Adaptive harvesting drives fishing down processes, regime shifts, and resilience changes in predator-prey systems

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Abstract

Many world fisheries display a declining mean trophic level of catches. This "fishing down the food web" is often attributed to reduced densities of high-trophic-level species, reflecting changes in the structure of harvested food webs. However, this pattern can also result from a restructuring of the fishery, that shifts from a focus on depleted upper trophic levels to abundant lower trophic levels. In fact, we show here that fishing down the food web can emerge from the adaptive harvesting of a predator-prey community, where changes in fishing patterns are driven by the relative profitabilities of the harvested species. The shift from a predator- to a prey-focused fishing pattern can yield abrupt changes in the system, and cause sudden losses in species densities. Such regime shifts occur when the predator species is highly valuable relative to the prey, and if it exerts a strong top-down control on the lower trophic level. Moreover, we find that when the two species are jointly harvested, high adaptation speeds can reduce the resilience of fisheries. Our results therefore suggest that flexibility in harvesting strategies will not necessarily benefit fisheries but may actually harm their sustainability.

Keywords

Adaptive harvesting; fishing pattern; fishing down the food web; regime shift; resilience; social-ecological system

Introduction

Many world fisheries are experiencing a general pattern of reduced mean trophic level of catches, called "fishing down the food web" (Pauly et al. 1998). This phenomenon is generally attributed to reduced abundances of high-trophic-level species, and is therefore understood as a symptom of ecosystem overfishing (Essington et al. 2006). As a consequence, fishing down the food web is often interpreted as only reflecting changes in the structure of harvested food webs, and the mean trophic level is commonly used as a proxy for the state of marine ecosystems (Butchart et al. 2010).

However, fishing down the food web may not only follow from changes in species abundances (Essington et al. 2006; Branch et al. 2010; Wilen and Wilen 2012). Reduced trophic level of catches can also result from changes in fishing patterns, fishermen adaptively shifting from depleted upper-trophic-levels to abundant lower-trophic-levels. In fact, empirical data suggest that fishermen often act as adaptive foragers in ecosystems, optimizing the rate of encounter with the species they exploit (Begossi 1992; Bertrand et al. 2007; Poos and Rijnsdorp 2007), and regularly switching the species they fish to maximize profits (Acheson 1988; Sethi et al. 2010).

Adaptive harvesting can also result from the adaptive management of fisheries, built on a constant feedback between changes in ecosystem states and changes in management strategies (Holling 1978). Based on population abundances, management authorities change quota or effort limits, thereby altering the distribution of fishing efforts (Walters 1986). However, as such an adaptive management requires coordination and decision processes, changes in fishing patterns are expected to be slower at the level of management authorities than at the level of individual fishermen.

Empirical evidence supports the view that fishing down the food web results from adaptive changes in fishing patterns. In the Scotian Shelf fishery, the decline in the groundfish

community produced a new fishery regime, dominated by shrimp and crab landings (Frank et al. 2005). Likewise, in the Argentinean-Uruguayan common fishing zone, data suggest that the fishing effort has been redistributed from overexploited to more abundant species (Jaureguizar and Milessi 2008). Exploitation of Antarctic marine resources is also a remarkable case of an adaptive fishing down the food web: starting with Atlantic fur seals, the fishery moved on to baleen whales and then to fishes, to end up with the current krill-oriented fishery (Ainley and Pauly 2014).

Adaptive harvesting is likely to impact the resilience of fisheries by linking ecological and economic dynamics. Resilience is generally understood as the ability of an ecosystem to absorb changes and still persist (Holling 1973). Fishing activities have been shown to affect various measures of resilience. (Hsieh et al. 2006) found for instance that fishing increases the variability of fish abundances, while (Lade and Gross 2012) evidenced potential fisheries-induced regime shifts. (Tromeur and Loeuille 2017) also demonstrated how different fishing patterns affect the recovery speed of harvested trophic communities. If one considers the fisher as a predator, then adaptive harvesting in fisheries is expected to stabilize dynamics, as often does adaptive foraging of predators in food webs. Adaptive foraging indeed reallocates predation pressures on more abundant species, thereby creating a negative feedback that eventually stabilizes the system (Loeuille 2010*a*). As a result, high adaptation speeds improve the resilience of complex food webs, as shown in (Kondoh 2003).

In the present work, we assess the bioeconomic consequences of adaptively harvesting a trophic community. To this aim, we use an analytically tractable model of an adaptively harvested predator-prey community. We first investigate the effect of increasing total fishing effort on the fishing pattern. According to fishing down the food web theory, the fishing pattern is expected to shift towards prey as predators get depleted. We then examine the impact of adaptive harvesting on the resilience of the fishery. We investigate three aspects of

resilience: the shape of the domain of attraction, the ability of returning to equilibrium following a pulse perturbation, and the speed of this return.

Model

We use a simple Lotka-Volterra predator-prey model, where both species are harvested:

$$\begin{cases} \dfrac{dN}{dt} &= rN\left(1-\dfrac{N}{K}\right)-\gamma NP-q_N e_N E_{tot} N \\ \dfrac{dP}{dt} &= \mu\gamma NP-mP-q_P e_P E_{tot} P \end{cases}, \qquad (1)$$

where N is prey density, P predator density, r the prey growth rate, K the prey carrying capacity, γ the predator attack rate, μ the prey-to-predator conversion efficiency, m the predator mortality, q_N and q_P the prey and predator catchabilities, and E_{tot} the total fishing effort. Fishermen can harvest both prey and predator, which is characteristic of intra-guild predation (see for instance Křivan and Schmitz (2003)). Considering a single fishing vessel, the effort may represent the number of hours spent at sea, while considering the entire fishing fleet, the effort may represent the number of active fishing vessels. The share of effort allocated to prey e_N varies following the equation:

$$\frac{de_N}{dt} = G E_{tot} e_N (1-e_N)\left[(p_N q_N N - c_N)-(p_P q_P P - c_P)\right] \qquad (2)$$

where p_N and p_P are the prices of prey and predators, and c_N and c_P are the per-unit-effort costs of harvesting prey and predators. The share of effort allocated to predator is then $e_P = 1-e_N$. These effort shares can represent the proportion of time spent using a prey- or predator-specific gear, or the proportion of vessels that specifically harvest prey or predators. Following Equation (2), the share of prey effort increases if the marginal utility of harvesting the prey is higher than the marginal utility of harvesting the predator.

Equation (2) derives from replicator dynamics, which is commonly used in economics (Noailly et al. 2003), as well as in ecology and evolution (Page and Nowak 2002). It has notably been used to describe the adaptive foraging of predators in food webs (Valdovinos et al. 2010), and of pollinators in mutualistic networks (Valdovinos et al. 2016).

Results

Fishing patterns emerging from adaptive harvesting

Three equilibrium fishing patterns emerge: a predator-focused, a prey-focused and a mixed fishing pattern. These stable equilibria are illustrated in Figure 1. The predator-focused equilibrium can be written as follows:

$$N^* = \frac{m + q_P E_{tot}}{\mu\gamma}$$

$$P^* = \frac{r}{\gamma}\left(1 - \frac{N^*}{K}\right) \qquad (3)$$

$$e_N^* = 0$$

It is stable provided $p_P q_P P^* - c_P > p_N q_N N^* - c_N$, which means that the marginal utility of harvesting the predator is higher than the marginal utility of harvesting the prey at equilibrium. Increasing fishing effort reduces predator density, and thereby enhances prey density. As a result, increasing fishing pressure improves the marginal utility of harvesting the prey, eventually destabilizing the predator-focused equilibrium (see Appendix S1 in the Supporting Information for detailed analytical calculations).

The prey-focused equilibrium can be written as follows:

$$N^* = \frac{m}{\mu\gamma} \qquad (4)$$

$$P^* = \frac{1}{\gamma}\left[r\left(1-\frac{m}{\mu\gamma K}\right)-q_N E_{tot}\right]$$

$$e_N^* = 1$$

It is stable provided $p_P q_P P^* - c_P < p_N q_N N^* - c_N$, which means that the marginal utility of harvesting the prey is higher than the marginal utility of harvesting the predator. Here increasing fishing effort on prey does not affect prey density, but it yields an indirect negative effect on predator density. Higher fishing pressure thus maintains the prey-focused fishing pattern, until the predator goes extinct (see Appendix S1). Therefore, as increased efforts eventually destabilize the predator-focused equilibrium (3) while maintaining the prey-focused equilibrium (4), we get that "fishing down the web" naturally emerges from adaptive harvesting in our system (see next section for an illustration of this result).

The mixed harvest equilibrium can be written as follows:

$$N^* = \frac{m + q_P\left(1-e_N^*\right)E_{tot}}{\mu\gamma}$$

$$P^* = \frac{p_N q_N N^* + c_P - c_N}{p_P q_P} \qquad (5)$$

$$e_N^* = \frac{1}{q_N E_{tot}}\left[r\left(1-\frac{N^*}{K}\right)-\gamma P^*\right]$$

In this equilibrium the two species are simultaneously harvested because the marginal utility of harvesting the prey is equal to the marginal utility of harvesting the predator: $p_P q_P P^* - c_P = p_N q_N N^* - c_N$. The complete expression of the equilibrium is given in the Appendix. This mixed fishing pattern is stable provided

$$\frac{q_P}{q_N} > \frac{\gamma K}{r}\left(\mu - \frac{p_N}{p_P}\right) \qquad (6)$$

This condition is dependent on ecological, economic and technical parameters. It holds whenever the price of the prey is large enough relative to the price of the predator modulated

by the conversion efficiency ($p_N > \mu\, p_P$). In particular, if the prey price is larger than the predator price (which is expected to be rare), this stability condition always holds. Stability is also favored by a high predator-to-prey catchability ratio (q_P / q_N), as well as by a low attack rate of the predator (γ), relative to the intraspecific competition rate of the prey (r / K). Therefore, the equilibrium is more likely to be stable when prey species are controlled by competition rather than by predation (i.e., in bottom-up controlled systems).

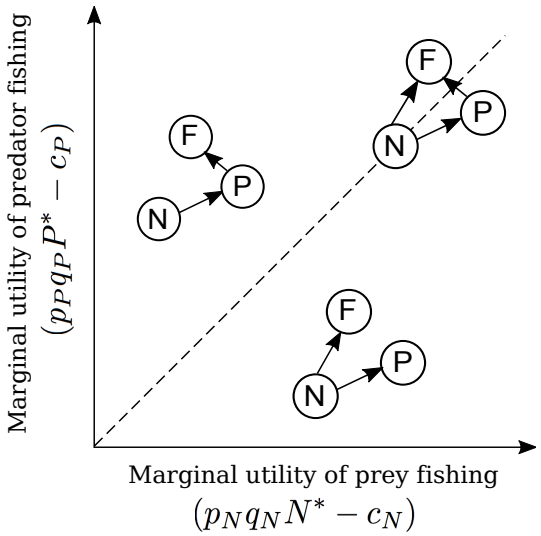

Figure 1: Illustration of the different fishing patterns that emerge from adaptive harvesting. Fishermen are described by the letter F, prey by N and predators by P. If the marginal utility of harvesting the predator is larger than the marginal utility of harvesting the prey, then the harvest is focused on predators. If it is smaller, then the harvest is focused on prey. If the marginal utilities of harvesting prey and predators are equal, then the fishing effort is shared between the two species.

Influence of fishing effort on fishing patterns

The equilibrium fishing pattern depends on the the total fishing effort. As illustrated in Figure 2 (and analytically shown in the Appendix), the fishing pattern shifts from a predator-

focused harvest to a prey-focused harvest with increasing fishing efforts. In between, a stable mixed harvest of predator and prey can be reached when condition (6) holds (Fig. 2a). In this case, the effort below which the predator-focused equilibrium is stable (E_{stab}^{PH} , see definition in Appendix S1) is lower than the effort above which the prey-focused equilibrium is stable (E_{stab}^{NH} , see definition in Appendix S1). Between these two efforts, a stable mixed harvest of prey and predator is reached. The progressive shift from a predator-focused to a prey-focused fishing pattern leads to a general reduction in predator density (Fig. 2c). However the shift towards a prey-focused harvest maintains predator populations at higher fishing efforts compared to scenarios in which harvest would remain focused on the predator. An adaptive harvest therefore allows the community to sustain higher fishing pressures than a fixed predator-focused harvest.

Sudden regime shifts between the predator- and the prey-focused equilibria occur whenever condition (6) does not hold. Then, the effort below which the predator-focused system is stable (E_{stab}^{PH}) is larger than the effort above which the prey-focused system is stable (E_{stab}^{NH}). In between, the predator- and the prey-focused equilibria are simultaneously stable, while the mixed harvest equilibrium is unstable (see Fig. 2b). This bistable system is characterized by a phenomenon called *hysteresis*: starting from a predator-focused system, increasing the fishing effort (arrow (1) in Fig. 2b) leads to a regime shift towards a prey-focused system when the effort reaches E_{stab}^{PH} (arrow (2) in Fig. 2b). This sudden shift induces severe losses in both prey and predator densities (Fig. 2d). To recover higher prey and predator densities, managers would have to reduce the fishing effort to E_{stab}^{NH} (arrows (3) and (4) in Fig 2b).

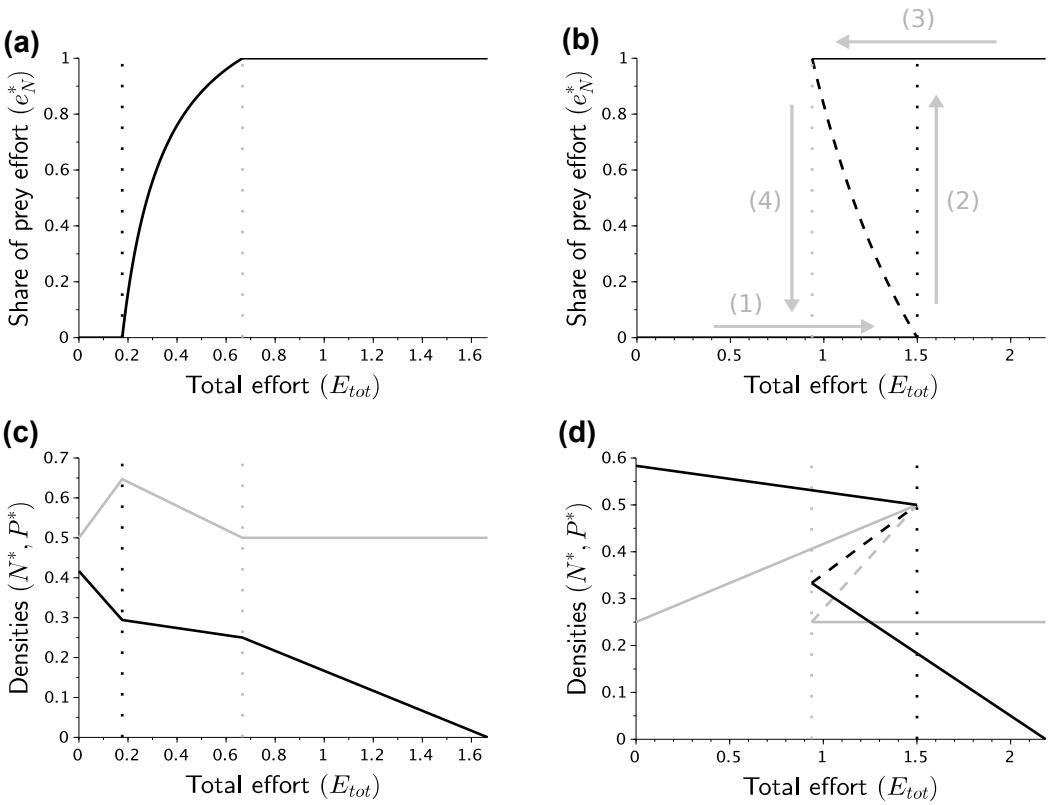

Figure 2: Share of prey effort (a,b) and equilibrium densities (c,d) for increasing fishing efforts. When condition (6) is verified (a,c), the mixed equilibrium is stable, and when it is not verified (b,d), the system exhibits alternative stable states. (c,d) gray line: prey density; black line: predator density. Dotted lines represent E_{stab}^{PH} (black dotted line) and E_{stab}^{NH} (gray dotted line). Dashed lines indicate unstable equilibria. Parameters in (a,c): $r=1$, $K=1$, $m=0.3$, $\mu=0.5$, $\gamma=1.2$, $q_N=0.3$, $q_P=0.5$, $p_N=1$, $p_P=2$, $c_N=0.1$, $c_P=0.2$. Parameters in (b,d): same as (a,c) except $K=2$, $\mu=0.8$, $\gamma=1.5$, $q_N=0.4$, $q_P=0.2$ and $p_P=3$.

Understanding sudden regime shifts

To better understand the mechanism behind these regime shift dynamics, we study the different feedback loops that stabilize or destabilize our system. To do this we consider the

non-diagonal elements of the Jacobian matrix of the system (see Appendix S1), which contains partial derivatives of our model, evaluated at the equilibrium. It informs us about the sign of the relationship between two variables, and about the parameters that are involved in this relationship. We show in Figure 3 the relationships between prey density, predator density, and share of prey effort. We also indicate the parameters involved both in the strength of the interaction and in stability condition (6).

Two loops are involved: the first one entails one negative feedback and is therefore stabilizing (gray lines); the second loop creates a global positive feedback and is therefore destabilizing (dashed black lines). Suppose that there is an increase in the share of effort allocated to prey harvesting. Following the gray loop, this reduces the fishing pressure on predators, as modulated by catchability q_P, therefore increasing predator density. This leads to increased top-down controls, mediated by attack rate γ, thus reducing prey density. This decreases the profitability of prey harvesting, as constrained by parameters p_N and q_N, thereby reducing the share of prey harvest. This first loop is therefore stabilizing. But following the black loop, the increase in the share of prey effort enhances the fishing pressure on prey, modulated by catchability q_N, thereby decreasing prey density. This induces a negative bottom-up effect mediated by parameters μ and γ, that reduces predator density. This decreases the profitability of predator harvesting, as constrained by parameters p_P and q_P, thus further increasing the share of prey harvest. This second loop is therefore destabilizing.

The relative influence of the stabilizing or of the destabilizing loop is dependent on the value of parameters involved in condition (6), that determine the stability of the mixed harvest equilibrium. For instance, a low predator price and a high prey price favor the stabilizing loop. On the contrary, a high conversion efficiency favors the destabilizing loop. The roles of the other parameters involved in condition (6) are dependent on the value of $\left(\mu - p_N / p_P\right)$,

which explains why they are involved in both stabilizing and destabilizing loops. For instance, increasing conversion efficiency μ promotes the stabilizing effect of predator catchability q_P, while increasing the prey-to-predator price ratio p_N/p_P enhances the destabilizing effect of predator catchability.

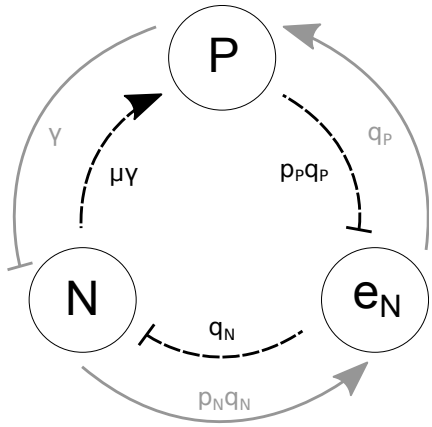

Figure 3: Illustration of the relationships between predator density, prey density and share of prey effort. Arrows indicate positive relationships, while bars indicate negative relationships. Gray lines form the stabilizing loop, and black dashed lines form the destabilizing loop.

Influence of adaptation speed on resilience

Adaptation speed G constrains the resilience of the system. Let us assume that condition (6) holds, which implies that a mixed harvest is possible. Resilience can then be measured by the return time to equilibrium after a perturbation (i.e., an assumed small change in either populations), small return times indicating high levels of resilience. To obtain this measure of resilience, we compute from the Jacobian matrix (see Appendix S1) the eigenvalue with the largest real part λ_m. The return time to equilibrium after a small perturbation is then $\tau = -1/\mathrm{Re}(\lambda_m)$ (Pimm and Lawton 1978; Loeuille 2010*b*).

As illustrated in Figure 4a, increasing the pace of adaptation is first stabilizing in a predator- and in a prey-focused fishery until resilience reaches a plateau. This pattern can also be inferred from the analytical expressions of the eigenvalues (see Appendix S1). In a mixed fishery, while low to intermediate adaptation speeds stabilize the system, higher adaptation rates turn out to be destabilizing. Because local stability (return time to equilibrium) is only one aspect of resilience, we also study how adaptation speeds affect population variability. We do so by modifying our model to include a Holling type II functional response, thereby allowing population cycles to occur under some conditions. The model is then expressed as:

$$\begin{cases} \dfrac{dN}{dt} &= rN\left(1-\dfrac{N}{K}\right)-\dfrac{\gamma NP}{N+N_0}-q_N e_N EN \\ \dfrac{dP}{dt} &= \mu\dfrac{\gamma NP}{N+N_0}-mP-q_P e_P EP \\ \dfrac{de_N}{dt} &= G\,E_{tot}\,e_N\left(1-e_N\right)\left[\left(p_N q_N N-c_N\right)-\left(p_P q_P P-c_P\right)\right] \end{cases} \tag{7}$$

where N_0 is the prey density at which the predator's attack rate reaches half of its maximum. As analytical work is made difficult by the non-linear functional response, we rely on numerical simulations. For different values of adaptation speed, we run 50000 time steps. We choose parameters so as to be in a mixed harvest situation, where $0<e_N^*<1$. Results are shown in Fig. 4b. For low adaptation rates, the system is stable and does not oscillate. But higher adaptation rates induce oscillations, with growing amplitude. In addition to increasing the return time to equilibrium, high adaptation speeds therefore drive the system into an unstable oscillating state. In Appendix S2, we show that the negative impact of adaptation speed on stability is robust to changes in parameters.

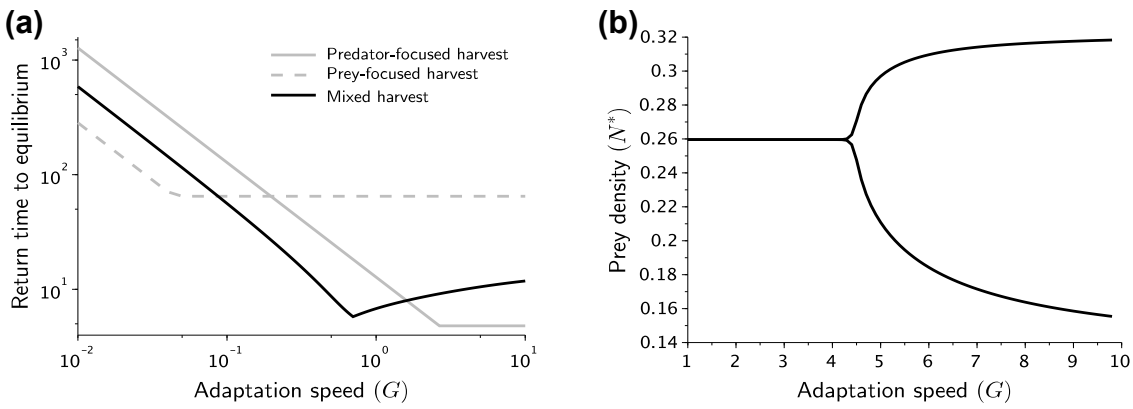

Figure 4: Influence of adaptation speed on stability. (a) Relationship between return time to equilibrium and adaptation speed in the predator-focused ($E_{tot}=0.3$), the prey-focused ($E_{tot}=2.7$) and the mixed equilibrium ($E_{tot}=1$). Parameters: $r=1$, $K=1$, $m=0.1$, $\mu=0.5$, $\gamma=1.2$, $q_N=0.3$, $q_P=0.5$, $p_N=1$, $p_P=2$, $c_N=0.1$, $c_P=0.2$. (b) Minimum and maximum prey densities for increasing adaptation speeds in a Rosenzweig-MacArthur model at the mixed equilibrium. Parameters: same as (a), except $K=1.5$, $m=0.2$, $N_0=0.4$, $E_{tot}=1.75$.

Discussion

This study highlights the relevance of integrating economic-ecological feedbacks to better understand the structure and dynamics of fisheries. We first show how adaptive harvesting changes fishing patterns, leading to fishing down the food web transitions. We then find that harvesting dynamics affects stability in several ways: it can trigger catastrophic regime shifts in fishing patterns, and it has constrasted effects on the resilience of fisheries and on population variability.

Our results suggest that fishing down the food web can directly result from feedbacks between ecological and economic dynamics. This view is already contained in the early formulations of the fishing down the food web theory. (Pauly et al. 1998) define this as a

gradual transition in landings from upper- to lower-trophic-levels, with simultaneous decreases in abundances, and changes in fishing patterns. However, as pointed out by (Essington et al. 2006), subsequent studies mainly interpreted fishing down the food web as resulting only from overfishing and changes in ecosystem structure. Accounting for economic dynamics and adaptive choice could thus help to understand and manage fisheries affected by this process.

Theoretical and empirical studies support the view that fishing down the food web emerges from feedbacks between changing fish abundances and adaptive fishing patterns. (Branch et al. 2010) found for instance that adaptive fishing patterns based on stock availability reduce the mean trophic level of catches in "Ecopath with Ecosim" models. (Andersen et al. 2015) also showed using a size-spectrum model of a harvested trophic community that increasing the global fishing pressure leads to a gradual re-allocation of effort from big predatory fish to medium and small prey fish. Likewise, (Wilen and Wilen 2012) found that if top predators in a food chain model have high values, then profit-driven effort dynamics first imply a focus on the top trophic level, followed by an increase in efforts targeting lower trophic levels. This result has been similarly obtained with an age-structured model of a food chain where harvesters can switch targets (Wiedenmann et al. 2016). Furthermore, as stated in the Introduction, empirical case studies suggest shifts in target from upper- to lower-trophic-levels in various fisheries. For instance, in the Scotian Shelf fishery, (Frank et al. 2005) noticed that reduced predatory groundfish abundance "has produced a new fishery regime in which the (...) monetary value of the combined shrimp and crab landings now far exceed that of the groundfish fishery it replaced". However, precise empirical investigations of this ecological-economic feedback are lacking.

This result of changing fishing patterns also echoes findings from studies of adaptive foraging in natural communities. In particular, (Křivan and Schmitz 2003) found that adaptive

foraging by a predator on a consumer-resource community could affect the topology of the food web. They show that at low densities, the top predator focuses on the consumer, at higher densities it focuses on the resource, and at intermediate densities it predates on both consumer and resource. This result is very similar to the relationship we find between the total fishing effort and the fishing pattern. The main difference is that while natural predators are expected to maximize energy inputs, in our model fishermen's behavior aims at maximizing profits. Moreover, our model allows to account for changes in adaptation speeds. while in (Krivan & Schmitz, 2003) adaptation is instantaneous.

While our expectation was that adaptive foraging would stabilize the system (Kondoh 2003; Loeuille 2010*a*), we show that it can also induce abrupt regime shifts. As pointed out in (Lade et al. 2013), social-ecological feedbacks may lead to regime shifts and bistability, while similar uncoupled systems do not. Using a harvested predator-prey model, (Horan et al. 2011) also found that modifying the feedback response between populations and management alters the stability lanscape of the system. However, many studies on fisheries-induced regime shifts focus on ecological drivers and on the ecological consequences of these shifts (Conversi et al. 2014). Reconsidering the role of human dynamics in triggering regime shifts in marine food webs could thus help to understand and prevent such phenomena.

Our investigation suggests that large top-down effects vs. bottom-up effects favor regime shifts. Such conditions lead to large increases in prey density with mounting fishing pressures, that favor a sudden shift towards prey fishing when predator profitability becomes too small. It also echoes studies stressing the importance of top-down forcing for triggering regime shifts in marine food webs (Pershing et al. 2014). Moreover, we find that the possibility of a social-ecological regime shift is dependent on the relative intensity of a stabilizing and a destabilizing feedback loop between prey and predator densities and the share of prey harvest. The dominance of one loop over the other relies on ecological

336 (conversion efficiencies, predation...), economic (prices) and technical parameters
337 (catchabilities). For instance, high conversion efficiencies promote the destabilizing loop,
338 while a high prey-to-predator price ratio enhances the stabilizing loop. This stresses the joint
339 influence of ecological and economic drivers in triggering regime shifts, as pointed out in
340 (Lade et al. 2015).

341 Understanding the various drivers of such social-ecological regime shifts is of major
342 importance for managers. In particular, our results suggest that providing high prices to upper-
343 trophic-levels and low prices to lower-trophic-levels increases the probability of entering a
344 social-ecological regime shift. This can be understood as follows: if upper-trophic-levels
345 display high prices, then fishermen have an incentive to focus on upper-trophic-levels until
346 these become too depleted, then triggering a sudden shift towards lower-trophic-levels.
347 Investigation of regime shifts in marine ecosystems could therefore benefit from the
348 integration of economic variables, such as prices or costs of the harvested species.

349 Regime shifts may however be difficult to detect and manage. If adaptation is slow,
350 the shift from a predator-focused to a prey-focused fishery (arrow (2) in Fig. 2b) can be long.
351 Moreover, because of hysteresis, coming back to the initial predator-focused state (arrow (4)
352 in Fig. 2b) implies harsh reductions in the total fishing effort. This also requires reductions in
353 prey fishing pressure, at the expense of fishermen that specialized on this prey. For instance
354 on the Scotian Shelf, the collapse of cod and the related increase in shrimps and crabs induced
355 a new fishing pattern, associated with an increase in the price of these macroinvertebrates
356 (Frank et al. 2005). Moving back to a predator-focused fishery could then come at a cost for
357 these fishermen and reduce the total profits earned from the fishery.

358 Preserving the resilience of fisheries is both an ecological and economic concern, as it
359 helps the recovery of harvested food webs, and as it insures fishermen against potential losses
360 in yield and profits (Baumgärtner and Strunz 2014). Resilience is however a multifaceted

concept, that requires diversified measures (Donohue et al. 2016). As discussed above, we examined the impact of adaptive harvesting on the domain of attraction of the system, and we evidenced potential regime shifts that could constrain predator populations to low abundances. While adaptation speed can accelerate the transition from an attractor to another, it does not modify the domain of attraction of the system. On the contrary, (Kramer 2008) showed with a model of an adaptively harvested reef ecosystem, that the basin of attraction of a coral-dominated state is larger when adaptation speed is high, therefore preventing the shift towards an undesired algae-dominated state. We further investigated the impact of adaptation speed on other aspects of resilience, namely the ability of a system to recover from a perturbation or to vary indefinitely, and the speed of this recovery.

In a prey- and a predator-focused equilibrium, adaptation speed is always stabilizing, as it reduces return times to equilibrium. In a mixed fishery, only low adaptation speeds are stabilizing. Likewise, it has been shown with a predator-prey model where fishermen can switch the species they harvest (but cannot harvest the two species simultaneously), that the speed of convergence is higher and that oscillations are reduced when the switching time approaches zero (Bischi et al. 2013). It is also coherent with adaptive foraging studies showing that predator's adaptation speed increases the resilience of food webs (Kondoh 2003).

High adaptation speeds however reduce the resilience of mixed fisheries, which contradicts our initial expectation of a stabilizing adaptive foraging. We find that high adaptation speeds increase the return time to equilibrium in a linear predator-prey system, and increase population variability by inducing oscillations in a non-linear predator-prey model. In the latter case, the amplitude of oscillations increases with adaptation speed. Likewise, (Kramer 2008) showed that a theoretical harvested reef ecosystem displays larger variations with high adaptation speeds. (Bischi et al. 2013) also showed with a harvested predator-prey model that fast switching from predator to prey induces oscillatory behaviors. Similarly, using

386 an age-structured food chain model, (Wiedenmann et al. 2016) found that biomass, catches
387 and profits are more variable when fishermen adaptively switch their target.
388 Social-ecological resilience therefore depends on how fast fishermen or management
389 authorities react to changes in relative abundances and profits. At the scale of individual
390 fishermen, following (Noailly et al. 2003), as agents imitate the most successful strategy,
391 adaptation speed may depend on the diffusion of information between fishermen, and
392 therefore on the social context of the fishery. Adaptation speed may however be slowed by
393 economic costs (Noailly et al. 2003). Changing gears can incur high costs for fishermen, thus
394 implying some inertia. Therefore, at the scale of management authorities, subsidizing
395 fishermen communities could be used to modulate adaptation speed, and potentially stabilize
396 the social-ecological system. Likewise, at large scales, regulatory or logistic constraints can
397 reduce adaptation speed (Bischi et al. 2013). In particular, if the decision of effort allocation is
398 taken by a management authority, delays inherent to collective and consensus decision-
399 making can impair the ability of the system to adapt and therefore slow down adaptation.
400 Harvesting strategies and policies rely on frequent population census and profitability
401 assessments, and are thus adaptive. Including such adaptive dynamics in management models
402 and plans is critical to achieve a sound management of multispecies fisheries. In particular,
403 our results suggest that such adaptation may severely constrain different aspects of fisheries
404 resilience. We therefore suggest that considering adaptive economic behaviors is a key step
405 towards the implementation of an ecosystem-based fisheries management (Pikitch et al.
406 2004).

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Supporting Information

Appendix S1: Analytical calculations

We here describe the three possible equilibria where predator and prey coexist, with their associated feasibility and stability conditions. The expressions of these equilibria can be found in the following table:

Table S1: Description of the three considered equilibria.

Predator harvest (PH)	Prey harvest (NH)	Mixed harvest (MH)
$N^*=\frac{m+q_P E_{tot}}{\mu\gamma}$	$N^*=\frac{m}{\mu\gamma}$	$N^*=\frac{m+q_P\left(1-e_N^*\right)E_{tot}}{\mu\gamma}$
$P^*=\frac{r}{\gamma}\left(1-\frac{N^*}{K}\right)$	$P^*=\frac{1}{\gamma}\left[r\left(1-\frac{m}{\mu\gamma K}\right)-q_N E_{tot}\right]$	$P^*=\frac{p_N q_N N^*+c_P-c_N}{p_P q_P}$
$e_N^*=0$	$e_N^*=1$	$e_N^*=\frac{1}{q_N E_{tot}}\left[r\left(1-\frac{N^*}{K}\right)-\gamma P^*\right]$

An equilibrium is feasible for parameter sets that ensure that prey and predator densities are positive. The mixed equilibrium is characterized by a supplementary feasibility condition, namely that the share of prey effort is between 0 and 1. We further assume that coexistence of prey and predator in the unharvested system is warranted, which implies that $m<\mu\gamma K$. The local stability of the system can be assessed by computing the eigenvalues of the Jacobian of the system at equilibrium. The general formulation of this Jacobian is:

$$J^*=\begin{pmatrix} \frac{-rN^*}{K} & -\gamma N^* & -q_N E_{tot} N^* \\ \mu\gamma P^* & 0 & q_P E_{tot} P^* \\ G E_{tot} e_N^*\left(1-e_N^*\right) p_N q_N & -G E_{tot} e_N^*\left(1-e_N^*\right) p_P q_P & G E_{tot}\left[\left(p_N q_N N^*-c_N\right)-\left(p_P q_P P^*-c_P\right)\right] \end{pmatrix} \quad (8)$$

1. Predator-focused harvest (PH)

1.1. Feasibility conditions

Prey density N^* is always positive and increases with the fishing effort. Predator density P^* is positive when

$$E_{tot} < E_{ext}^{PH} = \frac{1}{q_P}(\mu\gamma K - m), \tag{9}$$

and it decreases with the fishing effort. The effort below which the predator-focused harvest is feasible is denoted E_{ext}^{PH}.

1.2. Stability conditions

The eigenvalues of the system can be written:

$$\lambda_1 = \frac{-r N^*}{K}$$

$$\lambda_2 = -\mu \gamma^2 N^* P^* \tag{10}$$

$$\lambda_3 = G E_{tot}\left[\left(p_N q_N N^* - c_N\right) - \left(p_P q_P P^* - c_P\right)\right]$$

Eigenvalues λ_1 and λ_2 are negative if the feasibility conditions are fulfilled. The third eigenvalue λ_3 is negative as long as $p_P q_P P^* - c_P > p_N q_N N^* - c_N$. This translates into the following condition:

$$E_{tot} < E_{stab}^{PH} = \frac{\gamma K\left[\mu\gamma\left(c_N - c_P\right) - m\, p_N q_N\right] + r\, p_P q_P(\mu\gamma K - m)}{q_P\left[\gamma K\, p_N q_N + r\, p_P q_P\right]}, \tag{11}$$

where the effort below which the predator-focused harvest is stable is denoted E_{stab}^{PH}. All feasible states are not stable if $E_{ext}^{PH} > E_{stab}^{PH}$, which translates into the following condition:

$$\frac{c_N - c_P}{p_N q_N} < K \tag{12}$$

This condition always holds if the cost of harvesting the prey is smaller than the cost of harvesting the predator ($c_N < c_P$).

2. Prey-focused harvest (NH)

2.1. Feasibility conditions

Prey density N^* is always positive. Predator density P^* is positive when

$$E_{tot} < E_{ext}^{NH} = \frac{r}{q_N}\left(1 - \frac{m}{\mu\gamma K}\right), \tag{13}$$

and it decreases with the fishing effort. The effort below which the prey-oriented harvest is feasible is denoted E_{ext}^{NH} .

2.2. Stability conditions

The eigenvalues of the system can be written:

$$\lambda_1 = \frac{-r N^*}{K}$$

$$\lambda_2 = -\mu \gamma^2 N^* P^* \tag{14}$$

$$\lambda_3 = G E_{tot}\left[\left(p_P q_P P^* - c_P\right) - \left(p_N q_N N^* - c_N\right)\right]$$

Eigenvalues λ_1 and λ_2 are negative if the feasibility conditions are fulfilled. The third eigenvalue λ_3 is negative as long as $p_N q_N N^* - c_N > p_P q_P P^* - c_P$. This translates into the following condition:

$$E_{tot} > E_{stab}^{NH} = \frac{\gamma K\left[\mu\gamma\left(c_N - c_P\right) - m\, p_N q_N\right] + r\, p_P q_P\left(\mu\gamma K - m\right)}{\mu\gamma K\, q_N p_P q_P}, \tag{15}$$

where E_{stab}^{NH} stands for the effort above which the prey-focused harvest is stable. If $E_{ext}^{NH} < E_{stab}^{NH}$, none of the feasible states are stable. On the contrary, some feasible states can be stable if $E_{ext}^{NH} > E_{stab}^{NH}$, which translates into the following condition:

$$\frac{c_N - c_P}{p_N q_N} < \frac{m}{\mu\gamma} \tag{16}$$

If the harvesting the predator is costlier than harvesting the prey ($c_N < c_P$), this condition always holds.

3. Mixed predator-prey harvest (MH)

3.1. Feasibility conditions

As e_N^* is supposed to take values between 0 and 1, N^* is always positive. We can specify the effort at which the predator goes extinct by using the complete expression of the predator density at equilibrium:

$$P^* = \frac{(c_P - c_N)(r q_P - \mu\gamma K q_N) + K p_N q_N [r q_P - q_N (m + q_P E_{tot})]}{q_P [\gamma K q_N (p_N - \mu p_P) + r p_P q_P]} \tag{17}$$

Predator densities are positive if:

$$E_{tot} < E_{ext}^{MH} \quad \text{if} \quad \frac{q_P}{q_N} > \frac{\gamma K}{r}\left(\mu - \frac{p_N}{p_P}\right)$$

$$E_{tot} > E_{ext}^{MH} \quad \text{if} \quad \frac{q_P}{q_N} < \frac{\gamma K}{r}\left(\mu - \frac{p_N}{p_P}\right) \tag{18}$$

$$\text{with} \quad E_{ext}^{MH} = \frac{(c_N - c_P)(\mu\gamma K q_N - r q_P) + K p_N q_N (r q_P - m q_N)}{K p_N q_N^2 q_P}$$

Here E_{ext}^{MH} stands for the effort at which predators goes extinct in the mixed harvest equilibrium. Finally, as the share of prey effort can be written

$$e_N^* = \frac{\gamma K\left[\mu\gamma\left(c_P - c_N\right) + p_N q_N\left(m + q_P E_{tot}\right)\right] + r\, p_P q_P\left(m - \mu\gamma K + q_P E_{tot}\right)}{E_{tot} q_P\left[\gamma K q_N\left(p_N - \mu\, p_P\right) + r\, p_P q_P\right]}, \tag{19}$$

the feasibility condition on e_N^* becomes:

$$\begin{aligned} 0 < e_N^* < 1 \quad &\Leftrightarrow \quad E_{stab}^{PH} < E_{tot} < E_{stab}^{NH} \quad \text{if} \quad \frac{q_P}{q_N} > \frac{\gamma K}{r}\left(\mu - \frac{p_N}{p_P}\right) \\ 0 < e_N^* < 1 \quad &\Leftrightarrow \quad E_{stab}^{NH} < E_{tot} < E_{stab}^{PH} \quad \text{if} \quad \frac{q_P}{q_N} < \frac{\gamma K}{r}\left(\mu - \frac{p_N}{p_P}\right) \end{aligned} \tag{20}$$

Note that the second case is only possible if $p_N / p_P < \mu$, that is if the ratio of prey to predator prices is smaller than the prey-to-predator conversion efficiency.

3.2. Stability conditions

The analysis of stability can be done by computing the Jacobian matrix and the associated Routh-Hurwitz conditions. The characteristic polynomial $P(\lambda) = a_0\lambda^3 + a_1\lambda^2 + a_2\lambda^1 + a_3$ can be written as follows:

$$\begin{aligned} P(\lambda) = -\lambda^3 - \frac{r N^*}{K}\lambda^2 - \left(\mu\gamma^2 N^* P^* - E_{tot}{}^2\left(e_N^* - 1\right) e_N^* G\left(p_N q_N{}^2 N^* + p_P q_P P^*\right)\right)\lambda \\ + \frac{E_{tot}{}^2}{K}\left(e_N^* - 1\right) e_N^* G N^* P^* q_P\left(\gamma K\left(p_N - \mu\, p_P\right) q_N + r\, p_P q_P\right) \end{aligned} \tag{21}$$

The system is stable provided $a_0, a_1, a_2, a_3 < 0$ and $a_1 a_2 - a_0 a_3 > 0$. The coefficient a_0, a_1 and a_2 are negative as long as the feasibility conditions are verified. The coefficient a_3 is negative if

$$\frac{q_P}{q_N} > \frac{\gamma K}{r}\left(\mu - \frac{p_N}{p_P}\right) \tag{22}$$

The stability condition $a_1 a_2 - a_0 a_3 > 0$ is equivalent to

$$r\mu\gamma^2 N^* P^* + E_{tot}{}^2\left(e_N^* - 1\right) e_N^* G\, q_N\left(\gamma K P^*\left(p_N - \mu\, p_P\right) q_P - r\, p_N q_N N^*\right) > 0 \tag{23}$$

If $p_N \leq \mu p_P$, this condition is always verified, and stability only depends on condition (22). If $p_N > \mu p_P$ however, condition (22) is always true and stability then depends solely on condition (23), which is verified if

$$\frac{q_N N^*}{q_P P^*} \geq -\frac{p_P}{p_N}\frac{\gamma K}{r}\left(\mu - \frac{p_N}{p_P}\right). \tag{24}$$

From condition (22), this implies that

$$\frac{N^*}{P^*} > -\frac{p_P}{p_N}, \tag{25}$$

which is always true as N^* and P^* are positive. In short, if $p_N > \mu p_P$, then the equilibrium is stable, and if $p_N \leq \mu p_P$, then the stability of the equilibrium depends on condition (22). As shown in the main text, if condition (22) is not true, the system is bistable.

3.3. Effect of fishing effort on densities

Let us now investigate the precise effect of fishing pressure on the prey and predator densities. The following relationship can be established:

$$\begin{aligned} \frac{\partial N^*}{\partial E_{tot}} &= \frac{q_P}{\mu\gamma}\left(1 - \frac{\partial e_N^* E_{tot}}{\partial E_{tot}}\right) \\ \frac{\partial P^*}{\partial E_{tot}} &= \frac{p_N q_N}{p_P q_P}\frac{\partial N^*}{\partial E_{tot}} \end{aligned} \tag{26}$$

Prey and predator densities thus vary in the same direction with increasing efforts. This direction is dependent on the effect of effort on e_N^* . As we have

$$e_N^* = \frac{\gamma K\left[\mu\gamma\left(c_P - c_N\right) + p_N q_N\left(m + q_P E_{tot}\right)\right] + r\, p_P q_P\left(m - \mu\gamma K + q_P E_{tot}\right)}{E_{tot} q_P\left[\gamma K q_N\left(p_N - \mu p_P\right) + r\, p_P q_P\right]}, \tag{27}$$

we get the following derivative:

$$\frac{\partial e_N^* E_{tot}}{\partial E_{tot}} = \frac{\gamma K p_N q_N + r\, p_P q_P}{\left[\gamma K q_N\left(p_N - \mu p_P\right) + r\, p_P q_P\right]} \tag{28}$$

Then, two different cases appear:

$$\begin{aligned} &\frac{\partial N^*}{\partial E_{tot}}<0, \quad \frac{\partial P^*}{\partial E_{tot}}<0 \quad \text{and} \quad \frac{\partial e_N^*}{\partial E_{tot}}>0 \quad \text{if} \quad \frac{q_P}{q_N}>\frac{\gamma K}{r}\left(\mu-\frac{p_N}{p_P}\right) \\ &\frac{\partial N^*}{\partial E_{tot}}>0, \quad \frac{\partial P^*}{\partial E_{tot}}>0 \quad \text{and} \quad \frac{\partial e_N^*}{\partial E_{tot}}<0 \quad \text{if} \quad \frac{q_P}{q_N}<\frac{\gamma K}{r}\left(\mu-\frac{p_N}{p_P}\right) \end{aligned} \tag{29}$$

Thus, if the system is stable, predator and prey densities decrease while the share of prey harvest increases with the fishing effort, and if the system is bistable, predator and prey densities increase while the share of prey harvest decreases with the fishing effort.

4. Summary table

In the following table, we summarize the feasibility and stability conditions of the different possible equilibria. This helps to understand the relationships between these equilibria.

Table S2. Feasibility and stability conditions of the different equilibria. Expressions of the limit efforts are found in the Appendix. Only stability conditions that are not redundant with feasibility conditions are shown.

Equilibrium	Predator harvest (PH)	Mixed harvest (MH)	Prey harvest (NH)
Feasibility conditions	$E_{tot} < E_{ext}^{PH}$	if $\frac{q_P}{q_N} > \frac{\gamma K}{r}\left(\mu - \frac{p_N}{p_P}\right)$: $E_{tot} < E_{ext}^{MH}$ $E_{stab}^{PH} < E_{tot} < E_{stab}^{NH}$	$E_{tot} < E_{ext}^{NH}$
		if $\frac{q_P}{q_N} < \frac{\gamma K}{r}\left(\mu - \frac{p_N}{p_P}\right)$: $E_{tot} > E_{ext}^{MH}$ $E_{stab}^{NH} < E_{tot} < E_{stab}^{PH}$	
Stability conditions	$E_{tot} < E_{stab}^{PH}$	$\frac{q_P}{q_N} > \frac{\gamma K}{r}\left(\mu - \frac{p_N}{p_P}\right)$	$E_{tot} > E_{stab}^{NH}$
Relationships between conditions	$E_{ext}^{PH} > E_{stab}^{PH}$ $\Leftrightarrow$ $\frac{c_N - c_P}{p_N q_N} < K$	if $\frac{q_P}{q_N} > \frac{\gamma K}{r}\left(\mu - \frac{p_N}{p_P}\right)$: $E_{ext}^{MH} > E_{stab}^{PH} \Leftrightarrow \frac{c_N - c_P}{p_N q_N} < K$ $E_{ext}^{MH} > E_{stab}^{NH} \Leftrightarrow \frac{c_N - c_P}{p_N q_N} < \frac{m}{\mu\gamma}$	$E_{ext}^{NH} > E_{stab}^{NH}$ $\Leftrightarrow$ $\frac{c_N - c_P}{p_N q_N} < \frac{m}{\mu\gamma}$

It appears that a stable predator-focused system is reached at low efforts (for efforts smaller than E_{stab}^{PH}), while a stable prey-focused system is reached at high efforts (for efforts larger than E_{stab}^{NH}). In between, a mixed harvest is reached. Interestingly, the feasibility conditions of the mixed harvest equilibrium are defined by the limit efforts E_{stab}^{PH} and E_{stab}^{NH} that determine the stability of the predator-focused and the prey-focused systems. If $E_{stab}^{PH} < E_{stab}^{NH}$, this mixed harvest equilibrium is stable. But if on the contrary $E_{stab}^{PH} > E_{stab}^{NH}$, then the equilibrium is unstable. Moreover in this case, three equilibria overlap: stable predator- and prey-focused equilibria, and the unstable mixed harvest equilibrium. The system then exhibits bistability.

In the last row of the table, we investigate the relationships between the feasibility and stability conditions of the different equilibria. Importantly, it appears that if the predator goes extinct in one of the equilibria, then other equilibria cannot be reached for higher efforts. To illustrate this, let us consider three cases, where we suppose that a stable mixed harvest is possible ($q_P / q_N > (\gamma K / r)(\mu - p_N / p_P)$). In the first case, the difference between prey and predator costs relative to prey price and catchability is larger than prey carrying capacity ($(c_N - c_P)/(p_N q_N) > K$). This means that harvesting prey is costly and does not bring much profit relative to its maximum density. Therefore, the interest of harvesting prey is limited. As a result, the predator goes extinct before reaching the mixed equilibrium ($E_{ext}^{PH} < E_{stab}^{PH}$). It also implies that the mixed equilibrium is unfeasible ($E_{ext}^{MH} < E_{stab}^{PH}$). As predator mortality is considered to be lower than its maximum growth rate ($m < \mu\gamma K$) it also implies that the prey-focused equilibrium is unfeasible ($(c_N - c_P)/(p_N q_N) > m/(\mu\gamma) \Leftrightarrow E_{ext}^{NH} < E_{stab}^{NH}$).

In the second case, the difference between prey and predator costs relative to prey price and catchability is smaller than prey carrying capacity ($(c_N - c_P)/(p_N q_N) < K$), but

larger than predator mortality relative to the effect of predation ($(c_N - c_P)/(p_N q_N) > m/(\mu\gamma)$). Here the prey gets harvested in the mixed equilibrium, but the predator disappears before reaching the prey-focused equilibrium. Then, the prey-focused equilibrium is unfeasible.

In the third case the difference between prey and predator costs relative to prey price and catchability is smaller than prey carrying capacity ($(c_N - c_P)/(p_N q_N) < K$), and smaller than predator mortality relatively to the effect of predation ($(c_N - c_P)/(p_N q_N) < m/(\mu\gamma)$). This is always the case when the cost of harvesting prey is smaller than the cost of harvesting predators, which is often true as predators are generally bigger than their prey. In this case, all three equilibria are feasible.

Appendix S2: Robustness of results from the Rosenzweig-MacArthur model

In the main text, we show that increased adaptation speeds can induce oscillations and therefore destabilize the mixed harvest equilibrium of a Rosenzweig-MacArthur system. Here we assess the sensitivity of these results to other parameters of the model. To do so, we numerically compute the Jacobian of our system for each parameter value. When a pair of complex eigenvalues crosses the imaginary axis, the system undergoes a Hopf bifurcation and begins to oscillate.

Figure A1 shows the influence of all parameters of the model on the stability of the mixed harvest equilibrium, relative to adaptation speed. The main conclusion is that increased adaptation speed always displayed a destabilizing influence on the mixed harvest equilibrium. Moreover, high adaptation speeds broaden the range of parameters for which oscillations occur. These results therefore support the main text's conclusion of a destabilizing effect of adaptation speed in this model.

The influence of the other parameters can be organized in three categories. Figures A1a, d, g and j show parameters that are destabilizing at low values and stabilizing at higher values. Interestingly, the total fishing effort shows this kind of pattern, meaning that high fishing efforts can potentially stabilize an oscillating system. Figure A1b, e, h, and k show parameters that destabilize the equilibrium, jointly with adaptation speed. One of these parameters is the carrying capacity, which agrees with the well-known paradox of enrichment (Rosenzweig 1971). Also note that parameters that favor the relative profitability of prey, namely prey price and predator fishing cost, are destabilizing. Figure A1c, f, i, l and m shows stabilizing parameters. In accordance with other studies (Gross et al. 2009), we find that the predator mortality rate is stabilizing. Also note that parameters that favor the relative profitability of predators, namely predator price and prey fishing cost, are stabilizing.

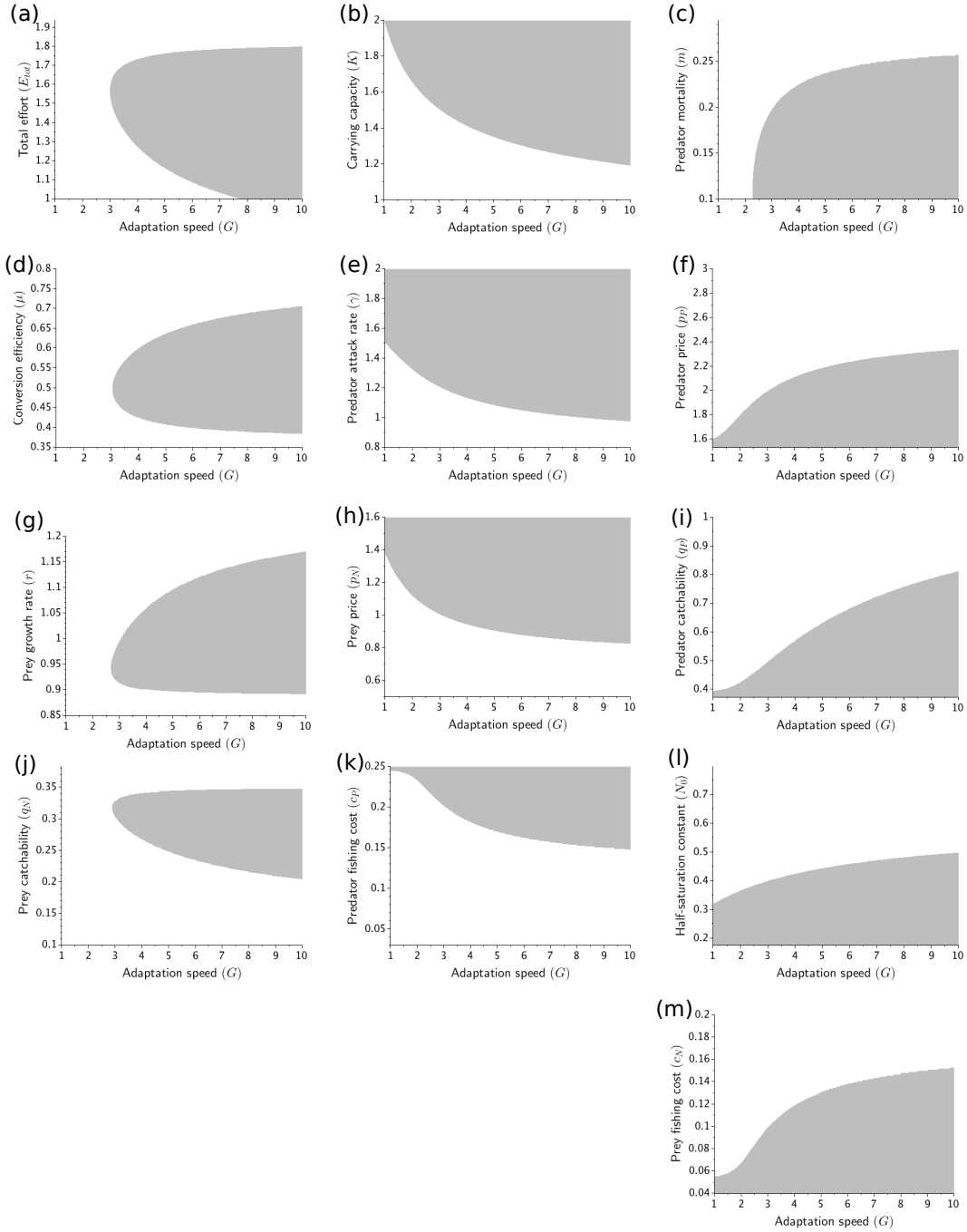

Figure S1: Influence of various parameters on the stability of the mixed harvest equilibrium, relative to adaptation speed. In the white zone, the system is stable, while in the grey zone it oscillates. Value of fixed parameters: $r=1$, $K=1.5$, $m=0.2$, $\mu=0.5$, $\gamma=1.2$, $q_N=0.3$, $q_P=0.5$, $p_N=1$, $p_P=2$, $c_N=0.1$, $c_P=0.2$, $N_0=0.4$, $E_{tot}=1.5$.