ORIGINAL ARTICLE

FISH and FISHERIES   WILEY

Synergies between price and life history enhance extinction risk in open-access fisheries

Leonardo Manir Feitosa[1] | **Matthew G. Burgess**[2] | **Christopher M. Free**[1,3] | **Steven D. Gaines**[1]

[1]Bren School of Environmental Science and Management, University of California, Santa Barbara, Santa Barbara, California, USA

[2]Department of Economics, University of Wyoming, Laramie, Wyoming, USA

[3]Marine Science Institute, University of California, Santa Barbara, Santa Barbara, California, USA

Correspondence
Leonardo M. Feitosa, Bren School of Environmental Science and Management, University of California, Santa Barbara, Santa Barbara, CA 93117, USA.
Email: lmfeitos@gmail.com

Abstract

There have been few documented extinctions of fished species, but many bioeconomic models predict that open-access incentives make extinction possible. Open-access multi-species fisheries can cause species' extinction if other, faster-growing species maintain profits at fatal effort levels. Even target species can be profitably harvested to extinction if their prices rise sufficiently as they are depleted. Here, we explore interactions between these potential extinction mechanisms by modelling an open-access multi-species fishery with one or multiple fleets exploiting two species, each with different growth rates, ex-vessel prices, and price dynamics. Increases in the strong stock's (the stock with higher productivity relative to fishing susceptibility) price as it is depleted increase the range of conditions under which the weak stock can be driven extinct and shrinks the range of bioeconomic parameters in which both species can coexist under open-access. Catch hyperstability – whereby species become easier to catch as they are depleted – makes the weak stock weaker as it is depleted and further narrows the scope for coexistence. Fleet diversity in targeting ability can prevent weak stock extinction, as competition or switching balances species abundances. With few documented global fished-species extinctions, our results raise important questions, which we discuss. Is the apparent lack of extinctions largely due to management? Are more species in lightly-managed fisheries threatened with extinction than previously acknowledged? Have more extinctions than we realize already happened in data- and management-poor fisheries? Or have fishes' high fecundity and the oceans' vastness provided protection against extinction that is uncaptured by existing theoretical models?

KEYWORDS
bioeconomic modelling, bycatch, extinction, hyperstability, multi-species fisheries, overexploitation

WILEY

1 | INTRODUCTION

Decades of fisheries economics research have cemented the idea that fisheries should rarely cause species extinctions, because fishing becomes unprofitable as stocks become depleted. In theory, this should reduce fishing pressure before stocks are completely extirpated (Gordon, 1954; Schaefer, 1957). There have indeed been few documented global extinctions of fish species caused by harvesting (Le Pape et al., 2017), and well-managed fisheries have had many successes in maintaining and rebuilding sustainable harvests (Cochrane, 2020; Hilborn et al., 2020).

However, there have been numerous severe depletions and local and regional extinctions of fished species (Dulvy et al., 2003; Webb & Mindel, 2015). Approximately 30% of global fisheries are considered to be overfished, and this proportion has grown through time (FAO, 2024). These depletions, combined with the lack of assessment information on most marine species, raise the possibility that extinctions are occurring on a larger scale than has been detected (McCauley et al., 2015; Webb & Mindel, 2015). Extinction risk seems to be highest among species with slow intrinsic population growth, high economic value, and high rates of unintentional or opportunistic catch in fisheries primarily targeting other species (Branch et al., 2013; Collette et al., 2011; Dulvy et al., 2003).

Recent bioeconomic theory explains how each of these conditions and others can allow fishing to cause extinction by preventing profits from dissipating as a species is depleted. For example, in single-species fisheries, fishing profits can be maintained as the target species' abundance declines if prices increase faster than costs, either due to supply and demand or rarity effects (Burgess, Costello, et al., 2017; Courchamp et al., 2006; Dao et al., 2023; Holden & McDonald-Madden, 2017). Hyperstability of catches can facilitate a similar dynamic, causing catch and profits to remain high even while abundance declines (Burgess, Costello, et al., 2017; Harley et al., 2001). Catch hyperstability is especially common in species with schooling behaviour (see Burgess, Costello, et al., 2017 for meta-analysis; Rose & Kulka, 1999). Harvest subsidies can also exacerbate overfishing or extinction threats for target species by reducing costs or subsidizing increases in fishing power (Sumaila et al., 2019).

The conditions for extinction may be even more common in multi-species than single-species fisheries (Berck, 1979; Clark, 1990; Larkin, 1963; May et al., 1979). Multi-species fisheries also constitute most global fisheries given the low selectivity of most fishing gears. In multi-species fisheries, species with higher productivity relative to their susceptibility to fishing can economically support fishing efforts that threaten the survival of species with lower productivity relative to their susceptibility to fishing (Burgess et al., 2013; Hastings et al., 2017). This dynamic represents a critical threat to many large-bodied marine species (which tend to have lower productivity) caught in multi-species fisheries (Branch et al., 2013), including chondrichthyans (sharks, rays, skates, sawfishes, chimeras), marine mammals, seabirds, turtles, and several species of large bony fish (Burgess et al., 2018; Dulvy et al., 2021). An analogous threat of opportunistic harvesting – whereby hunters target an abundant,

fast-growing species, but will kill a rare, slow-growing species if they encounter one – affects land animals (Thurner et al., 2021) and may have contributed to the Pleistocene megafaunal extinction (Alroy, 2001). Multi-species fisheries can also indirectly cause extinction threats by affecting species competition (Burgess et al., 2019) and other interactions.

Theory on extinction threats from fishing has tended to explore threats to target species in single-species contexts (e.g., from rising prices or stable costs) separately from threats from multi-species fishing (e.g., Burgess, Costello, et al., 2017 versus Burgess et al., 2013). Here, we analyse the interactions between these threats. We extend the classic Gordon-Schaefer bioeconomic model to a two-species fishery in which one or both species have increasing prices or hyperstable catches as they become rarer. We also explore the effect of fisheries subsidies and fleet diversity on extinction conditions and equilibrium abundances. We focus on three broad questions: (1) How do single-species and multi-species extinction mechanisms interact, and under what conditions are they synergistic or antagonistic? (2) How broad are the sets of conditions that can cause extinction under open-access management? (3) Does having multiple fleets exploiting both stocks affect extinction threats from multi-species fishing? We derive analytical results and perform simulations to explore these questions.

2 | METHODS

2.1 | The model

We first consider a two-species, open-access, single-fleet fishery, in which one species, s (hereafter 'stock'), has higher fishing susceptibility relative to its productivity than another stock, w

(Zhou et al., 2016). For convenience of terminology, we refer to the stock with lower susceptibility relative to its productivity as the 'strong stock' (hence, *s*) and the other as the 'weak stock' (hence, *w*), as is common in the literature (Hastings et al., 2017). However, we do not intend for this terminology to convey any normative implications (e.g., a negative one for 'weak' stocks).

We assume that both stocks co-occur and are exploited by the same fishery operating within a single fleet. We explore behaviour under both open-access and maximum sustainable yield (MSY)-based management. Both stocks grow according to continuous logistic growth – governed by a maximum growth rate (r_i for stock *i*) and a maximum abundance or carrying capacity (K_i for stock *i*). Each stock has a catchability (q_i for stock *i*) that reflects its susceptibility to each unit of fishing effort (E). We include an additional parameter, β_i for stock *i*, that allows catch per unit effort (CPUE) to be non-linearly related to abundance (N_i for stock *i*) to account for catch flexibility (Burgess, Costello, et al., 2017; Harley et al., 2001). As β gets progressively smaller than one, catches become increasingly hyperstable (i.e., catches remain high despite declining abundance). The rate of change of abundance of stock *i*, N_i, is expressed in continuous time as the following derivative:

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_i}{K_i}\right) - q_i N_i^{\beta_i} E, \tag{1}$$

where *i* = *s* or *w*.

Under open-access conditions, we assume that the dynamics of effort are given by Equation (2), which mirrors the Gordon-Schaefer model, with the addition of catch non-linearity (β_i) and the assumption that price can be non-constant. Specifically, we assume that there is a constant per-unit-effort fishing cost, *c*, and that the price of catch is a function of the stock size [$p_i (N_i)$], either directly (Courchamp et al., 2006; Holden & McDonald-Madden, 2017) or indirectly as a function of catch (Burgess, Costello, et al., 2017). Fishing revenue from species *i* is equal to price multiplied by catch [$p_i (N_i) q_i N_i^{\beta_i} E$]. Profits are equal to revenues from both species added together, minus fishing costs (*cE*). The rate of change of effort, *E*, is proportional to fishing profits, with a constant, α, determining the response rate of effort to profits:

$$\frac{dE}{dt} = \alpha E \left[p_s (N_s) q_s N_s^{\beta_s} + p_w (N_w) q_w N_w^{\beta_w} - c \right] \tag{2}$$

Effort decreases when profits are negative and increases when profits are positive.

While our analytical evaluations do not specify a form of the price function [$p_i(N_i)$], one of the simulation scenarios described below assumes, as in Burgess, Costello, et al. (2017), that price is a function of catch with a constant price flexibility of demand (Eales et al., 1997; Houck, 1965), f_i:

$$p_i (N_i) = A_i C_i^{-f_i} = A_i \left(q_i N_i^{\beta_i} E \right)^{-f_i} \tag{3}$$

Here, C_i denotes catch (per unit time) of stock *i*, where $C_i = q_i N_i^{\beta_i} E$, according to Equation (1).

Under MSY-based management targeting stock *i*, we assume that effort is set to the level that creates MSY-generating fishing mortality (F_{MSY}). This cannot be solved for analytically when CPUE is non-linear in abundance ($\beta_i \neq 1$), but when CPUE is linear in abundance ($\beta_i = 1$):

$$F_{MSY} = \frac{r_i}{2q_i} \tag{4}$$

To distinguish the strong and weak stocks, we define differences in vulnerability, where the 'vulnerability' of stock *i* is specified as in Burgess et al. (2013):

$$V_i = \frac{CPUE_i}{r_i N_i} = \frac{q_i}{r_i} N_i^{\beta_i - 1} \tag{5}$$

If CPUE is linearly related to abundance ($\beta_i = 1$), then $V_i = \frac{q_i}{r_i}$, and the identity of the stock with higher vulnerability is fixed. By contrast, if $\beta_i \neq 1$, then the identity of the more vulnerable stock can change depending on the relative abundance of each stock. Therefore, for simplicity, our analyses refer to the 'weak' and 'strong' stock according to their $\frac{q_i}{r_i}$ ratios (the weak stock's ratio is set to be higher: $\frac{q_w}{r_w} > \frac{q_s}{r_s}$).

We perform analytical evaluations of the model to derive equilibria and extinction conditions and identify synergies or antagonisms between price-driven and weak-stock-driven extinction conditions. These analytical solutions are derived in the results Section 3.1.

2.2 | Extension to multiple fleets

To see how multi-fleet competition with malleable selectivities (i.e., a situation where fleets can change catchabilities, q_{ij}, by changing their fishing practices) might affect our results, we explore a fishery with multiple fleets exploiting both stocks at different rates, extending the results of Burgess (2015). Here, a 'fleet' can be thought of as a distinct combination of timing, location, gear, and target species, similar to the concept of a 'fishing opportunity' (Branch et al., 2005) or a 'métier' (Marchal et al., 2013).

With *M* fleets, where E_j denotes the effort in fleet *j* and q_{ij} denotes the catchability of stock *i* in fleet *j*, the dynamics of stock abundance and effort are given by:

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_i}{K_i}\right) - \sum_{j=1}^{M} q_{ij} N_i^{\beta_i} E_j, \tag{6}$$

where *i* = *s* or *w*;

$$\frac{dE_j}{dt} = \alpha E_j \left[p_s (N_s) q_{sj} N_s^{\beta_s} + p_w (N_w) q_{wj} N_w^{\beta_w} - c \right] \tag{7}$$

For analytical convenience, we assume that all fleets have the same cost, *c*, and incorporate differences in their catch efficiency into the *q* parameters. We also assume that all fleets have the same response rate to profits, α, since this parameter does not affect the equilibrium outcomes. Following Burgess (2015), we decompose each *q* parameter as:

$$q_{ij} = a_i m_{ij} e_j \qquad (8)$$

Here, a_i is a species-specific parameter that represents how easy species i is to catch across all fleets; m_{ij} represents the degree to which fleet j targets species i compared with other species (we therefore require $m_{sj} + m_{wj} = 1$ for all fleets j); and e_j represents the efficiency of fleet j (i.e., how much catch does it obtain per unit of effort – and therefore per unit of cost), all else equal. We now assume that the weak stock is defined by $\frac{a_w}{r_w} > \frac{a_s}{r_s}$.

2.3 | Simulated evaluations of the model

We performed three groups of simulations to examine overexploitation and extinction risk under bioeconomic scenarios in which equilibria could not be analytically derived. First, we evaluate a 'constant price' scenario, which assumes that prices are constant and CPUE is linearly correlated with abundance. This scenario allows us to implicitly explore interactions between price dynamics and weak stock dynamics without having to specify the price function. In this scenario, we simulate weak-stock equilibria – based on Equations (1) and (2) – over a range of vulnerability ratios (V_w/V_s) and strong and weak stock prices, with other parameter values

fixed (Figure 1a–d). Second, in a 'fisheries subsidies' scenario, we examine the impact of fisheries subsidies on overexploitation and extinction risk. This scenario is equivalent to the 'constant price' scenario except that we decrease fishing costs by 25% to mimic fisheries subsidies. We selected 25% because it reflects that magnitude of subsidies for multi-species trawl fisheries in Sumaila et al. (2010) (Figure 2).

Finally, we evaluate a 'non-constant price' scenario in which we evaluate various combinations of price flexibility and catch flexibility using Equation (3). This scenario is of special interest because price flexibility (f_i) and catch flexibility (β_i) can interact to threaten a target species (Burgess, Costello, et al., 2017). In the context of weak-stock dynamics, catch flexibility has the additional interesting property that it makes both the vulnerability ratio of the two stocks and the identity of the weak stock dependent on the stocks' relative abundance (Figure 3). To explore these conditions and their interactions, we simulate four sub-scenarios: (1) a reference scenario with $f_s = f_w = 0$ (constant prices) and $\beta_s = \beta_w = 1$ (CPUE linear in abundance); (2) a scenario in which both stocks have positive price flexibilities ($f_s = f_w = 0.22$) and only the strong stock has hyperstable catches ($\beta_s = 0.56; \beta_w = 1$); (3) the same scenario as (2) where the catch
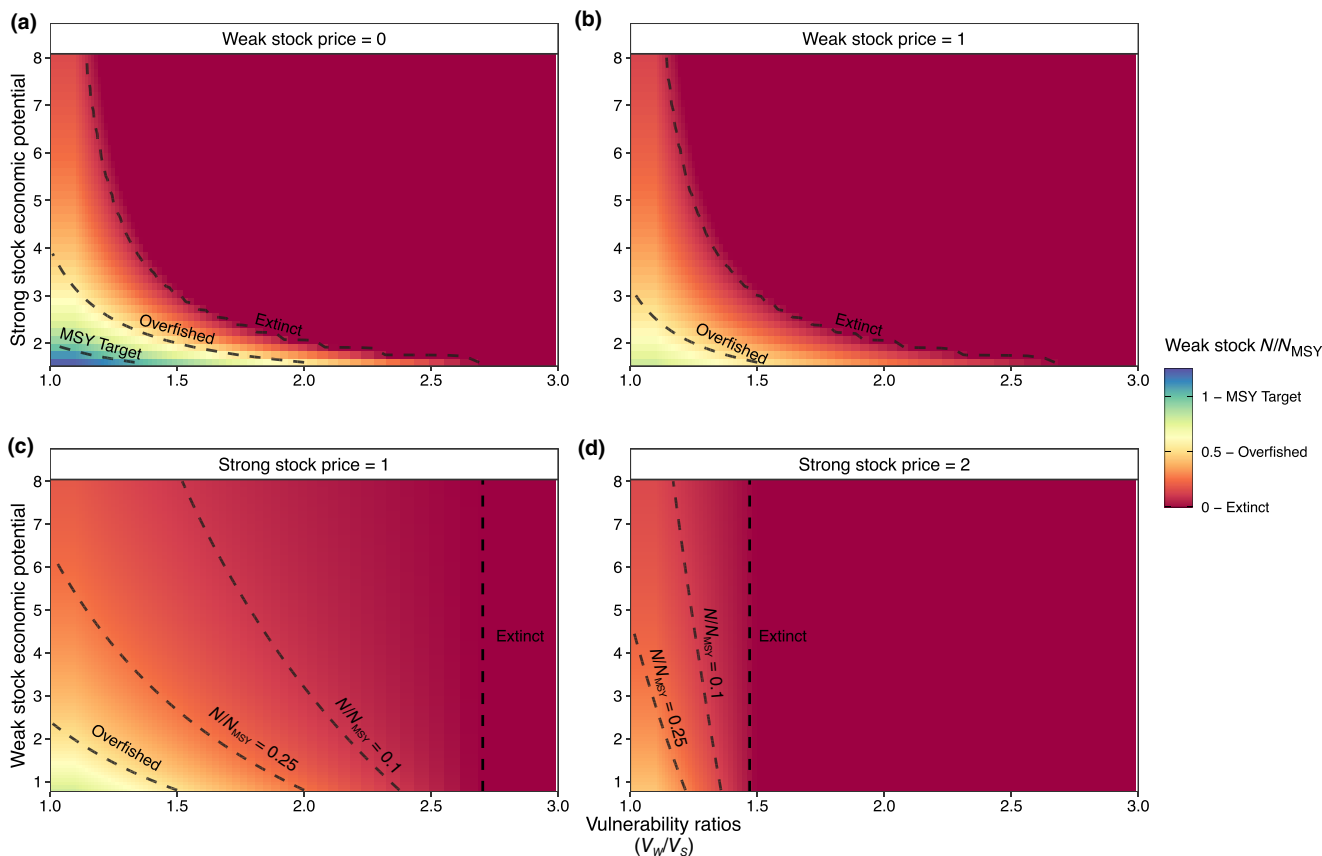

FIGURE 1 Equilibrium abundance for the constant price scenario. Weak stock depletion (N/N_{MSY}) is shown for a range of vulnerability ratios and revenue potential for both stocks. The synergy zone that drives the weak stock extinct with higher prices of the strong stock is shown by the outer convex curve. Higher vulnerability ratios indicate higher vulnerability for the weak stock. Parameter values for all panels are: $q_s = q_w = 0.02$, $c = 0.05$, $K_s = 4$, $K_w = 2$, $r_s = 1$; $r_w = 0.1$–0.99 at 0.1 intervals. Parameter values for panels a and b: $p_s = 0.1$ to 10 at 0.2 intervals, $p_w = 0$ (a) and 1 (b). Parameter values for panels c and d: $p_w = 0.1$ to 10 at 0.1 intervals, $p_s = 1$ (c) and 2 (d).

flexibilities are reversed and it is now the weak stock with hyper-stable catches ($\beta_s = 1$; $\beta_w = 0.56$); and (4) the same scenario where both stocks have hyperstable catches ($\beta_s = \beta_w = 0.56$). These f_i and β_i values are medians from a meta-analysis of actual fisheries (Burgess, Costello, et al., 2017). All parameter values for each simulation are shown in Table 1. Simulations were run in R version 4.2.3 (R Core Team, 2021) with the deSolve (Soetaert et al., 2010) package. All code used is available at https://github.com/lmfeitos/bycatch-biocon-model.

3 | RESULTS

3.1 | Analytical results

Given an equilibrium effort, E^*, the equilibrium abundance of stock i, N_i^*, can be found by setting the right-hand side of Equation (1) equal to zero. This cannot be done analytically when CPUE is non-linear in abundance ($\beta_i \neq 1$). However, with $\beta_i = 1$, N_i^* is given by:

$$N_i^* = K_i\left(1 - \frac{q_i}{r_i}E^*\right) = K_i\left(1 - V_iE^*\right),\tag{9}$$

where $i = s$ or w.

The smallest equilibrium effort that drives stock i to extinction, denoted $E_{x,i}$, is found by setting the right-hand side of Equation (9) equal to zero:

$$E_{x,i} = \frac{1}{V_i},\tag{10}$$

where $i = s$ or w.

Extinction of the weak stock occurs at a smaller E^*, because it has greater vulnerability ($V_w > V_s$). Therefore, three extinction outcomes are possible, depending on E^*: (1) neither species goes extinct, (2) only the weak stock goes extinct, or (3) both stocks go extinct. The strong stock cannot go extinct while the weak stock survives.

Extinction of stock i under open-access requires profits (denoted π, for shorthand) to remain positive ($\pi > 0$) as stock i is depleted ($N_i \to 0$):

$$N_i 0 \underset{}{\lim} \pi > 0 \tag{11}$$

Since the weak stock must go extinct at lower effort than the strong stock, the weak stock will go extinct if the strong stock alone can support an equilibrium effort greater than the effort that would drive
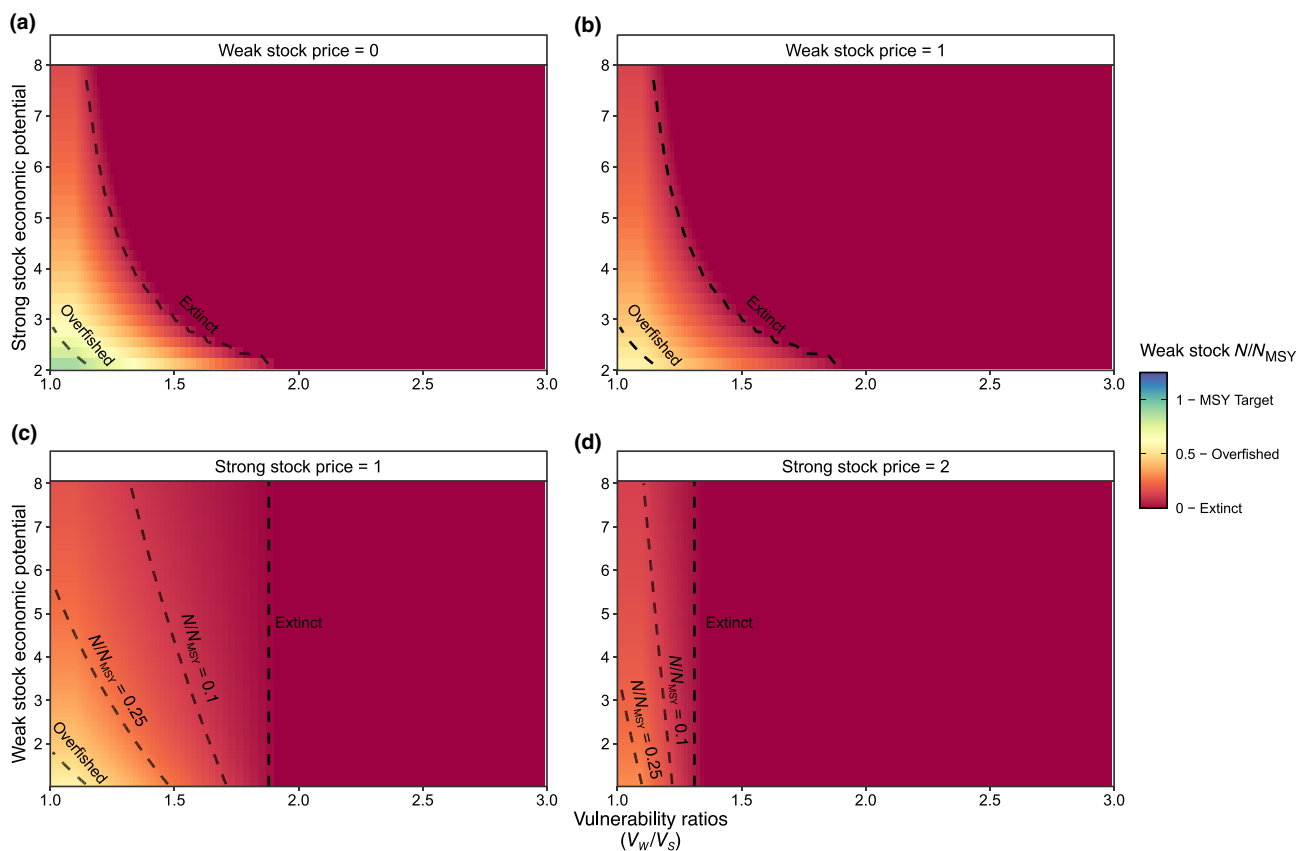

FIGURE 2 Equilibrium abundance for the constant price with a fishing subsidy scenario. Weak stock depletion (N/N_{MSY}) is shown for a range of vulnerability ratios and revenue potential for both stocks. The synergy zone that drives the weak stock extinct with higher prices of the strong stock is shown by the outer convex curve. Higher vulnerability ratios indicate higher vulnerability for the weak stock. Parameter values for all figures are: $q_s = q_w = 0.02$, $c = 0.0375$, $K_s = 4$, $K_w = 2$, $r_s = 1$; $r_w = 0.1$ to 0.99 at 0.1 intervals. Parameter values for panels a and b: $p_s = 0.1$ to 10 at 0.2 intervals, $p_w = 0$ (a) and 1 (b). Parameter values for panels c and d: $p_w = 0.1$ to 10 at 0.1 intervals, $p_s = 1$ (c) and 2 (d).

FIGURE 3 Vulnerability and CPUE dynamics as a function of stock abundance for different values of β. Hyperstable catch is simulated with $\beta = .56$ and not hyperstable with $\beta = 1$.

Catch flexibility — Hyperstable — Not hyperstable
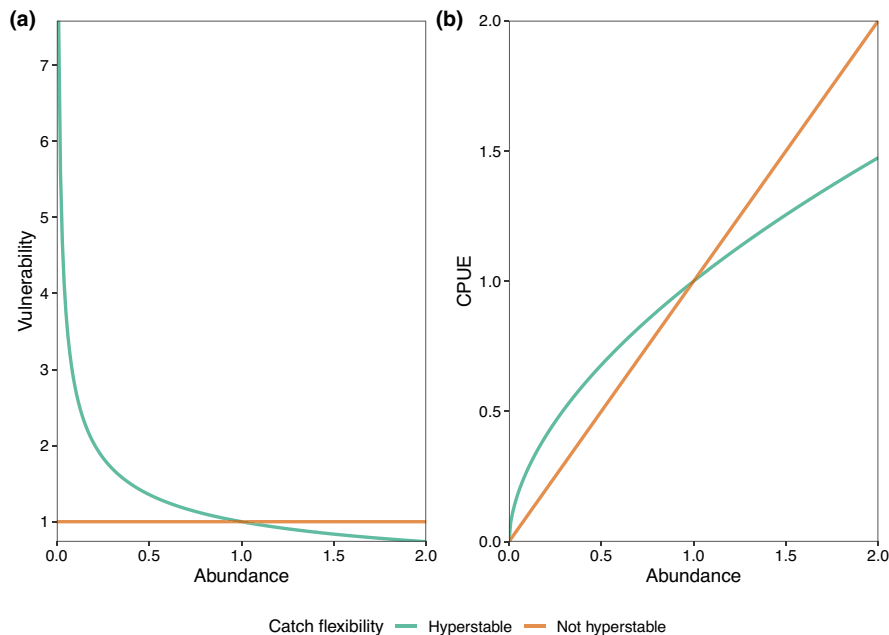
the weak stock extinct, $E_{x,w}$. We can solve for the equilibrium effort with the strong stock alone, which we denote E_s^*, by setting the right-hand side of Equation (2) equal to zero, with $N_w = 0$, solving for N_s, inserting the result into Equation (9), and solving for E (again assuming $\beta_s = \beta_w = 1$). This yields the following expression for E_s^*:

$$E_s^* = \frac{1}{V_s}\left[1 - \frac{c}{p_s(N_s^*)q_s K_s}\right] \tag{12}$$

The weak stock is extinct at equilibrium if $E_s^* \geq E_{x,w}$ (i.e., if the equilibrium effort the strong stock supports on its own, E_s^*, is large enough to drive the weak stock extinct, $E_{x,w}$). Using Equations (10) and (12), we can rewrite this extinction condition for the weak stock as:

$$\frac{V_w}{V_s}\left[1 - \frac{c}{p_s(N_s^*)q_s K_s}\right] \geq 1 \tag{13}$$

From inequality (13), we can see the potential for the price and weak stock mechanisms to synergistically cause the weak stock's extinction under conditions where neither mechanism could cause the weak stock's extinction on its own. As the strong stock's price, $p_s(N_s^*)$, increases, the term $\frac{c}{p_s(N_s^*)q_s K_s}$ decreases and the term $\left[1 - \frac{c}{p_s(N_s^*)q_s K_s}\right]$ approaches 1. We can think of $\frac{p_s(N_s^*)q_s K_s}{c}$ as measuring the strong stock's economic potential. For example, with constant prices, $\frac{p_s q_s K_s}{c}$ represents the maximum profit margin (revenues divided by costs) that the strong stock can generate on its own, if its abundance were at carrying capacity, K_s. Inequality (13) implies that the range of vulnerabilities allowing the weak stock to persist shrinks as the economic potential of the strong stock becomes greater.

If $\left[1 - \frac{c}{p_s(N_s^*)q_s K_s}\right] = 1$, then the weak stock must go extinct, because $\frac{V_w}{V_s} > 1$, by the definitions of the weak and strong stocks. With a constant (and finite) strong stock price, p_s, inequality (13) implies a range of weak stock vulnerabilities that will not cause extinction:

$$V_s < V_w < \frac{V_s}{\left[1 - \frac{c}{p_s q_s K_s}\right]} \tag{14}$$

However, increasing p_s narrows this range (Figure 1a,b). Therefore, adding price flexibility of the strong stock increases the range of vulnerabilities that cause a weak stock to go extinct and narrows the scope for co-existence. Indeed, if the strong stock's price flexibility were large enough to cause its own extinction as a target species (i.e., regardless of the profit contributions of the weak stock), then all stocks in the same fishery having higher vulnerability would go extinct as well.

In contrast, adding price flexibility to the weak stock cannot generally create a synergistic extinction condition for either stock. The price of the weak stock does not affect whether it can be driven extinct via effort supported by the strong stock (Figure 1c,d). Mathematically, we can see that $p_w(N_w^*)$ (the price of the weak stock) does not appear in inequality (13) (the extinction condition of the weak stock). Moreover, price flexibility of the weak stock cannot cause extinction of the strong stock, because it would first have to cause extinction of the weak stock at a lower fishing effort. If price flexibility of the weak stock were sufficiently high to cause the weak stock's extinction as a target species, then the characteristics of the strong stock would not matter – the weak stock would go extinct. A synergy – between the existence of a strong stock and weak-stock price flexibility – causing the weak stock's extinction, can only occur in the extremely narrow case of a weak stock with high enough f_w to cause its extinction at low abundance, but where there is also a stable equilibrium at high abundance and a tipping-point abundance in between (illustrated in Burgess, Costello, et al.'s, 2017; Figure 1a). In this case, the extra fishing revenue from the strong stock could eliminate the positive equilibrium and make extinction the only possible outcome.

With MSY management of the strong stock [from Equation (4)], $E^* = \frac{1}{2V_s}$, the weak stock survives if $V_w < 2V_s$ (Burgess et al., 2013). Therefore, if the strong stock is profitable enough to require MSY

TABLE 1 Parameter values used in each simulation scenario.

Parameter	Scenarios		
	Constant prices	Subsidy	Price ~ catch
Price, strong stock (p_s)	0.1–10 by 0.5	0.1–10 by 0.5	–
Price, weak stock (p_w)	0.1–10 by 0.5	0.1–10 by 0.5	–
Carrying capacity, strong stock (K_s)	4	4	4
Carrying capacity, weak stock (K_w)	2	2	2
Intrinsic growth rate, strong stock (r_s)	0.1–1 by 0.01	0.1–1 by 0.01	1
Intrinsic growth rate, weak stock (r_w)	0.1–0.9 by 0.01	0.1–0.9 by 0.01	0.99
Catchability, both stocks ($q_{s,w}$)	0.02	0.02	0.02
Cost per unit effort (c)	0.05	0.0375	0.05
Price flexibility, strong stock (f_s)	–	–	0; 0.22
Price flexibility, weak stock (f_w)	–	–	0; 0.22
Catch flexibility, strong stock (β_s)	–	–	1; 0.56
Catch flexibility, weak stock (β_w)	–	–	1; 0.56
Response rate of effort to profits (α)	–	–	1
Price function scalar, strong stock (A_s) = weak stock (A_w)	–	–	1

Note: Values of $f = 0.22$ and $\beta = .56$ were chosen based on the median values obtained by Burgess, Costello, et al. (2017) through a meta-analysis of such values for aquatic species. Values of growth rate for the strong stock were always maintained higher than those for the weak stock since weaker stocks are less productive than stronger stocks by definition.

management (i.e., if its open-access equilibrium abundance is lower than its MSY abundance), then the critical weak stock vulnerability resulting in weak stock extinction must be lower than $2V_s$. Given the differences in growth rates (r) among species caught in multi-species fisheries, which are often much larger than a factor of two (Zhou et al., 2012), this viability condition under open-access seems potentially quite restrictive.

3.2 | Multiple fleets

So far, we have only considered a scenario with one type of fleet, whose selectivities for the two species (represented by the q parameters) are fixed. With multiple fleets, and dynamics governed by Equations (6) through (9), we find that it matters substantially, for

extinction risk, whether there are selectivity constraints (i.e., constraints on m_{ij} values) or not.

With no selectivity constraints (i.e., where all m_{ij} values are possible), it follows from the results of Burgess (2015) that competition between all possible fleets will result in a competitive equilibrium where all fleets have the highest possible efficiency (which we denote e_{MAX}) and where:

$$p_s(N_s)\alpha_s N_s^{\beta_s} = p_w(N_w)\alpha_w N_w^{\beta_w} \tag{15}$$

Equation (15) is satisfied at the point where all effort isoclines (i.e., the sets of points where $\frac{dE_j}{dt} = 0$) having the same efficiency intersect. The intuition of Equation (15) is that it represents conditions under which all fleets having the same efficiency have the same profitability, because fleet profits are insensitive to which stock they target (determined by the m_{ij} parameters). See Burgess (2015) for an expanded demonstration of this result.

Our model explicitly considers, via Equation (7), that fleets – each with fixed selectivity and targeting – compete for fish and profitability determines entry or exit. However, Burgess and Plank (2020) show that the conditions defined by Equation (15) would also be an attractor in a situation where individual vessels could switch between fleets by adjusting their targeting (m_{ij}). If $p_s(N_s)\alpha_s N_s^{\beta_s} > p_w(N_w)\alpha_w N_w^{\beta_w}$, then vessels would have an incentive to shift their behaviour to target the strong stock more, and vice versa. The ideal free distribution of vessels among fleets would cause the system to approach Equation (15). Therefore, whether fleets (i.e., combinations of gear, timing, target species, etc.) compete for fish or for vessels (via vessels switching between them), Equation (15) will be an attractor of the dynamics.

As long as each species' price has a finite maximum as it approaches extinction (which requires $f_i < \beta_i$ if prices follow Equation (3)), the set of points satisfying Equation (15) goes through the origin. Therefore, the fact that equilibrium must satisfy Equation (15) implies that fleet diversity prevents extinction (see Burgess, 2015). For example, if the weak stock were approaching extinction, vessels would have an incentive to shift their behaviour to participate in fleets that targeted the strong stock more. On the other hand, if $f_i > \beta_i$ for one of the species, then rising prices as stock i is depleted creates incentives to specialize on it right up until it is extinct. In other words, fleet diversity prevents extinction from technical interactions, but does not prevent extinctions from price dynamics.

In practice, however, weak stock problems arise because selectivities are constrained. For example, if it were possible to set $m_{sj} = 1$, then there would be no catch of the weak stock, which is not usually possible in real fisheries. Therefore, assuming all m_{ij} values are possible is unrealistic. Instead, suppose that there was a minimum m_{wj} for all fleets j, denoted m_{wmin}. (There could also be a maximum m_{wj} but it would be irrelevant to the resulting competitive equilibrium, as we will see). If the weak stock were approaching extinction, then vessels would have incentives to participate in fleets that targeted the strong stock more – i.e., with higher m_{sj}, and consequently lower m_{wj}. Therefore, assuming the weak stock has a finite maximum price, the weak stock can only be driven extinct if its one-fleet

extinction conditions, as described above, are satisfied by a fleet, j, with $q_{wj} = a_w m_{wmin} e_{MAX}$ – a fleet with the highest possible efficiency and lowest possible targeting of the weak stock. Competition between all possible fleets would favor this fleet, and therefore this fleet's parameters would determine the weak stock's viability under competition (see Burgess, 2015).

The results of the previous paragraph imply that – even if selectivities are constrained – diversity in selectivity among fleets reduces (but generally does not eliminate) weak stock extinction threats. To see this, compare the case with competition among all possible fleets with a particular efficiency (e_j) – which would result in a fleet with m_{wmin} winning out – and a case with one fleet with m_{wj} selected at random, which would target the weak stock to a greater extent, on average ($m_{wj} > m_{wmin}$). The randomly selected fleet will result in a higher q_{wj}, and a lower q_{sj}, on average, and therefore a greater chance of weak stock extinction. As Burgess (2015) shows, increasing the diversity of fleet efficiencies has the opposite effect – increasing extinction risk – because competition favours the highest efficiency and diversity increases the chances of sampling a high-efficiency fleet.

3.3 | Simulation results

In our single-fleet simulations exploring a range of relative stock vulnerabilities and prices (Figure 1), we find that the parameter space allowing coexistence between a strong and weak stock in a multi-species fishery operating under open-access conditions is quite small, even if the strong stock's economic potential is small. Any weak stock that is ~2.5 times more vulnerable than the strong stock would go extinct given our assumptions and the evaluated parameter values (Figure 1a). If a strong stock has sufficient economic potential to be overfished (beyond F_{MSY}) under open-access, then the weak stock's critical vulnerability is less than $2V_s$ (Burgess et al., 2013). This vulnerability threshold shrinks as the strong stock's economic potential increases, approaching 1 (i.e., all weak stocks go extinct) as the strong stock's economic potential or price approaches infinity (Figure 1a,b). We call this mechanism – whereby the strong stock's economic potential or price reduces the scope of weak stock coexistence – 'the synergy of endangerment', illustrated by the dashed lines in Figure 1a.

With multiple fleets and no selectivity constraints, there would be no synergy of endangerment, because competition would shift towards fleets that did not target the weak stock as much. However, with constrained selectivity, the synergy of endangerment would still apply to the one-fleet case with a fleet having targeting parameter m_{wmin} and efficiency e_{MAX}.

In contrast to the synergy of endangerment, Figure 1c,d illustrates how the weak stock's price and economic potential do not affect the vulnerability threshold at which it is driven extinct. Thus, there is no synergy between the own-price- and vulnerability-related extinction conditions for the weak stock, as shown above analytically. Of course, raising the weak stock's economic potential does reduce its equilibrium abundance, introducing a 'synergy of overfishing' (Figure 1c,d).

Figure 2 shows that introducing fishing subsidies increases depletion in all cases and narrows the range of vulnerabilities allowing coexistence. The intuition is that subsidies lower costs, which effectively increases the economic potential of both stocks. In general, a 1% decrease in per capita costs results in a 1.2% decrease in the vulnerability ratio that allows the weak stock to persist (Figure 2), all else equal.

Our simulations in Figure 4 illustrate how realistic values of price flexibility (f) and catch flexibility (β) affect the interaction between price-driven threats and weak-stock threats. Hyperstability causes a stock's vulnerability to increase as its abundance decreases (Equation 5). When the strong stock is hyperstable, this reduces the weak stock's equilibrium depletion by lowering its relative vulnerability as effort increases (Figure 4b vs. a). Conversely, a hyperstable weak stock is depleted or driven extinct faster and at lower vulnerability (q/r), because its relative vulnerability increases as effort increases (Figure 4c vs. a). When both stocks are hyperstable, the weak stock's relative vulnerability still increases as it depletes, because its abundance depletes – and therefore its vulnerability rises – faster than the strong stock's (Figure 4d vs. a). Price flexibility causes the weak stock's price to rise quickly when it is very rare. This economically powers a temporary increase in effort, and a temporary decrease in the strong stock's abundance, which subsides when the weak stock is driven completely extinct (Figure 4c,d).

4 | DISCUSSION

We analyse the interaction between price-related and multi-species fishery related threats to harvested species under open-access conditions. Our results suggest that these threats can act synergistically, jointly posing extinction threats to weak stocks under conditions where neither could pose a threat alone. Our results also suggest that there is a relatively small range of biological and economic conditions (parameters) under which weak stocks can survive open-access. Subsidies and catch hyperstability both exacerbate threats and shrink the parameter range that allows coexistence. Our results further raise concerns about the detrimental effects of fisheries subsidies beyond allowing overfishing to continue (Sumaila et al., 2024), since we also predict a higher risk of fisheries-induced extinctions facilitated by such subsidies. Indeed, the higher presence of harmful (capacity-enhancing) subsidies is linked to a higher number of threatened shark species, with the beneficial (management) subsidies being linked to a lower number of threatened species (Pacoureau et al., 2023). With multiple fleets, diversity in their abilities to target the different species will tend to prevent extinction, whereas diversity in their efficiencies could exacerbate extinction risk (Burgess, 2015).

Although we do not analyse species interactions here, previous research suggests that introducing ecological competition between species in multi-species fisheries would further narrow the scope of conditions under which they could coexist (Burgess et al., 2019). The same applies to multi-species fisheries systems exploiting species with trophic interactions (Burgess, 2015), which leads to disproportionately higher top predator extinction compared with their prey or
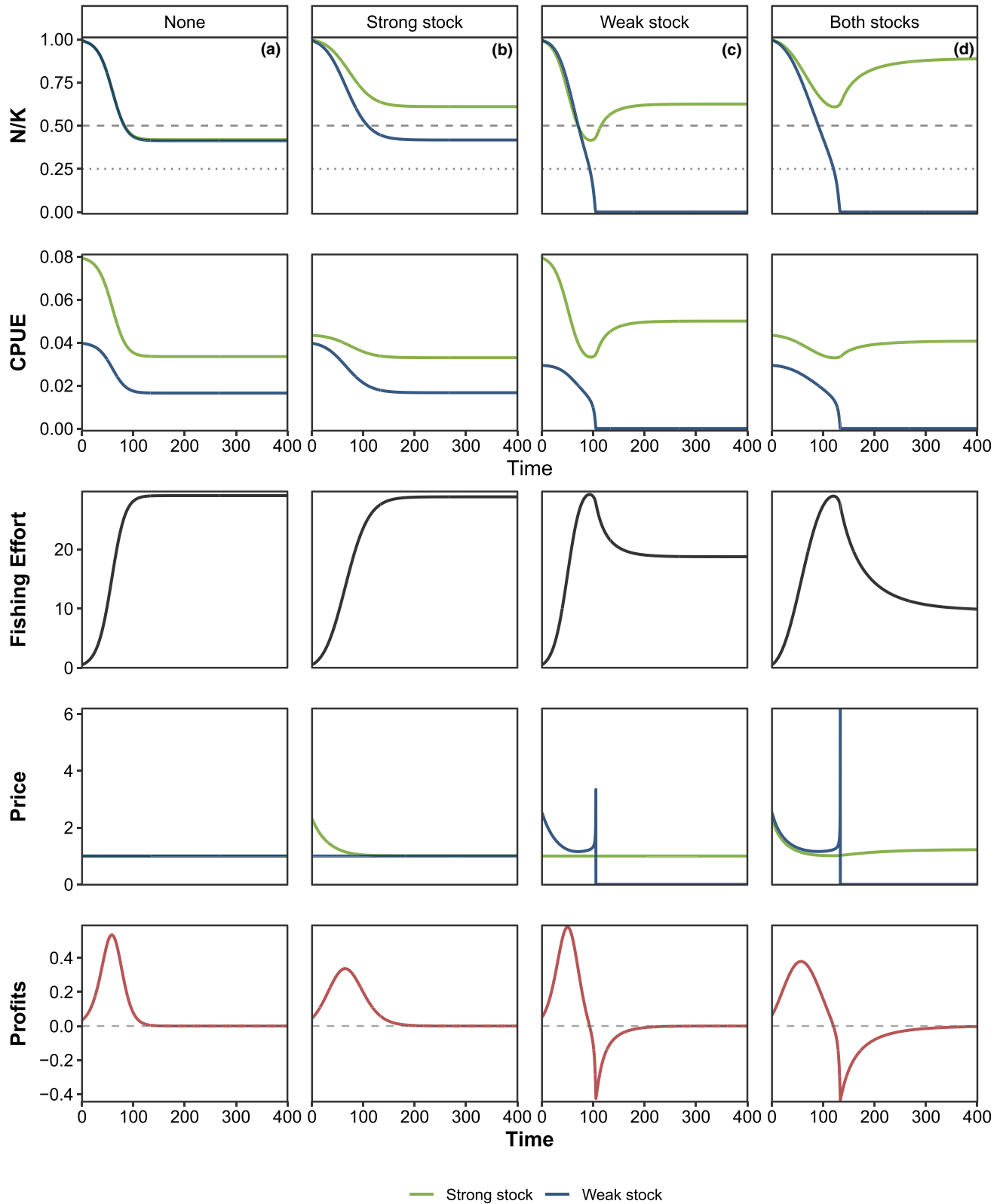
FIGURE 4 Simulations of non-constant price under different hyperstability scenarios. Time series simulations for the equilibria of fishing effort, strong and weak stock depletion, and profits for different values of price flexibility (f) and catch flexibility (β). Each column represents a scenario simulation. Dashed and dotted lines in panel A represent commonly used fisheries abundance target ($N/K=0.5$) and limit ($N/K=0.25$) reference points. Parameter values: $q_s=q_w=0.02$, $r_s=1$, $r_w=0.99$, $K_s=4$, $K_w=2$, $\alpha=1$, $A_s=A_w=1$, $c=0.05$. Initial variable values for N_s and N_w equaled their respective K values, and the initial effort $E=0.5$ for all scenarios.

higher commercial value to the fishery (Matsuda & Abrams, 2006). While such consequences are often context dependent, the extinction of longer-lived taxa, which often exert top-down control in marine food webs, can amplify fisheries-induced trophic cascades and destabilize the community trophic structure (Salomon et al., 2010; Zhou & Smith, 2017).

Our results raise important questions for fisheries science and management. Perhaps most importantly: if open-access fishing should so easily cause extinction, why have there been relatively few documented global extinctions of harvested marine species (Le Pape et al., 2017; McCauley et al., 2015)?

One possible explanation – for teleost fish – is that they are protected from extinction by high fecundity: a small number of females can produce millions of juveniles (Le Pape et al., 2017). This would protect fish from extinction only if juveniles achieved higher survival rates at very low abundance, such that species' maximum growth rates are much higher than they currently appear – a possibility some scholars find unlikely (Sadovy, 2001). Indeed, studies have tended to estimate fish species' maximum population growth rates as similar to those of terrestrial vertebrates (which do not produce millions of eggs) (e.g., Myers et al., 1999). On the other hand, many fish species have weak empirical relationships between recruitment and spawning biomass (Szuwalski et al., 2015) – a pattern more consistent with the possibility of high fecundity allowing for fast growth from low abundance. If high fecundity manifested as high steepness (i.e., stronger-density-dependence of growth than our logistical model assumes), without affecting apparent maximum growth rates, this could blunt some price-driven extinction threats, but not multispecies-harvesting threats (see Burgess, 2014; Burgess et al., 2013; Burgess, Fredston-Hermann, et al., 2017). High fecundity would also not protect large-bodied marine fauna such as chondrichthyans, marine mammals, and sea turtles caught as bycatch, which do not have similarly high fecundity to teleosts and are often subject to growth overfishing (Froese, 2004). Furthermore, it would not protect any fished species from severe depletion and, if these species have economic value, they could become trapped in a 'poaching pit' (Bulte, 2003).

A second factor that intuitively seems to naturally protect marine species from extinction is the vastness of the ocean, which contributes to high fishing costs and offers refugia away from fishing. The vastness of the ocean might protect species against price-driven extinctions in practice but would not on its own protect against extinctions driven by multi-species dynamics. Burgess, Costello, et al. (2017) showed that extinction of a target species from price dynamics can occur if price flexibility (f) is larger than catch flexibility (β). As the target species' abundance declines, the cost of catching the next fish increases, approaching infinity as abundance approaches zero (provided $\beta > 0$). In their model, harvesting can remain profitable as abundance declines when $f > \beta$, because this makes the price of the next catch approach infinity faster than the cost of obtaining it. However, in reality, neither the price of a unit of catch nor its cost can actually reach infinity. Even the literal last fish of a species would sell for a finite price, and catching the last fish would have a finite cost. In a vast ocean, though, it seems likelier

(than in a river or lake, for example) that the finite maximum cost would exceed the finite maximum price, thereby preventing extinction (but not preventing severe depletion). In contrast, a strong stock can indefinitely support an extinction-threatening effort for a weak stock. Thus, the vastness of the ocean cannot protect a weak stock from extinction indefinitely.

Besides the possibility that something (e.g., high fecundity, ocean vastness) inherently protects fished species from extinction, even under open-access, the other possibility is that many fished species would face extinction if subjected to open-access for long enough. If so, determining which species these are, and how many there are, is an urgent research question. Implementing management in time to prevent these extinctions is of the utmost priority. These species likely include high-vulnerability bycatch species, such as sharks (Juan-Jordá et al., 2022), marine mammals, turtles, and birds (Burgess et al., 2018). The first documented extinction of a marine fish – the Java stingaree (*Urolophus javanicus*, Urolophidae) (Constance et al., 2023), the widespread local extirpations of sawfish species (Pristidae spp.) (Yan et al., 2021), and the existence of several elasmobranchs with high probability of extinction due to bycatch overfishing already sounds this alarm (Dulvy et al., 2021; Lessa et al., 2016; Santana et al., 2020). Models such as ours, parametrized with real-world data, could help to proactively identify such species by identifying sets of extinction-threatening bioeconomic conditions even before depletion materializes (Burgess et al., 2013; Burgess, Costello, et al., 2017).

We consider that such examples of this dynamic can occur in both tropical fisheries and those operating under western-style monitoring and management. For example, daggernose (*Isogomphodon oxyrhynchus*, Carcharhinidae) and smalltail (*Carcharhinus porosus*, Carcharhinidae) sharks were common bycatch in gillnet fisheries targeting a mix of more productive and valuable teleost species, mainly the acoupa weakfish (*Cynoscion acoupa*, Sciaenidae), in the Brazilian Amazon coast during the 1980s and 1990s (Lessa, 1997; Stride et al., 1992). Since then, overfishing caused their populations to respectively decline over 90% and 99% within three generations, thus becoming some of the most endangered sharks in the world (Lessa et al., 2016; Santana et al., 2020). Both shark species have low economic value but are much less productive than the teleost species targeted by these fisheries (Oliveira et al., 2020). An example from a more strongly managed fishery is the threat posted to smalltooth sawfish (*Pristis pectinata*, Pristidae) from bycatch in shrimp trawl fisheries in the southeast USA (Graham et al., 2022). Abundance of smalltooth sawfish declined substantially in the 1990s due to high fisheries bycatch, prompting its listing as endangered in the USA's Endangered Species Act in 2003 due to high extinction risk (Brame et al., 2019). Recently, stronger fishery management efforts appear to have reversed the decline, but the slow life history of the species and poor enforcement of the fishing ban are likely to hamper rebuilding (Carlson, 2023). Both of these represent scarcely well-documented examples that demonstrate the nefarious effects that poorly managed multi-species fisheries can have on incidentally caught weak stocks, with or without economic value.

A fourth related possibility is that there have already been more extinctions than we realize. While not clearly indicating extinctions, the latest global IUCN assessment of sharks and rays found that ~25% of species previously classified as Data Deficient actually belonged to one of the threatened categories (Dulvy et al., 2021), thus reinforcing the existence of undocumented and ongoing declines. Indeed, fisheries science, monitoring, and management often go together, and consequently, many of the most overfished fisheries are also relatively data poor (Costello et al., 2016). Determining whether there has been cryptic biodiversity loss is an important research question. These questions gain urgency as human populations and seafood demands continue to grow (Costello et al., 2020), and multi-species fishing technologies, such as fish aggregating devices (FADs), continue to become more efficient (Dagorn et al., 2013). These trends will increase the economic potential of fisheries, and consequently increase the number of species that are non-viable without management.

Our model has several limitations that should be noted. As mentioned above, we do not consider species interactions, which might exacerbate threats (Burgess et al., 2019) or high fecundity and survival at low abundances, which might abate threats (Le Pape et al., 2017). We model multi-species fisheries with only two species, whereas real multi-species fisheries often catch dozens of species. Adding more species to our model – all else equal – would likely exacerbate threats by improving the economic potential of the fishery and extending the incentive to keep fishing. We also focused much of our analysis on equilibrium statics as opposed to transient dynamics. A recent spatially-explicit simulation study (Thurner et al., 2021), exploring opportunistic harvesting combined with a different conceptualization of price dynamics, found that transient dynamics can make abundance of a strong stock a more important driver of extinction risk for the weak stock than its growth rate. Lastly, although our model includes several interacting features – such as hyperstability, price dynamics, subsidies, and multi-species catch – it includes each fairly simply (e.g., constant price flexibility and catch flexibility). Each of these limitations presents an opportunity for future research. Nonetheless, our results shed novel and instructive light on how these model components interact.

Our results underscore the importance of fully incorporating bycatch into fisheries management and treating it under a precautionary approach as done for target stocks. This should occur regardless of whether such management would prevent extinction or merely severe depletion. Indeed, where fisheries have been well managed, there is a broad track record of success in rebuilding depleted stocks and preventing overfishing (Costello et al., 2016; Hilborn et al., 2020; Juan-Jordá et al., 2022), including for weak stocks caught as bycatch in multi-species fisheries (Pacoureau et al., 2023; Warlick et al., 2018). There is a rich literature and history of practice proposing and documenting strategies for successful management of low or high value threatened species caught in multi-species fisheries (Dulvy et al., 2021; Link & Marshark, 2021; Wallace et al., 2011). Open-access fisheries can have pervasive ecological and economic consequences, and successful fisheries management should be a priority, especially in areas where fishing is a key activity for cultural, economic, and food security purposes.

ORCID

Leonardo Manir Feitosa https://orcid.org/0000-0002-1988-5326
Matthew G. Burgess https://orcid.org/0000-0002-3750-4347
Christopher M. Free https://orcid.org/0000-0002-2557-8920
Steven D. Gaines https://orcid.org/0000-0002-7604-3483

REFERENCES

Alroy, J. (2001). A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. *Science*, *292*(5523), 1893–1896. https://doi.org/10.1126/science.1059342

Berck, P. (1979). Open access and extinction. *Econometrica*, *47*(4), 877–882. https://doi.org/10.2307/1914136

Brame, A., Wiley, T., Carlson, J., Fordham, S., Grubbs, R., Osborne, J., Scharer, R., Bethea, D., & Poulakis, G. (2019). Biology, ecology, and status of the smalltooth sawfish Pristis pectinata in the USA. *Endangered Species Research*, *39*, 9–23. https://doi.org/10.3354/esr00952

Branch, T. A., Hilborn, R., & Bogazzi, E. (2005). Escaping the tyranny of the grid: A more realistic way of defining fishing opportunities. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*(3), 631–642. https://doi.org/10.1139/f04-232

Branch, T. A., Lobo, A. S., & Purcell, S. W. (2013). Opportunistic exploitation: An overlooked pathway to extinction. *Trends in Ecology & Evolution*, *28*(7), 409–413. https://doi.org/10.1016/j.tree.2013.03.003

Bulte, E. H. (2003). Open access harvesting of wildlife: The poaching pit and conservation of endangered species. *Agricultural Economics*, *28*(1), 27–37. https://doi.org/10.1016/S0169-5150(02)00036-1

Burgess, M. G. (2014). *Simple solutions to complex problems in fisheries*. University of Minnesota. conservancy.umn.edu/handle/11299/164778

Burgess, M. G. (2015). Consequences of fleet diversification in managed and unmanaged fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(1), 54–70. https://doi.org/10.1139/cjfas-2014-0116

Burgess, M. G., Costello, C., Fredston-Hermann, A., Pinsky, M. L., Gaines, S. D., Tilman, D., & Polasky, S. (2017). Range contraction enables harvesting to extinction. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(15), 3945–3950. https://doi.org/10.1073/pnas.1607551114

Burgess, M. G., Fredston-Hermann, A., Pinsky, M. L., Gaines, S. D., & Tilman, D. (2017). Reply to Le Pape et al.: Management is key to preventing marine extinctions. *Proceedings of the National Academy of Sciences of the United States of America*, 114(31), E6275–E6276. https://doi.org/10.1073/pnas.1708147114

Burgess, M. G., Fredston-Hermann, A., Tilman, D., Loreau, M., & Gaines, S. D. (2019). Broadly inflicted stressors can cause ecosystem thinning. *Theoretical Ecology*, 12(2), 207–223. https://doi.org/10.1007/s12080-019-0417-4

Burgess, M. G., McDermott, G. R., Owashi, B., Peavey Reeves, L. E., Clavelle, T., Ovando, D., Wallace, B. P., Lewison, R. L., Gaines, S. D., & Costello, C. (2018). Protecting marine mammals, turtles, and birds by rebuilding global fisheries. *Science*, 359(6381), 1255–1258. https://doi.org/10.1126/science.aao4248

Burgess, M. G., & Plank, M. J. (2020). What unmanaged fishing patterns reveal about optimal management: Applied to the balanced harvesting debate. *ICES Journal of Marine Science*, 77(3), 901–910. https://doi.org/10.1093/icesjms/fsaa012

Burgess, M. G., Polasky, S., & Tilman, D. (2013). Predicting overfishing and extinction threats in multispecies fisheries. *Proceedings of the National Academy of Sciences of the United States of America*, 110(40), 15943–15948. https://doi.org/10.1073/pnas.1314472110

Carlson, J. K. (2023). Trouble in the trawls: Is bycatch in trawl fisheries preventing the recovery of sawfish? A case study using the US population of smalltooth sawfish, *Pristis pectinata*. *Global Ecology and Conservation*, 48, e02745. https://doi.org/10.1016/j.gecco.2023.e02745

Clark, C. W. (1990). *Mathematical bioeconomics: The optimal management of renewable resources* (2nd ed.). John Wiley & Sons.

Cochrane, K. L. (2020). Reconciling sustainability, economic efficiency and equity in marine fisheries: Has there been progress in the last 20 years? *Fish and Fisheries*, 22(2), 298–323. https://doi.org/10.1111/faf.12521

Collette, B. B., Carpenter, K. E., Polidoro, B. A., Juan-Jordá, M. J., Boustany, A., Die, D. J., Elfes, C., Fox, W., Graves, J., Harrison, L. R., McManus, R., Minte-Vera, C. V., Nelson, R., Restrepo, V., Schratwieser, J., Sun, C.-L., Amorim, A., Brick Peres, M., Canales, C., ... Yáñez, E. (2011). High value and long life—Double jeopardy for tunas and billfishes. *Science*, 333(6040), 291–292. https://doi.org/10.1126/science.1208730

Constance, J., Ebert, D. A., Fahmi, Finucci, B., Simeon, B., & Kyne, P. M. (2023). Urolophus javanicus. *The IUCN Red List of Threatened Species*, 2023, e.T60095A229337053.

Costello, C., Cao, L., Gelcich, S., Cisneros-Mata, M. Á., Free, C. M., Froehlich, H. E., Golden, C. D., Ishimura, G., Maier, J., Macadam-Somer, I., Mangin, T., Melnychuk, M. C., Miyahara, M., de Moor, C. L., Naylor, R., Nøstbakken, L., Ojea, E., O'Reilly, E., Parma, A. M., ... Lubchenco, J. (2020). The future of food from the sea. *Nature*, 588(7836), 95–100. https://doi.org/10.1038/s41586-020-2616-y

Costello, C., Ovando, D., Clavelle, T., Strauss, C. K., Hilborn, R., Melnychuk, M. C., Branch, T. A., Gaines, S. D., Szuwalski, C. S., Cabral, R. B., Rader, D. N., & Leland, A. (2016). Global fishery prospects under contrasting management regimes. *Proceedings of the National Academy of Sciences of the United States of America*, 113(18), 5125–5129. https://doi.org/10.1073/pnas.1520420113

Courchamp, F., Angulo, E., Rivalan, P., Hall, R. J., Signoret, L., Bull, L., & Meinard, Y. (2006). Rarity value and species extinction: The anthropogenic Allee effect. *PLoS Biology*, 4(12), e415. https://doi.org/10.1371/journal.pbio.0040415

Dagorn, L., Holland, K. N., Restrepo, V., & Moreno, G. (2013). Is it good or bad to fish with FADs? What are the real impacts of the use of drifting FADs on pelagic marine ecosystems? *Fish and Fisheries*, 14(3), 391–415. https://doi.org/10.1111/j.1467-2979.2012.00478.x

Dao, T., Quaas, M., Koemle, D., Ehrlich, E., & Arlinghaus, R. (2023). Can price feedbacks cause human behavior-induced tipping points in exploited fish stocks? An extension of the bioeconomic Gordon-Schaefer model. *Fisheries Research*, 259, 106550. https://doi.org/10.1016/j.fishres.2022.106550

Dulvy, N. K., Pacoureau, N., Rigby, C. L., Pollom, R. A., Jabado, R. W., Ebert, D. A., Finucci, B., Pollock, C. M., Cheok, J., Derrick, D. H., Herman, K. B., Sherman, C. S., VanderWright, W. J., Lawson, J. M., Walls, R. H. L., Carlson, J. K., Charvet, P., Bineesh, K. K., Fernando, D., ... Simpfendorfer, C. A. (2021). Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Current Biology*, 31(21), 4773–4787.e8. https://doi.org/10.1016/j.cub.2021.08.062

Dulvy, N. K., Sadovy, Y., & Reynolds, J. D. (2003). Extinction vulnerability in marine populations. *Fish and Fisheries*, 4(1), 25–64. https://doi.org/10.1046/j.1467-2979.2003.00105.x

Eales, J., Durham, C., & Wessells, C. R. (1997). Generalized Models of Japanese Demand for Fish. *American Journal of Agricultural Economics*, 79(4), 1153–1163. https://doi.org/10.2307/1244272

FAO. (2024). *The state of world fisheries and aquaculture 2024*. FAO. https://doi.org/10.4060/cd0683en

Froese, R. (2004). Keep it simple: Three indicators to deal with overfishing. *Fish and Fisheries*, 5(1), 86–91. https://doi.org/10.1111/j.1467-2979.2004.00144.x

Gordon, H. S. (1954). The economic theory of a common-property resource: The fishery. *The Journal of Political Economy*, 62(2), 124–142.

Graham, J., Kroetz, A. M., Poulakis, G. R., Scharer, R. M., Carlson, J. K., Lowerre-Barbieri, S. K., Morley, D., Reyier, E. A., & Grubbs, R. D. (2022). Commercial fishery bycatch risk for large juvenile and adult smalltooth sawfish (*Pristis pectinata*) in Florida waters. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 32(3), 401–416. https://doi.org/10.1002/aqc.3777

Harley, S. J., Myers, R. A., & Dunn, A. (2001). Is catch-per-unit-effort proportional to abundance? *Canadian Journal of Fisheries and Aquatic Sciences*, 58(9), 1760–1772. https://doi.org/10.1139/f01-112

Hastings, A., Gaines, S. D., & Costello, C. (2017). Marine reserves solve an important bycatch problem in fisheries. *Proceedings of the National Academy of Sciences of the United States of America*, 114(34), 8927–8934. https://doi.org/10.1073/pnas.1705169114

Hilborn, R., Amoroso, R. O., Anderson, C. M., Baum, J. K., Branch, T. A., Costello, C., de Moor, C. L., Faraj, A., Hively, D., Jensen, O. P., Kurota, H., Little, L. R., Mace, P., McClanahan, T., Melnychuk, M. C., Minto, C., Osio, G. C., Parma, A. M., Pons, M., ... Ye, Y. (2020). Effective fisheries management instrumental in improving fish stock status. *Proceedings of the National Academy of Sciences of the United States of America*, 117(4), 2218–2224. https://doi.org/10.1073/pnas.1909726116

Holden, M. H., & McDonald-Madden, E. (2017). High prices for rare species can drive large populations extinct: The anthropogenic Allee effect revisited. *Journal of Theoretical Biology*, 429, 170–180. https://doi.org/10.1016/j.jtbi.2017.06.019

Houck, J. P. (1965). The Relationship of Direct Price Flexibilities to Direct Price Elasticities. *American Journal of Agricultural Economics*, 47(3), 789–792. https://doi.org/10.2307/1236288

Juan-Jordá, M. J., Murua, H., Arrizabalaga, H., Merino, G., Pacoureau, N., & Dulvy, N. K. (2022). Seventy years of tunas, billfishes, and sharks as sentinels of global ocean health. *Science*, 378(6620), eabj0211. https://doi.org/10.1126/science.abj0211

Larkin, P. A. (1963). Interspecific competition and exploitation. *Journal of the Fisheries Research Board of Canada*, 20(3), 647–678. https://doi.org/10.1139/f63-044

Le Pape, O., Bonhommeau, S., Nieblas, A.-E., & Fromentin, J.-M. (2017). Overfishing causes frequent fish population collapses but rare extinctions. *Proceedings of the National Academy of Sciences of the United States of America*, 114(31), E6274. https://doi.org/10.1073/pnas.1706893114

Lessa, R., Batista, V. S., & Santana, F. M. (2016). Close to extinction? The collapse of the endemic daggernose shark (*Isogomphodon oxyrhynchus*) of Brazil. *Global Ecology and Conservation*, 7, 70–81. https://doi.org/10.1016/j.gecco.2016.04.003

Lessa, R. P. (1997). Sinopse dos estudos sobre elasmobrânquios da costa do Maranhão. *Boletim Do Laboratório de Hidrobiologia*, *10*, 19–36.

Link, S. J., & Marshark, A. R. (2021). *Ecosystem-based fisheries management: Progress, importance, and impacts in the United States*. Oxford University Press. https://doi.org/10.1093/oso/9780192843463.001.0001

Marchal, P., De Oliveira, J. A. A., Lorance, P., Baulier, L., & Pawlowski, L. (2013). What is the added value of including fleet dynamics processes in fisheries models? *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(7), 992–1010. https://doi.org/10.1139/cjfas-2012-0326

Matsuda, H., & Abrams, P. A. (2006). Maximal yields from multispecies fisheries systems: Rules for systems with multiple trophic levels. *Ecological Applications*, *16*(1), 225–237. https://doi.org/10.1890/05-0346

May, R. M., Beddington, J. R., Clark, C. W., Holt, S. J., & Laws, R. M. (1979). Management of multispecies fisheries. *Science*, *205*(4403), 267–277. https://doi.org/10.1126/science.205.4403.267

McCauley, D. J., Pinsky, M. L., Palumbi, S. R., Estes, J. A., Joyce, F. H., & Warner, R. R. (2015). Marine defaunation: Animal loss in the global ocean. *Science*, *347*(6219), 1255641.

Myers, R. A., Bowen, K. G., & Barrowman, N. J. (1999). Maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences*, *56*(12), 2404–2419. https://doi.org/10.1139/f99-201

Oliveira, C. D., Lessa, R., Almeida, Z., & Santana, F. M. (2020). Biology and fishery of Acoupa weakfish Cynoscion acoupa (Lacepède, 1801): A review. *Neotropical Biology and Conservation*, *15*(3), 333–349. https://doi.org/10.3897/neotropical.15.e55563

Pacoureau, N., Carlson, J. K., Kindsvater, H. K., Rigby, C. L., Winker, H., Simpfendorfer, C. A., Charvet, P., Pollom, R. A., Barreto, R., Sherman, C. S., Talwar, B. S., Skerritt, D. J., Sumaila, U. R., Matsushiba, J. H., VanderWright, W. J., Yan, H. F., & Dulvy, N. K. (2023). Conservation successes and challenges for wide-ranging sharks and rays. *Proceedings of the National Academy of Sciences of the United States of America*, *120*(5), e2216891120. https://doi.org/10.1073/pnas.2216891120

R Core Team. (2021). *R: A language and environment for statistical computing* (Version 4.2.3) [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Rose, G. A., & Kulka, D. W. (1999). Hyperaggregation of fish and fisheries: How catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. *Canadian Journal of Fisheries and Aquatic Sciences*, *56*, 118–127.

Sadovy, Y. (2001). The threat of fishing to highly fecund fishes. *Journal of Fish Biology*, *59*, 90–108. https://doi.org/10.1111/j.1095-8649.2001.tb01381.x

Salomon, A. K., Gaichas, S. K., Shears, N. T., Smith, J. E., Madin, E. M. P., & Gaines, S. D. (2010). Key features and context-dependence of fishery-induced trophic cascades. *Conservation Biology*, *24*(2), 382–394. https://doi.org/10.1111/j.1523-1739.2009.01436.x

Santana, F. M., Feitosa, L. M., & Lessa, R. P. (2020). From plentiful to critically endangered: Demographic evidence of the artisanal fisheries impact on the smalltail shark (*Carcharhinus porosus*) from Northern Brazil. *PLoS One*, *15*(8), e0236146. https://doi.org/10.1371/journal.pone.0236146

Schaefer, M. B. (1957). Some considerations of population dynamics and economics in relation to the management of the commercial marine fisheries. *Journal of the Fisheries Research Board of Canada*, *14*(5), 669–681. https://doi.org/10.1139/f57-025

Soetaert, K., Petzoldt, T., & Setzer, R. W. (2010). Solving differential equations in R: Package deSolve. *Journal of Statistical Software*, *33*, 1–25. https://doi.org/10.18637/jss.v033.i09

Stride, R. K., da Batista, V. S., & Raposo, L. A. B. (1992). *Pesca experimental de tubarão com redes de emalhar no litoral maranhense* (3rd ed., pp. 165). CORSUP/EDUFMA.

Sumaila, U. R., Alam, L., Abdallah, P. R., Aheto, D., Akintola, S. L., Alger, J., Andreoli, V., Bailey, M., Barnes, C., Ben-Hasan, A., Brooks, C. M., Carvalho, A. R., Cheung, W. W. L., Cisneros-Montemayor, A. M., Dempsey, J., Halim, S. A., Hilmi, N., Ilori, M. O., Jacquet, J., ... Pauly, D. (2024). WTO must complete an ambitious fisheries subsidies agreement. *npj Ocean Sustainability*, *3*(1), 1–3. https://doi.org/10.1038/s44183-024-00042-0

Sumaila, U. R., Ebrahim, N., Schuhbauer, A., Skerritt, D., Li, Y., Kim, H. S., Mallory, T. G., Lam, V. W. L., & Pauly, D. (2019). Updated estimates and analysis of global fisheries subsidies. *Marine Policy*, *109*, 103695. https://doi.org/10.1016/j.marpol.2019.103695

Sumaila, U. R., Khan, A., Teh, L., Watson, R., Tyedmers, P., & Pauly, D. (2010). Subsidies to high seas bottom trawl fleets and the sustainability of deep-sea demersal fish stocks. *Marine Policy*, *34*(3), 495–497. https://doi.org/10.1016/j.marpol.2009.10.004

Szuwalski, C. S., Vert-Pre, K. A., Punt, A. E., Branch, T. A., & Hilborn, R. (2015). Examining common assumptions about recruitment: A meta-analysis of recruitment dynamics for worldwide marine fisheries. *Fish and Fisheries*, *16*(4), 633–648. https://doi.org/10.1111/faf.12083

Thurner, S. D., Converse, S. J., & Branch, T. A. (2021). Modeling opportunistic exploitation: Increased extinction risk when targeting more than one species. *Ecological Modelling*, *454*, 109611. https://doi.org/10.1016/j.ecolmodel.2021.109611

Wallace, B. P., DiMatteo, A. D., Bolten, A. B., Chaloupka, M. Y., Hutchinson, B. J., Abreu-Grobois, F. A., Mortimer, J. A., Seminoff, J. A., Amorocho, D., Bjorndal, K. A., Bourjea, J., Bowen, B. W., Dueñas, R. B., Casale, P., Choudhury, B. C., Costa, A., Dutton, P. H., Fallabrino, A., Finkbeiner, E. M., ... Mast, R. B. (2011). Global conservation priorities for marine turtles. *PLoS One*, *6*(9), e24510. https://doi.org/10.1371/journal.pone.0024510

Warlick, A., Steiner, E., & Guldin, M. (2018). History of the West Coast groundfish trawl fishery: Tracking socioeconomic characteristics across different management policies in a multispecies fishery. *Marine Policy*, *93*, 9–21. https://doi.org/10.1016/j.marpol.2018.03.014

Webb, T. J., & Mindel, B. L. (2015). Global patterns of extinction risk in marine and non-marine systems. *Current Biology*, *25*(4), 506–511. https://doi.org/10.1016/j.cub.2014.12.023

Yan, H. F., Kyne, P. M., Jabado, R. W., Leeney, R. H., Davidson, L. N. K., Derrick, D. H., Finucci, B., Freckleton, R. P., Fordham, S. V., & Dulvy, N. K. (2021). Overfishing and habitat loss drive range contraction of iconic marine fishes to near extinction. *Science Advances*, *7*(7), eabb6026. https://doi.org/10.1126/sciadv.abb6026

Zhou, S., Hobday, A. J., Dichmont, C. M., & Smith, A. D. M. (2016). Ecological risk assessments for the effects of fishing: A comparison and validation of PSA and SAFE. *Fisheries Research*, *183*, 518–529. https://doi.org/10.1016/j.fishres.2016.07.015

Zhou, S., Milton, D. A., & Fry, G. C. (2012). Integrated risk analysis for rare marine species impacted by fishing: Sustainability assessment and population trend modelling. *ICES Journal of Marine Science*, *69*(2), 271–280. https://doi.org/10.1093/icesjms/fss009

Zhou, S., & Smith, A. (2017). Effect of fishing intensity and selectivity on trophic structure and fishery production. *Marine Ecology Progress Series*, *585*, 185–198. https://doi.org/10.3354/meps12402