possibility of transient stock collapses, effects of fleet diversity on the temporal variance in yields and profits, or the stability of fished ecosystems. Fleet diversity likely plays an important role in determining the stability of fishing yields and profits, and fished stocks. Ecological theory suggests that increasing biological diversity decreases the stability of individual species' populations (May 1973), but increases the stability of aggregate ecosystem services such as productivity (Lehman and Tilman 2000). This suggests that increasing fleet diversity may analogously destabilize the populations of individual stocks or the profits of fishers in individual fishing units, but may increase the stability of fishery-wide yields and profits. Recent evidence from California Current fisheries suggests that fisheries can indeed destabilize individual fish populations (Hsieh et al. 2006; Anderson et al. 2008). By decreasing the stability of individual stocks, increasing fleet diversity may also increase the likelihood of transient stock collapses. The effects of fleet

diversity on the stability of the economic and ecological impacts of fisheries merit further study.

5.6 Conclusion

Fisheries are an important global provider of food, employment, and other social benefits (Beddington et al. 2007; Worm et al. 2009; Costello et al. 2012a; Chan et al. 2012), but also have large and increasing ecological impacts (Worm et al. 2006, 2009; Costello et al. 2012b; Halpern et al. 2012; Ricard et al. 2012). With global fish demand rising (Delgado et al. 2003) and global protein demand expected to double in the next half-century (Tilman et al. 2011), fisheries management faces the delicate challenge of providing the highest possible levels of sustainable production at the lowest possible ecological cost. The theory presented here, for which there is some empirical support in the literature, broadly suggests that diversifying métiers can have positive impacts on the yields and ecological sustainability of both managed and open-access multispecies fisheries. My analysis also suggests that the potential of management to improve fisheries' socio-economic and ecological outcomes relative to open-access is likely to be highest in diverse fishing fleets. Large international fishing fleets targeting widespread or migratory stocks, such as those targeting tunas, are likely to be some of the most diverse, but are also some of the most difficult to manage (Beddington et al. 2007; Worm et al. 2009). Continued advances in the management of these fisheries will be critical to ensuring the long-term sustainability of the socioeconomic benefits of fisheries and the ecosystems that support them. In the meantime, continuing to diversify métiers in multispecies fisheries may reduce threats to some weak stocks even without management (e.g. Burgess et al. 2013).
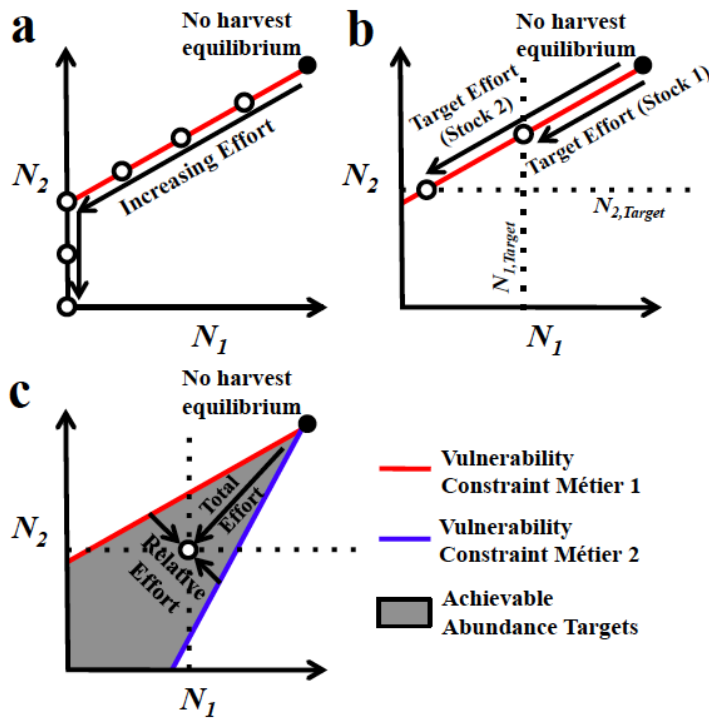
Figure 5.1. Total and relative efforts and achievable abundances in managed fisheries. (**a**) With a single métier in a fishery, stocks' relative equilibrium abundances are constrained (the vulnerability constraint (red line)) by their relative vulnerabilities to the métier. (**b**) As a result, with few métiers in a multispecies fishery it is often impossible to simultaneously achieve target abundances for multiple stocks, instead trading off overexploiting some with under-exploiting others. (**c**) With multiple métiers, management influencing both their relative and total effort levels can produce any set of equilibrium stock abundances within the region (shaded) bounded by the vulnerability constraints each would produce in isolation (red and blue lines).
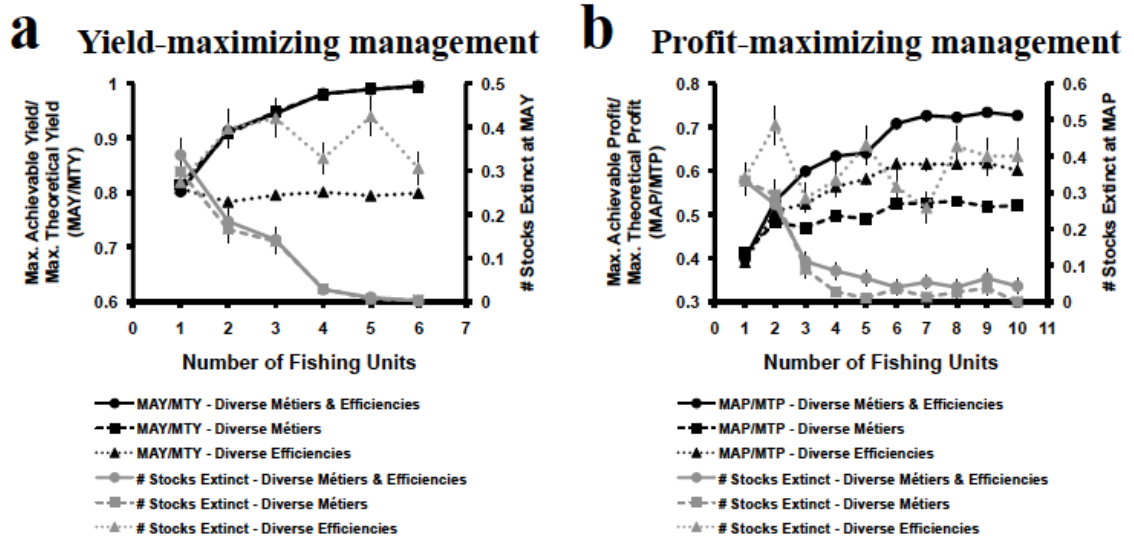
Figure 5.2. Fleet diversity increases achievable yields and profits in managed fisheries. Results of a 5-stock stochastic simulation of average relationships between fleet diversity and achievable yields and profits with (**a**) optimal management for obtaining maximum achievable yield (MAY) and (**b**) optimal management for obtaining maximum achievable profit (MAP). Average maximum achievable (**a**) yields (MAY) and (**b**) profits (MAP) are shown (black) along with the average number of extinctions achieving MAY or MAP requires (grey). Each point represents a sample of 500 models with randomly chosen parameter values. Vertical lines indicate standard errors.
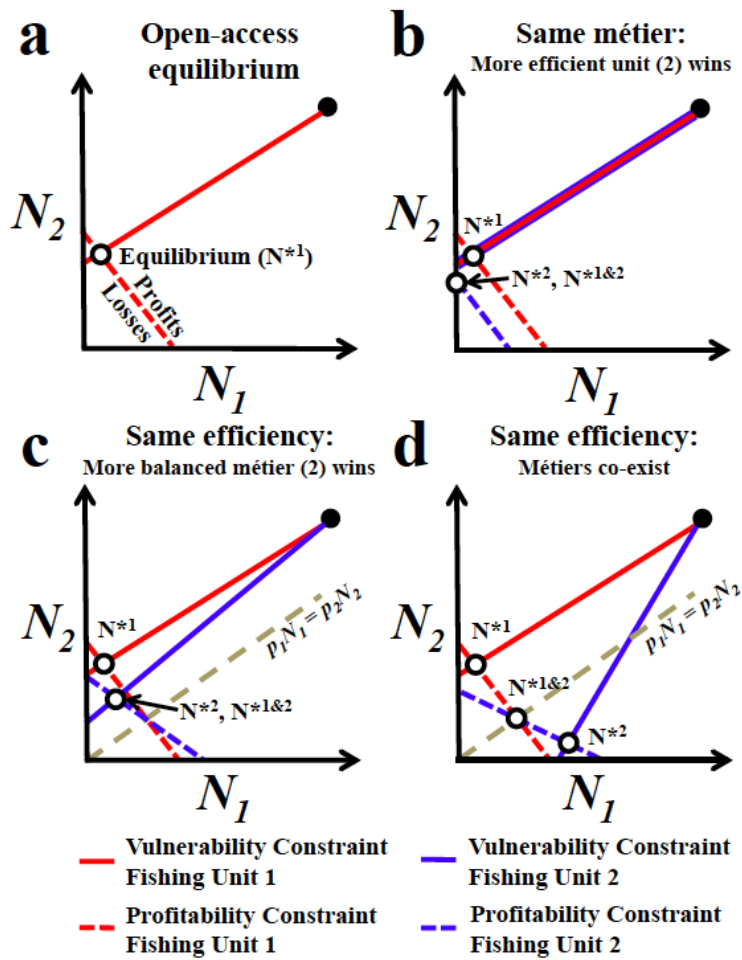
Figure 5.3. Competition in open-access fisheries. (a) With one fishing unit, equilibrium occurs at the intersection of the vulnerability constraint and profitability constraints (N^{*1} for fishing unit 1). **(b)** If fishers are in the same métier, more efficient fishers will outcompete less efficient fishers (competitive equilibrium is denoted $N^{*1\&2}$). **(c)**, **(d)** As métiers diversify with equal efficiency, equilibrium abundances will tend toward equalization of price*abundance is equal for all stocks (tan dashed line), either via **(c)** competitive exclusion, **(d)** co-existence, or both. The profitability constraints of all fishing units with equal efficiency (red and blue dashed lines in **(c)** and **(d)**) intersect at a single point where price*abundance is equal for all stocks (as drawn, $p_2 > p_1$).

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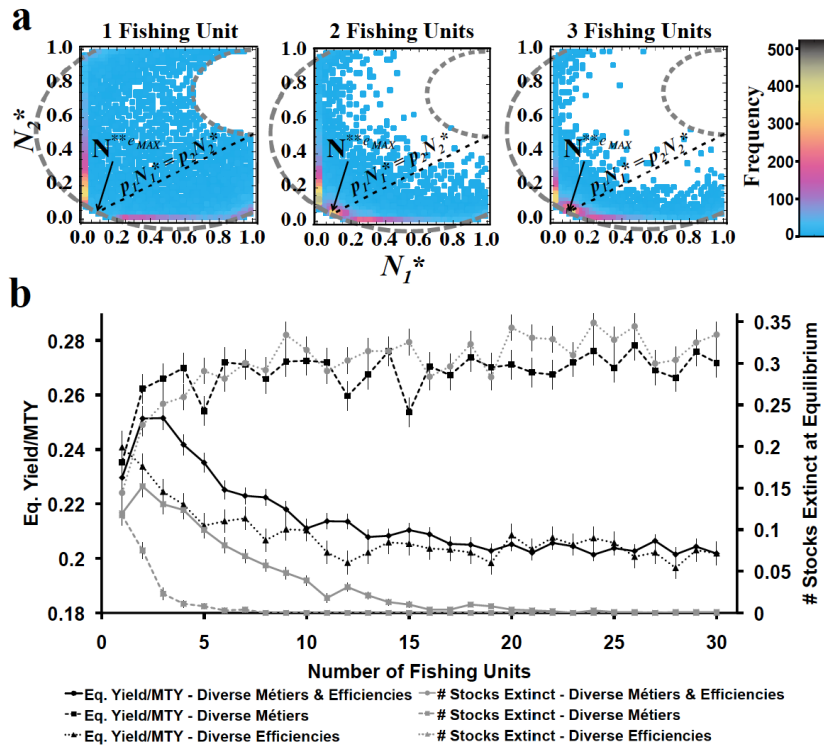**Figure 5.4. Consequences of fleet diversification in open-access fisheries.** (**a**) A stochastic simulation showing the frequency distribution of equilibria (**N***) in a 2 stock fishery in which 1, 2, and 3 fishing units respectively (from left to right) were randomly drawn 15 000 times from a uniform distribution of all possible métiers ($m_{ij} \sim U[0,1]$) and a bounded range of efficiencies ($e_j \sim U[1,12]$). Stocks were assumed to have logistic growth with r_i, $K_i = 1$ for $i = 1, 2$ and $p_1 = 1$, $p_2 = 2$. Grey lines represent all possible intersections of vulnerability and profitability constraints for the most (large dashes) and least (small dashes) efficient fishers. As a result of competition among fishers, increasing fleet diversity increases causes the probability of having the most efficient possible exploitation and stock abundances where price*abundance are equal at equilibrium ($\mathbf{N}^{**e_{MAX}}$, intersection of grey and black dashed lines) approaches 1. (**b**) A stochastic simulation with the same parameter values and distributions as (**a**), where each of 1 to 30 fishing units are drawn randomly 1000 times, with métiers and efficiencies varying separately and jointly. When only métiers vary, diversification leads to higher yields (black) and fewer extinctions (grey) on average by balancing exploitation. When only efficiencies vary, diversification has the opposite effect, by reducing equilibrium abundances. When both métiers and efficiencies vary, the probability density of equilibrium abundances concentrates at $\mathbf{N}^{**e_{MAX}}$ as diversity increases. As a result, the effect of métiers' diversity reducing extinctions dominates (grey), but in this case the effect of efficiencies reducing average equilibrium yields also dominates (black). Error bars shown are standard errors ($n = 1000$).

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5.7 Supplementary Material

Appendix A – Vulnerability and profitability constraints under different ecological and economic assumptions

Vulnerability constraints

        The vulnerability constraint of a particular fishing unit, j, is the set of possible equilibrium abundance vectors, $\mathbf{N}^*$, at different efforts with only unit j in the fishery. The vulnerability constraint can be mathematically described by the system of equations resulting from setting the right hand side of equation 2a equal to 0 simultaneously for all combinations of extant stocks, x and y, at equilibrium:

$$\frac{g_x(\mathbf{N}^*)}{g_y(\mathbf{N}^*)} = \frac{m_{xj}}{m_{yj}} \quad (5.\text{S.A.1})$$

As can be seen from equation (S.A.1), the vulnerability constraint is determined solely by the métier, and is not influenced by efficiency. Additionally, because it is defined by a system of $S-1$ unique equations, it will be a one dimensional curve with any number of stocks, S. Figure 5.S1a-e illustrates vulnerability constraints in 2-stock models under different ecological assumptions (i.e. values of $g_i(.)$), listed below.

Fig.5.S1a – No interaction: $g_i(\mathbf{N}(t)) = r_i(1 - (N_i(t)/K_i))$, for $i = 1, 2$, where r_i and K_i are positive constants respectively representing the maximum intrinsic per-capita growth rate and carrying capacity of stock i (sensu Schaefer 1954).

Fig.5.S1b – Competition: $g_i(\mathbf{N}(t)) = r_i\left(1 - \frac{(N_i(t) + \alpha_{ij}N_j(t))}{K_i}\right)$, for $i, j = 1, 2, j \neq i$, where r_i

and K_i are the same as above, and α_{ij} is a positive constant representing the strength of the competitive effect of individuals of stock j on the growth rate of stock i (sensu MacArthur and Levins 1967). Stable co-existence of both stocks in the absence of harvesting requires $\alpha_{ij} \leq (K_i/K_j)$ for $i, j = 1, 2$.

Fig.5.S1c – Mutualism: $g_i(\mathbf{N}(t)) = r_i\left(1 - \dfrac{(N_i(t) - \alpha_{ij}N_j(t))}{K_i}\right)$, for $i, j = 1, 2, j \neq i$, where r_i

and K_i are the same as above, and α_{ij} is a positive constant representing the strength of the mutualistic effect of individuals of stock j on the growth rate of stock i.

Fig.5.S1d – Predator and non-essential prey:

$$g_{pred}(\mathbf{N}(t)) = r_{pred}\left(1 - \frac{(N_{pred}(t) - \alpha_{predprey}N_{prey}(t))}{K_{pred}}\right),$$

$$g_{prey}(\mathbf{N}(t)) = r_{prey}\left(1 - \frac{(N_{prey}(t) + \alpha_{preypred}N_{pred}(t))}{K_{prey}}\right),$$ where r_i and K_i are the same as above (i

$= pred, prey$), and $\alpha_{predprey}$ and $\alpha_{preypred}$ are positive constants respectively representing the strength of the positive effect of prey on predator growth rates and predators on prey growth rates. Note that the predator does not require any particular abundance of prey to survive (with no prey, the predator has logistic growth).

Fig.5.S1e – Predator and essential prey: $g_{pred}(\mathbf{N}(t)) = r_{pred}\left[\dfrac{(N_{prey}(t) - N_{prey,MINpred})}{(K_{prey} - N_{prey,MINpred})}\right],$

$$g_{prey}(\mathbf{N}(t)) = r_{prey}\left(1 - \frac{(N_{prey}(t) + \alpha_{preypred}N_{pred}(t))}{K_{prey}}\right),$$ where the prey growth is the same as in

Fig. 5.S1d, but the predator now needs a minimum abundance of prey, $N_{prey,MINpred}$ to survive.

As illustrated in Figure 5.S1 and in the main text for the logistic model (equation (3)), the shape of the vulnerability constraint is largely determined by the type of interaction (predation, competition, etc.), and by relative values of (m_{ij}/r_i) in most communities.

Profitability constraints

The profitability constraint of a particular fishing unit, j, is the set of abundance vectors, **N**, that result in zero profits for fishers in unit j. It is defined mathematically by setting the right hand side of equation 2b equal to 0 (equivalent to equation (5.4)):

$$e_j \sum_{i=1}^{S} p_i(N_i) m_{ij} N_i = 1 \quad (5.S.A.2).$$

As can be seen from equation (5.S.A.2), the profitability constraint is determined by both the métier (its slope; Figure 5.3c,d) and the efficiency (its position relative to the origin; Figure 5.3b) of fishers in fishing unit j. It is an $S-1$ dimensional surface, which is linear if prices are constant (Figure 5.3). If prices increase as abundance decreases ($p_i'(.) < 0$), but not fast enough to cause profits to increase with decreasing abundance (i.e. $d[p_i(N_i)N_i]/dN_i > 0$ for all N_i, i), the profitability constraint is generally convex, as illustrated for a 2-stock fishery in Figure 5.S1f, because the decrease in price as abundance of a stock increases generally results in diminishing marginal returns to stock abundance (i.e. $d^2[p_i(N_i)N_i]/dN_i^2 < 0$ for all N_i, i). This is analogous to the property of convex isoquants as a result of diminishing marginal returns to production factors (e.g. capital, labour) in microeconomics (see Mas-Colell et al. 1995).

If a stock, i, has the property that the revenues it generates increase as its abundance decreases (i.e. $d[p_i(N_i)N_i]/dN_i < 0$), then it is likely to be driven extinct (Courchamp et al. 2006), and this likelihood can be exacerbated by increasing the diversity of métiers. If $d[p_i(N_i)N_i]/dN_i < 0$ at current and all lower abundances, N_i, of stock i, then any fishing unit whose current revenues from only stock i are greater than its costs can profitably harvest stock i to extinction. Increasing efficiency or métiers would increase the likelihood of sampling such a fishing unit. If $d[p_i(N_i)N_i]/dN_i < 0$ at current abundance of stock i but not abundances lower than a certain abundance (because of price saturation, for example), increasing the diversity of efficiency or métiers would increase the likelihood of sampling a fishing unit that could drive stock i to this abundance, at which point the theory presented in the main text would apply, and equilibrium at infinite fleet diversity would satisfy equation (5.5). Thus, equation (5.5) (equality of price*abundance across all extant revenue-generating stocks at equilibrium) is likely to be satisfied even if prices can increase faster than abundances decline for some stocks.

Appendix B – Importance of influencing relative and total efforts, and the number of different métiers being equal to or exceeding the number of stocks, to achieve a target set of stock abundances or mortality rates

Consider the model of an S-stock fishery from the main text, where there are now J different fishing units, such that equation (5.2a), describing the population growth of species i becomes:

$$\frac{dN_i(t)}{dt} = N_i(t)\left(g_i(\mathbf{N}(t)) - \sum_{j=1}^{J} m_{ij} e_j E_j(t)\right) \quad (5.S.B.1)$$

Suppose there is a desired 'target' (denoted T) abundance for every stock, N_{Ti} for stock i, that is achieved by inflicting instantaneous per-capita fishing mortality rates, $\mathbf{F_T} = (F_{T1},\ldots, F_{TS})$ on all stocks. The per-capita fishing mortality rate of stock i at time t, $F_i(t)$, is given by:

$$F_i(t) = \sum_{j=1}^{J} m_{ij} e_j E_j(t) \quad (5.S.B.2).$$

Because effort in each fishing unit is defined in units of monetary cost, effort in fishing unit j, E_j, can be represented as the total cost-budget of the fishery as a whole (total effort), denoted $E(t)$ at time t, multiplied by the fraction of this cost-budget allocated to fishing unit j (relative effort), denoted $b_j(t)$ at time t, where $\sum_j b_j(t) = 1$. With this substitution, the fishing mortality rate of stock i is given by:

$$F_i(t) = E(t)\sum_{j=1}^{J} m_{ij} e_j b_j(t) \quad (5.S.B.3).$$

In order for the target mortality rates, $\mathbf{F_T}$, to be achieved for all stocks, effort must be allocated such that,

$$\mathbf{F_T} = E^*(\mathbf{Q} \bullet \mathbf{b}^*) \quad (5.S.B.4),$$

where $\mathbf{Q} = \{m_{11}e_1,\ldots,m_{1J}e_J\},\ldots,\{m_{S1}e_1,\ldots,m_{SJ}e_J\}\}$, $\mathbf{b}^* = \{b_1^*,\ldots,b_J^*\}$, and $\mathbf{b}^*$ and E^* respectively define relative and total efforts needed to achieve the target. This equation requires $\mathbf{Q}$ to have a rank of S or greater to be solved for $\mathbf{b}^*$, which requires at least S different métiers. Figure S2 illustrates this graphically in a 3-stock fishery. When the dimensionality of the set of achievable abundance targets (determined by the number of

different métiers) is smaller than the number of stocks, it is highly unlikely that a particular set of target abundances will be contained in this set (Figure 5.S2a,b vs. c).

Appendix C. Priority effects on the outcome of competition can only occur if fishers from different fishing units receive different prices for the same catch.

Priority effects occur when two fishing units compete and neither can invade the other's equilibrium, resulting in an outcome of competition determined by which unit enters the fishery earlier or can expand faster. Priority effects are unlikely if all fishers face the same prices. This property is illustrated in Figure 5.S3 in a model of a fishery targeting two stocks with logistic growth. Analogously to priority effects between two ecological consumers (see Tilman 1980), priority effects between two fishing units result in the existence of an unstable equilibrium, where the profitability constraints of both fishing units are satisfied, and additional effort in each fishing unit would shift stock abundances away from the equilibrium to levels where it unit made higher profits than the other fishing unit (Figure 5.S3). This implies that for priority effects to exist between two competing fishing units, x and y, there must be at least one stock, i, for which $m_{ix} > m_{iy}$ and $p_i m_{ix} < p_i m_{iy}$ (i.e. more effort in fishing unit x would reduce the abundance of stock i relative to others, which would have a greater negative impact on fishing unit y's revenues than its own), or $m_{ix} < m_{iy}$ and $p_i m_{ix} > p_i m_{iy}$ (the converse). This is impossible if p_i is the same for all fishing units.

Appendix D – Exceptions to common effects of fleet diversification on yield and ecological impacts of open-access fisheries, as a result of ecology or technological feasibility

Provided efficiency is finite, infinitely diverse métiers in a multispecies fishery drive stocks' abundances to a point in the first quadrant where they generate equal marginal revenue (equation (5.7)), preventing extinction of weak stocks directly caused by the fishery. This property is illustrated in Figure 4 in a model with no interspecific interactions in Figure 5.4, but also holds under many types of interactions. For example, Figure 5.S4a shows the results of a similar stochastic simulation of a fishery targeting

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two competing stocks, with the same qualitative results as in Figure 5.4b. The procedure is the same as in Figure 5.4b, except the population growth of both stocks in the absence of fishing is described by a simplified Lotka-Volterra competition model (sensu MacArthur and Levins 1967), where $g_i(\mathbf{N}(t)) = 1 - N_i(t) - 0.3N_j(t)$ ($i, j = 1, 2, i \neq j$), and other parameter values/distributions are: $\{p_1 = 1, p_2 = 2, m_{1j} \sim U[0, 1], e_j \sim U[2, 12]\}$. As the number of fishing units increased, average yields decreased when efficiency varied, and increased when only métiers varied. The average number of extinctions decreased as the number of fishing units increased when métiers varied, and increased when only efficiency varied (Figure 5.S4a, right panel).

However, some ecosystem structures or restrictions on the range of technologically feasible fishing units can cause diversification of métiers to lead to more frequent stock collapses. Ecological specialist stocks that either have obligate prey or mutualists also caught or otherwise impacted by the fishery may still be driven extinct. Specifically, a stock, i, having long-term persistence that requires an obligate mutualist or prey, k, to have at least a minimum population size, $N_{k,MINi}$, will be driven extinct at infinite fleet diversity if $N_k^{**e_{MAX}} < N_{k,MINi}$. This is illustrated in a stochastic simulation of a fishery targeting a predator (Stock 2) and its essential prey (Stock 1) in Figure S4b. The procedure was the same as in Figures 5.4b and 5.S4a, except that stocks' population growth in the absence of fishing was now described by: $g_1(\mathbf{N}(t)) = 1 - N_1(t) - N_2(t)$,

$g_2(\mathbf{N}(t)) = \dfrac{(N_1(t) - N_{1,MIN2})}{(1 - N_{1,MIN2})}$, and other parameter values/distributions are: $\{p_1 = 1, p_2 = 0.5, m_{1j} \sim U[0, 1], e_j \sim U[2, 5]\}$. In this model, increases in all types of diversification led to increases in average likelihood of predator extinction (Figure 5.S4b). This occurred because competition among diverse métiers and efficiency drives the prey's abundance to a level that is below $N_{1,MIN2}$ (Figure 5.S4b, left panel). Additionally, all types of fleet diversification increased average yields, as the prey's average yields increased in response to reduced predation pressure, which more than compensated for lost predator yields (Figure 5.S4b, right panel). This latter result is somewhat dependent on parameter values, but is likely to hold in systems where transfers of biomass up food chains are

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inefficient, a common property in nature (e.g. Lindeman 1942; Odum 1957; Christensen and Pauly 1992).   Thus, diversification of métiers in fisheries impacting multiple trophic levels may increase both yields and the likelihood of stock collapses.

Diversification of métiers can also increase the likelihood of stock collapses when some relative catch rates are not technologically feasible. Some relative catch rates may not be feasible if, for example, two stocks have sufficiently high niche overlap that it would be difficult or impossible to design a fishing technology that catches one without also catching the other at a certain rate. If relative catch rates that lead stocks to have relative depletions satisfying equation (5.5) or (5.7) are not technologically feasible, then it is possible for métiers that drive one or more stocks extinct to be favoured by competition. Figure 5.S4c illustrates this point in a stochastic simulation identical to Figure 5.S4a, in which métiers for which $m_{1j} < 0.55$ are now technologically infeasible (i.e. $m_{1j} \sim U[0.55, 1]$). As a result, the relationships between diversification in yield seen in Figure S4a are similar, but now all types of diversification increase the likelihood of stock 1's collapse (Figure 5.S4c). An analytical example of this is also given below.

Suppose 2 stocks, x and y, having logistic growth ($g_i(\mathbf{N}(t)) = r_i\left(1 - \left(N_i(t)/K_i\right)\right)$ for all i) where $r_x = 2r_y$, $K_x = K_y = a_x = a_y = 1$, and $p_x = p_y = p$, are exploited in a fishery, and, due to technological constraints, $m_{xj} \leq m_{yj}$ for any fishing unit j. At any efficiency, $p_x N_x^*$ $= p_y N_y^*$ would require either a single fishing unit, j, where $m_{xj} = 2m_{yj}$, or 2 fishing units, j and k, where $m_{xj} > 2m_{yj}$ and $m_{xk} < 2m_{yk}$, or vice versa. However, this is infeasible because $m_{xj} \leq m_{yj}$ for all j. Thus, $p_x N_x^* > p_y N_y^*$ at all feasible equilibria, implying that competition favours fishing units with the largest possible harvest rate of stock x, which in this case corresponds to $m_x = m_y$ (i.e. $m_x = m_y = 0.5$ because $m_{xj} + m_{yj} = 1$ for all j by definition). Thus, if the maximum efficiency is e_{MAX}, infinite fleet diversity would result in equilibrium stock sizes, $N_x^* = (2/3pe_{MAX}) + (1/3)$, $N_y^* = (4/3pe_{MAX}) - (1/3)$. Infinite fleet diversity results in the extinction of stock y if $e_{max} \geq 4/p$.
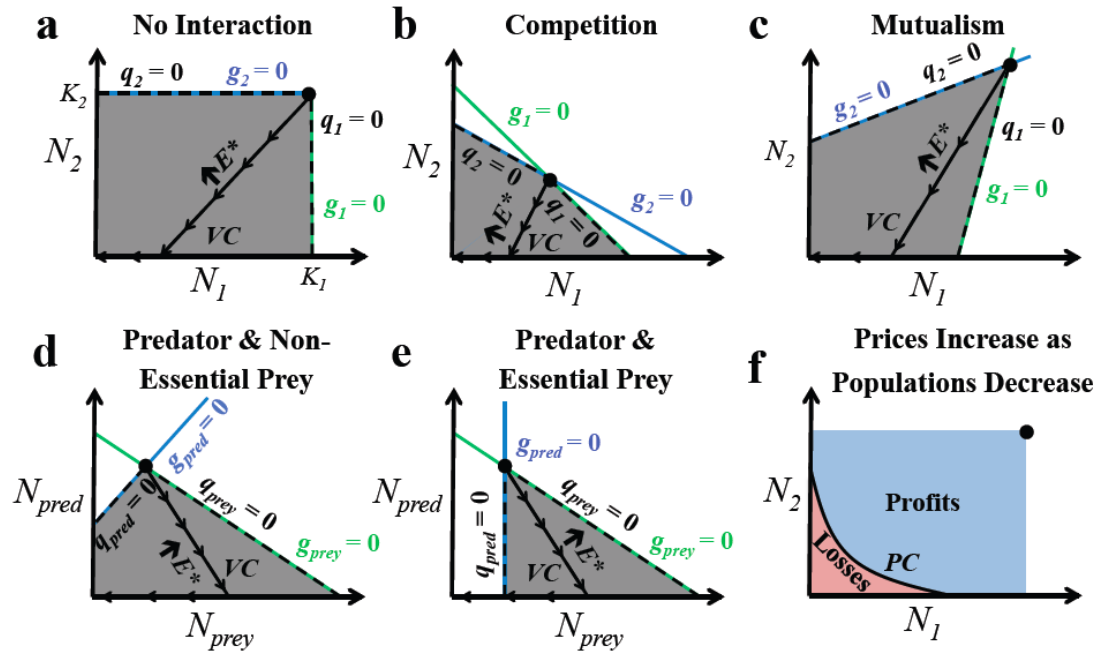
Figure 5.S1. Vulnerability and profitability constraints with different assumptions. Vulnerability (**a-e**) (VC) and profitability constraint (**f**) (PC) with different ecological and economic assumptions. In each figure, stocks' zero net growth isoclines (ZNGI) ($g_i = 0$) (blue and green lines) and equilibrium abundances (filled circle) in the absence of harvesting are shown. If one of the stocks is not caught in the fishery ($q_i = 0$), increasing fishing effort causes equilibrium abundances to move along its ZNGI ($g_i = 0$) towards the origin (dashed lines). If both stocks are caught, increasing fishing effort causes equilibrium abundances to move along the vulnerability constraint, which must lie somewhere in the gray shaded region, and whose slope is determined by the stocks' relative catch rates and growth rates. Specific functional forms on which the shapes of ZNGIs are based for different classes of species interactions are given in Appendix A. (**f**) When prices increase as stocks' abundances decrease, the profitability constraint – the set of stock abundances that result in zero profits, separating abundances yielding positive profits (blue shaded region) and losses (red shaded region) – is generally convex.
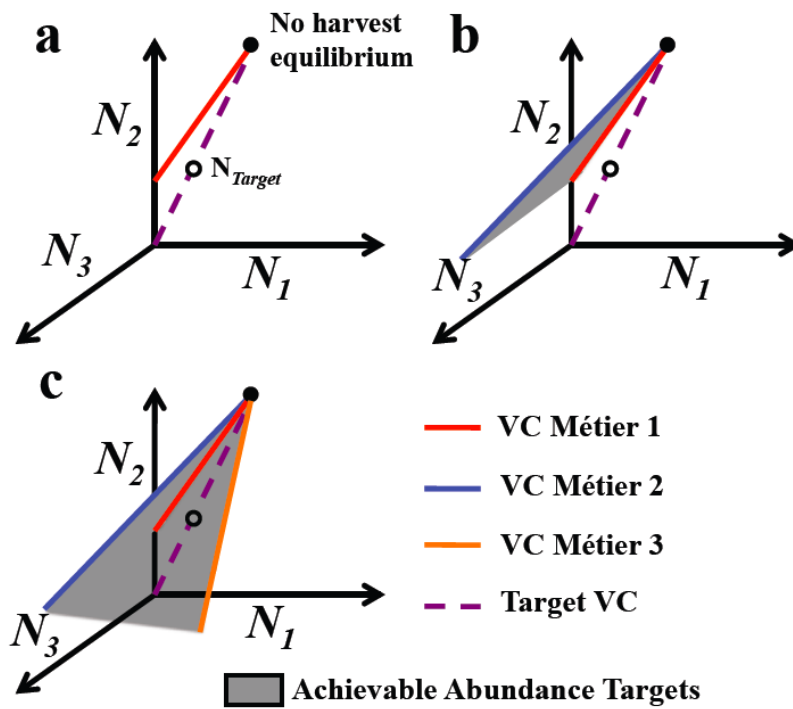
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Figure 5.S2. Diversity of métiers and achievable abundances in managed fisheries. The relationship between the number of métiers and the achievability of a multi-stock abundance target (N_{Target}, open circles) is shown in a 3-stock model. A hypothetical vulnerability constraint producing the target is also shown (dashed purple line). With only 1 métier (**a**), achievable outcomes are constrained to a single one-dimensional vulnerability constraint curve (red), which is unlikely to coincide exactly with the desired curve (purple) in 3-dimensional space by chance. Similarly, with 2 métiers (**b**) it is also unlikely, though less unlikely, that the 2-dimensional plane of possible achievable outcomes (shaded region) contains the desired outcome. However, with 3 (**c**) or more métiers, the chance that the desired outcome is achievable becomes sizeable, provided the 3 métiers differ in their relative catch rates.
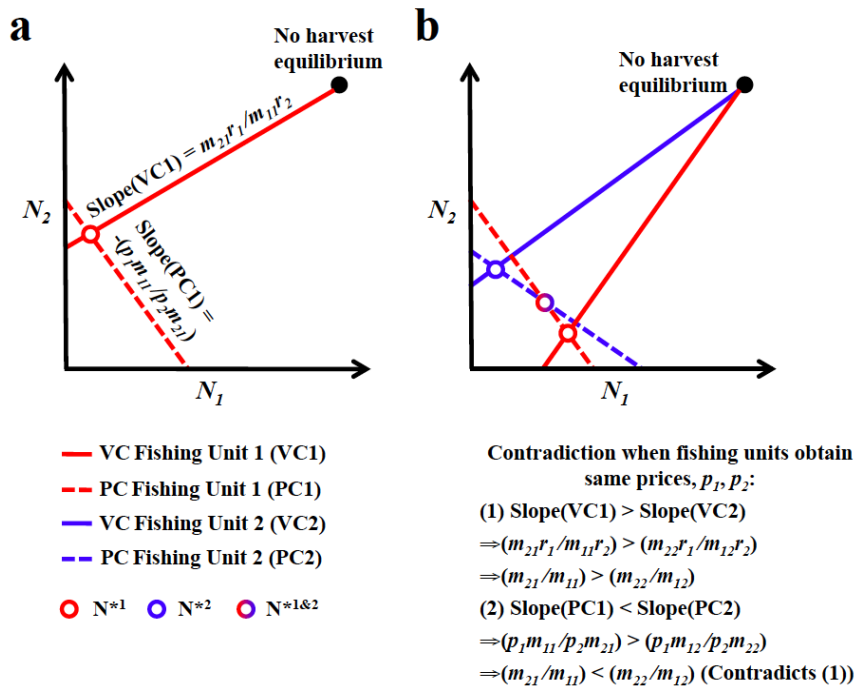
a

No harvest equilibrium

N_2

Slope(VC1) $= m_{21}r_1/m_{11}r_2$

Slope(PC1) $= (p_1m_{11}/p_2m_{21})$

N_1

b

No harvest equilibrium

N_2

N_1

— VC Fishing Unit 1 (VC1)
-- PC Fishing Unit 1 (PC1)
— VC Fishing Unit 2 (VC2)
-- PC Fishing Unit 2 (PC2)

○ N*^{1} ○ N*^{2} ○ N*$^{1\&2}$

Contradiction when fishing units obtain same prices, p_1, p_2:
(1) Slope(VC1) > Slope(VC2)
$\Rightarrow (m_{21}r_1/m_{11}r_2) > (m_{22}r_1/m_{12}r_2)$
$\Rightarrow (m_{21}/m_{11}) > (m_{22}/m_{12})$
(2) Slope(PC1) < Slope(PC2)
$\Rightarrow (p_1m_{11}/p_2m_{21}) > (p_1m_{12}/p_2m_{22})$
$\Rightarrow (m_{21}/m_{11}) < (m_{22}/m_{12})$ (Contradicts (1))

Figure 5.S3. Priority effects require fishing units to face different prices. A 2-stock 2-fishing unit model illustrating the reason for which priority effects are only possible if fishers in different fishing units face different prices. Slope equations for the vulnerability constraint (Slope(VC)) and profitability constraint (Slope(PC)) are derived respectively from equations (3) and (4), assuming there are 2 stocks, each having logistic growth and constant prices, where abundances (N_i, $i = 1,2$) are normalized as fractions of carrying capacity (i.e. $K_1 = K_2 = 1$). Circles indicate equilibrium stock sizes with: only fishing unit 1 (N*^{1}, red), only fishing unit (N*^{2}, blue), and the unstable co-existence equilibrium (N*$^{1\&2}$, red and blue).
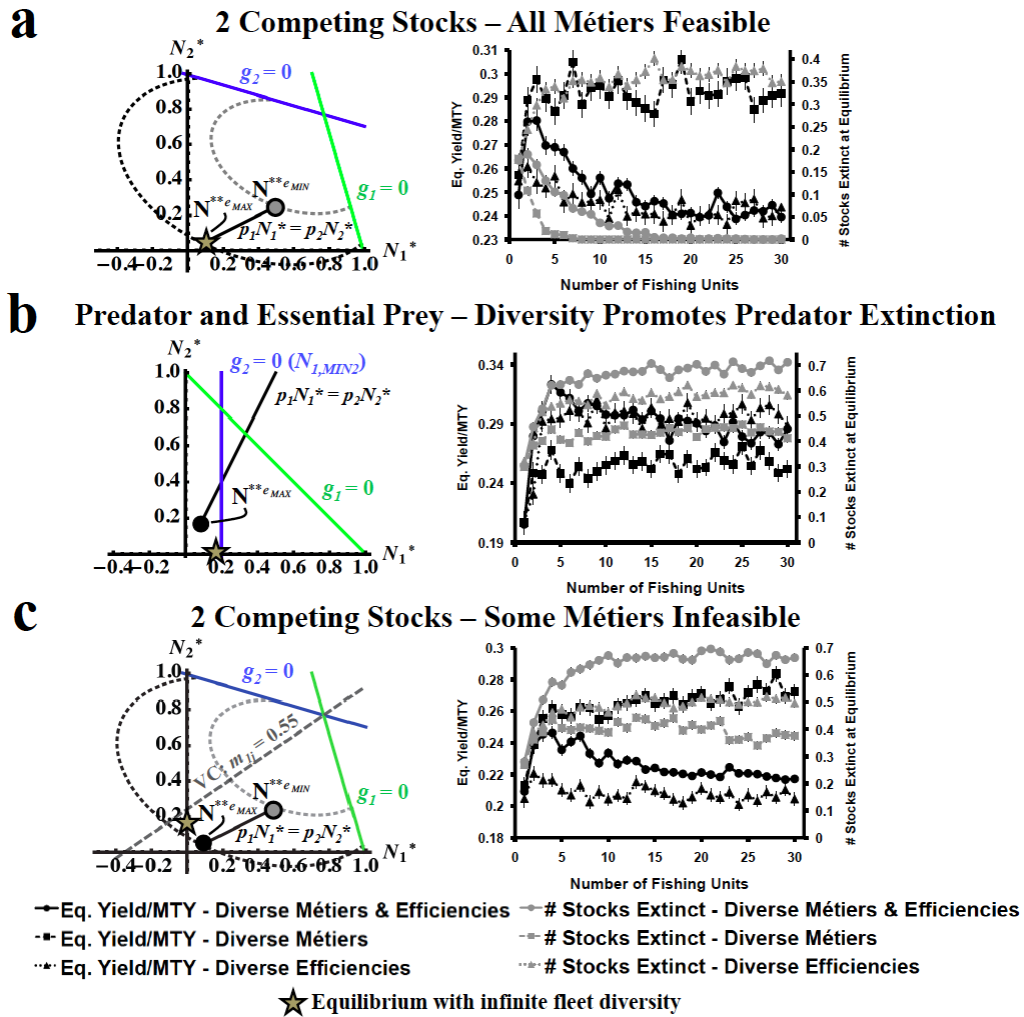
Figure 5.S4. Relationships between fleet diversity and yields and ecological impacts in different types of open-access fisheries. These are illustrated in 2-stock fisheries in which (**a**, **c**) stocks are competing or are (**b**) predator (Stock 2) and essential prey (Stock 1). In panel (**c**), only métiers j with $m_{1j} \geq 0.55$ are technologically feasible, illustrated by the grey dashed line in (**c**) (left). Points at which $p_1N_1^* = p_2N_2^*$ are illustrated (black solid lines), as well as all possible intersection points of vulnerability and profitability constraints for fishing units with minimum (e_{MIN}) (grey dotted lines) and maximum (e_{MAX}) (black dotted lines) feasible technological efficiency are shown in the left-hand panels. Stocks' zero net growth isoclines (ZNGI) ($g_i = 0$) (blue and green lines) are also shown. The right-hand panels show the relationships between fleet diversity and yield (black) and the average number of extinctions (grey) in stochastic simulations of the fisheries illustrated in the corresponding left-hand panels. Each point represents a sample of 1000 models with randomly chosen parameter values. Vertical lines indicate standard errors.

Chapter 6

Conclusion: Improving the informational efficiency of fisheries science

Fisheries science and management are inherently data-limited pursuits. Fisheries exist within complex social-ecological systems, in locations that are particularly difficult and expensive to sample. Conventional approaches to fisheries management have mostly relied on fitting single-species assessment models to data to estimate sustainable harvest rates and population trends (Hilborn & Ovando 2014). Despite their relative simplicity, conventional assessment approaches have been estimated to cost up to 15% of the landed value of the stocks assessed (Arnason et al. 2000; Hilborn & Ovando 2014). Moreover, though conventional assessments are becoming more widespread, with large databases (FAO 2011; Ricard et al. 2012) including nearly 400 stocks encompassing 35% of the world's catch (Hilborn & Ovando 2014), there are still thousands of unassessed fish stocks encompassing a majority of the world's catch (Costello et al. 2012). For unassessed stocks, a number of data-poor stock assessment approaches (DPSA) have emerged that approximate population statuses and threats from life-histories and catch-histories and how these correlate with the statuses and threats of better-studied species (e.g. Caddy 1999, 2002; Cheung et al. 2005; Costello et al. 2012; Le Quesne & Jennings 2012; Martell & Froese 2013). At the other end of the spectrum, there have been calls for more holistic, ecosystem-based approaches to fisheries management (Pikitch et al. 2004; Palumbi et al. 2008), which may require significantly more data and complex models than conventional management approaches (Pauly et al. 2000; Christensen & Walters 2004), and are thus likely even less broadly applicable.

Clearly, there is a fundamental tradeoff in fisheries assessment approaches between reach and predictive power that is driven by information requirements (Figure 6.1). Approaches requiring little information are likely to be widely applicable, but also much less reliable for specific fisheries (Costello et al. 2012; Hilborn & Ovando 2014). Conversely, approaches that provide the greatest predictive power often require the most

input information (e.g. Pauly et al. 2000; Christensen & Walters 2004), making them less widely applicable. Thus, the best assessment approach for any given fishery is sure to be dependent on the amount and type of available information, in addition to other factors such as budget, location, and management institutions (Hilborn & Ovando 2014). However, as with any tradeoff situation, it is important to ensure that efficiency is being achieved (e.g. Polasky et al. 2008). In this case, efficiency means achieving the maximum predictive power possible for a given amount of information (Figure 6.1).

The studies in this volume highlight two important pathways to improving the informational efficiency of fisheries science: theoretical concision, and ecological abstraction. Theoretical concision means striving for parametric simplicity in mechanistic models, and rooting models in measurable parameters. The rationale for doing this is analogous to the information theoretic rationale for preferring simpler statistical models (Burnham & Anderson 2002). The approaches to predicting extinction and overfishing threats presented in Chapter 2 (Burgess et al. 2013) and Chapter 3 focus on identifying the threat potential of current fishing practices (gear, relative catchabilities) and other biological and socioeconomic conditions (price flexibilities, catch elasticities, management). The modeling framework used in Chapter 3 also considers profits and abundances in relative, rather than absolute terms. These focuses and formulations both promote parametric simplicity, reducing the data requirements of the approaches without necessarily compromising their predictive power. Mechanistic approaches to assessing extinction and overfishing threats are important because they allow conditions conducive to eventual unsustainable harvest rates and population declines to be identified before such harvest rates and declines are realized (Burgess et al. 2013).

Ecological abstraction occurs when models of only a subset of species in a larger ecosystem are successfully able to predict the dynamics of this subset of species (Schaffer 1981). Understanding when simple models reliably predict sustainable harvest rates of fished populations, and other important fishery impacts, within complex ecological realities is important in prioritizing data collection efforts and designing precautionary management approaches, where necessary. The study presented in Chapter

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4 provides evidence that single-species assessment models will often provide reliable estimates of sustainable harvests of competing populations caught in multispecies fisheries, but only over ranges of fishing effort in which all populations in the fishery are extant. At efforts beyond those needed to cause the extinction of the most susceptible population to overfishing, estimates of sustainable yields and harvest rates are highly unreliable. In the least susceptible populations, overestimates of sustainable yields and harvest rates are particularly likely. However, because conditions leading to unreliable assessments, bounds on the magnitude of sustainable yield and mortality-rate overestimates, and management solutions are possible within single-species assessment and management frameworks, incorporating competition explicitly into assessments in multispecies fisheries may not be necessary. In contrast, other studies have shown that single-species assessments can be unreliable when foraging behaviors are dynamic (Abrams 2009c; Tschirhart 2012), and in many predator-prey systems (Abrams 2009a,b,c). More complex assessment models may thus be useful in such situations. More research is needed to broadly characterize the conditions under which simplistic assessment models reliably predict important population and community responses to fishing.

Previous studies have highlighted two other promising pathways to improving the informational efficiency of fisheries science: interpolating or approximating missing data using data from similar species or fisheries (e.g. Cheung et al. 2005; Costello et al. 2012; Le Quesne & Jennings 2012; Martell & Froese 2013), and making use of recent advances in non-linear, non-parametric forecasting methods (e.g. Sugihara & May 1990; Sugihara et al. 2012; Deyle et al. 2013). Non-linear, non-parametric forecasting methods, which can be applied with only a single time series (e.g. abundance or CPUE in one population), have been used with considerable success in making short-term forecasts in ecology (e.g. Sugihara & May 1990; Sugihara 1994) and recently in some fisheries (e.g. Glaser et al. 2011; Liu et al. 2012; Deyle et al. 2013; but see Glaser et al. 2013). A related approach to empirically identifying causal relationships in complex systems has also been developed (Sugihara et al. 2012), which could allow for functional relationships between species to be identified. Future approaches to fisheries science and management combining

theoretical concision, ecological abstraction, interpolation of missing data using information from closely related species or fisheries, and non-linear, non-parametric forecasting are likely to be highly successful in the face of data limitations, and highly informative in prioritizing future data gathering efforts.
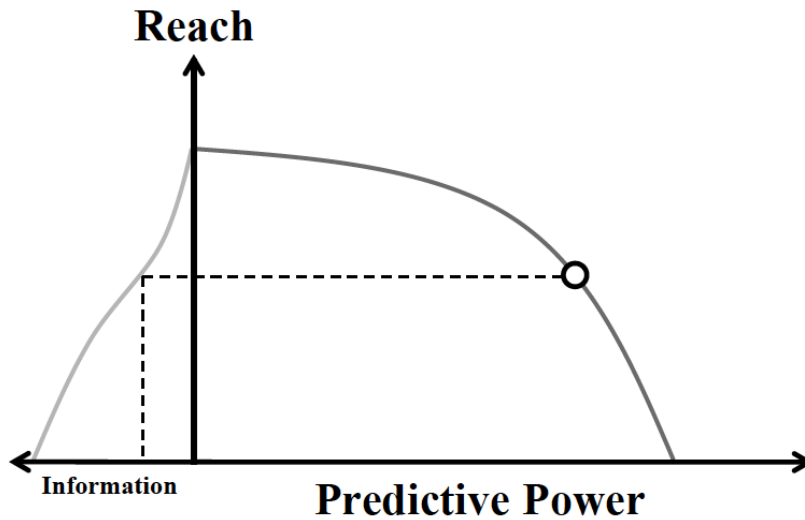

Figure 6.1. Information-based tradeoff between reach and predictive power in fisheries assessments. Assessment approaches face a tradeoff between reach (i.e. how widely applicable they are) and predictive power. Any hypothetical assessment technique requiring no information would theoretically be applicable to any population, but would have no predictive power. More information allows for greater predictive power in assessments, but limits the breadth of applicability to species for which the information is available. The maximum predictive power achievable in an assessment with different amounts of information defines the efficiency frontier with respect to this tradeoff, represented by a dark-grey line in the above figure). The open circle shows a point on the hypothetical efficiency frontier and the black dashed lines illustrate the amount of information corresponding to this point.

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