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Eric Tromeur, Nicolas Loeuille

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Eric Tromeur[1,2,a], Nicolas Loeuille[2,b]

[1] AgroParisTech, Univ Paris-Saclay, 16 rue Claude Bernard, 75231, Paris, France

[2] Sorbonne Universités, UPMC Univ Paris 06, Univ Paris Diderot, Univ Paris-Est Créteil, CNRS, INRA, IRD, Institute of Ecology and Environmental Sciences of Paris (iEES Paris), 7 quai St Bernard, 75252, Paris, France

[a] ORCID: 0000-0003-0620-7902; Email: eric.tromeur@agroparistech.fr

[b] ORCID: 0000-0001-9588-6542; Email: nicolas.loeuille@upmc.fr

Abstract

The global overexploitation of fish stocks is endangering many marine food webs. Scientists and managers now call for an ecosystem-based fisheries management, able to take into account the complexity of marine ecosystems and the multiple ecosystem services they provide. By contrast, many fishery management plans only focus on maximizing the productivity of harvested stocks. Such practices are suggested to affect other ecosystem services, altering the integrity and resilience of natural communities. Here we show that while yield-maximizing policies can allow for coexistence and resilience in predator-prey communities, they are not optimal in a multi-objective context. We find that although total prey and predator maximum yields are higher with a prey-oriented harvest, focusing on the predator improves species coexistence. Also, moderate harvesting of the predator can enhance resilience. Furthermore, increasing maximum yields by changing catchabilities improves resilience in predator-oriented systems, but reduces it in prey-oriented systems. In a multi-objective context, optimal harvesting strategies involve a general trade-off between yield and resilience. Resilience-maximizing strategies are however compatible with quite high yields, and should often be favored. Our results further suggest that balancing harvest between trophic levels is often best at maintaining simultaneously species coexistence, resilience and yield.

Introduction

The overexploitation of fish stocks is a global phenomenon that has major impacts on the structure and the functioning of marine ecosystems (Pauly et al. 1998, Worm et al. 2009). It has been shown to reduce the numbers of top predators such as sharks (Myers et al. 2007), thus triggering trophic cascades that compromise the conservation of marine biodiversity (Pauly et al. 1998, Estes et al. 2011) and affect its global functioning. Resulting biodiversity losses impair the delivery of ocean ecosystem services, altering the resilience and the productivity of fisheries (Worm et al. 2006). As a consequence, scientists are now calling for a consistent ecosystem-based fisheries management (EBFM), able to tackle the complexity of multispecies fisheries, and to balance multiple ecosystem services (Pikitch et al. 2004, Bennett et al. 2009).

However, many fisheries only focus on a single service, namely the productivity of the fishery. As a result, the maximum sustainable yield (hereafter MSY), has become the most common management target in world fisheries (Mace 2001). This reference point corresponds to the maximum level of catches that can be harvested from a fish stock while allowing the stock to regenerate. However, MSY targets generally rely on single-species assessments (Larkin 1977), which in multispecies contexts has been found to deteriorate the structure of marine ecosystems (Walters et al. 2005). This may in turn have far-reaching consequences on other ecosystem services such as ecosystem regulation and biomass preservation (Bennett et al. 2009). The compatibility of yield-maximizing strategies with the principles of ecosystem-based management is thus in question. This issue is particularly pressing given ecological network structures, where harvesting a species can affect other interacting species.

First, maximizing catches of a given species can endanger other trophic levels through indirect density-dependent effects. Predator species are particularly sensitive as they compete with harvesters for prey (Christensen 1996). Such indirect effects of prey harvesting have been empirically suggested to reduce predator numbers in multispecies fisheries (Pauly 1979, Trites et al. 1997, Essington and Munch 2014). Collapse of predator populations can also directly result from predator harvest (Myers and Worm 2003). As a consequence of the competition between predator species and harvesters, the culling of predator species has also been proposed to increase the productivity of some fisheries (Yodzis 1994).

Accordingly, former theoretical studies suggested that maximizing prey yield requires culling predators (May et al. 1979, Beddington and Cooke 1982, Legović et al. 2010, Kar and Ghosh 2013), except if the predator can rely on other resources or if the trophic interaction is ratio-dependent (Larkin 1966, Kar and Ghosh 2013). On the contrary, if the predator is the only harvested species, harvesting it at MSY enables the coexistence of prey and predator species (Legović et al. 2010, Kar and Ghosh 2013). Harvesting both prey and predator species to reach a multispecies MSY can enable the coexistence of the two species if the predator species is productive enough and can sustain sufficient harvesting levels (Larkin 1966, May et al. 1979, Matsuda and Abrams 2006, Kar and Ghosh 2013).

Second, yield-maximizing strategies can impact the resilience of the harvested food webs. Resilience is generally construed as the ability of food webs to recover from disturbances (McCann 2000). Empirical evidence usually suggests that harvesting reduces the resilience of marine ecosystems. Hsieh et al. (2006) found for instance that fishing increases variability in the abundance of harvested species. This effect has been interpreted as the result of changes in the size structure of fish populations (Anderson et al. 2008, Kuparinen et al. 2016). In predator-prey communities, harvesting predators has also been shown to promote regime shifts towards persistently low predator populations (Estes et al. 2011), as shown with cod in the Baltic Sea (Gardmark et al. 2014). Likewise, the resilience of coral communities can be affected by the harvest of herbivorous fish (Mumby et al. 2013, 2016). A local stability analysis of a coastal fish community based on empirical data also revealed a destabilizing effect of predator decline over time (Britten et al. 2014).

Theoretical studies have shown that the resilience of harvested predator-prey food webs is highly dependent on the relative intensity of prey and predator harvest. In many studies, increasing the rate of prey harvesting leads to less stable predator-prey dynamics (Brauer and Soudack 1979a, May et al. 1979). The impact of predator harvest is less clear however. Increasing the rate of harvest has been found to destabilize the dynamics of the system (Brauer and Soudack 1979b, May et al. 1979), which is coherent with the view that predators tend to stabilize ecosystems (Christensen 1996, Rooney et al. 2006). However, harvesting predators has also been found to stabilize the dynamics of the system (Brauer and Soudack 1979b, Plank and Law 2012). This latter result is coherent with the assumption that a decreased energy flux relative to the predator loss rate increases the resilience of the system to perturbations (Rosenzweig 1971, Rip and McCann 2011).

In the present work, we intend to discuss management from a simple point of view, accounting for multiple ecosystem services. We not only assess the productivity of the fishery (ressource supply ecosystem service), a classical target of MSY models, but also the integrity of the community (maintenance of all species, a conservation target) and its resilience. To allow for a more thorough mathematical analysis, resilience is measured as the time it takes for the system to come back to equilibrium after a small disturbance. We investigate the effects of maximizing yield on one of the two interacting species and on the whole community. We explore synergies and trade-offs between yield, conservation and resilience that arise from different harvesting strategies. More specifically, we predict: (1) from a conservation point of view, as predator populations limit potential prey yields, yield-maximizing strategies can be expected to deplete predator populations, resulting in a trade-off between yield and conservation objectives. (2) This in turn could affect resilience; in particular, increased prey harvests can be expected to reduce resilience, while the effects of predator harvest remain unclear. Thus, trade-offs are also likely to arise between resilience and yield and to depend on the relative intensities of prey and predator harvest. (3) That given these two trade-off axes, one may only need to sacrifice a little yield compared to MSY targets, to allow a better and more integrative management of marine ecosystems (in line with Pretty Good Yield concepts (Hilborn 2010)).

Our results indeed highlight a general trade-off between yield and resilience that depends on the relative harvesting intensities of prey and predator species, and suggest that a sensible strategy meeting all three targets usually balances the harvesting between predator and prey species.

Methods

Model

To allow for a tractable analysis of relevant management strategies, we consider a simple Lotka-Volterra model of predator-prey dynamics where the two species are harvested (we however consider an additional model with a type II functional response in the Supplementary Material). This model can be written as:

$$\begin{cases} \dfrac{dN}{dt} = rN\left(1 - \dfrac{N}{K}\right) - \gamma NP - q_N EN \\ \dfrac{dP}{dt} = e\gamma NP - mP - q_P EP \end{cases} \tag{1}$$

where N and P are the respective densities of the prey and predator species, r is the prey intrinsic growth rate, K its carrying capacity, γ is the attack rate of the predator, e the efficiency of conversion of prey into predator, and m the predator natural mortality rate. Predator and prey species are harvested with a single fishing effort E and with respective catchabilities q_N and q_P. In fisheries, this would mean that a single fleet harvests multiple species at once, which is the case of most fishing fleets such as trawlers.

Equilibrium

At the equilibrium, the variations of densities in time (Eq. (1)) are set to zero. A trivial equilibrium exists where the two populations are extinct. This trivial equilibrium is stable provided the effort remains below the growth rate of the prey species, given its catchability ($E < r/q_N$, see Appendix 1 in Supplementary Material). Otherwise, prey population increases when rare. In the single-species equilibrium, the density of the prey is equal to $N^* = K(1 - q_N E/r)$, while the predator remains extinct. This equilibrium is feasible and stable if the harvesting effort is smaller than the maximum effort the prey can sustain ($E < r/q_N$) and larger than the maximum effort the predator can sustain ($E > r(e\gamma K - m)/(rq_P + e\gamma K q_N)$). This latter limit decreases with predator and prey catchabilities and predator mortality as these parameters undermine predator growth, and increases with the growth rate of the prey. If $e\gamma K < m$, the predator is extinct even in a unharvested system. Finally, a coexistence equilibrium also exists:

$$N^* = \frac{m + q_P E}{e\gamma} \quad ; \quad P^* = \frac{1}{\gamma}\left[r\left(1 - \frac{(m + q_P E)}{e\gamma K}\right) - q_N E\right] \tag{2}$$

This equilibrium is feasible and stable if the harvesting effort is smaller than the maximum effort the predator can sustain ($E < r(e\gamma K - m)/(rq_P + e\gamma K q_N)$). From Eq. (2), prey density positively depends on predator harvest, as harvesting relaxes the top-down control exerted by predators. The density of the predator species is negatively correlated with the intensity of prey and predator harvesting. Thus, harvesting predator populations increases prey density and decreases predator density, while harvesting prey populations only decreases predator density.

Maximum sustainable yield

We now determine the management allowing for maximum sustainable yield (MSY). When both populations are exploited, assuming that individuals of both species are valued equivalently, this strategy satisfies

$$\max_E \ (q_N E N^* + q_P E P^*) \tag{3}$$

As specific scenarios, we also study simpler situations in which only one of the two species is exploited. In that case, one of the catchabilities is set to zero. If the computed effort leads to the extinction of one of the two species, a new effort is computed for the remaining species. For precise MSY computations, see Appendix 1.

Resilience

We wish to measure how harvesting impacts the resilience of the system, understood as the ability of a system to sustain perturbations (here, small variations of densities around the equilibrium). To do this, we compute the leading eigenvalue λ_m of the Jacobian matrix at the equilibrium, that is the eigenvalue with the largest real part.

The return time to the equilibrium after a small perturbation is then (Pimm and Lawton 1978, Loeuille 2010):

$$\tau = \frac{1}{-Re(\lambda_m)} \tag{4}$$

A large return time to the equilibrium suggests a low resilience in the face of perturbations.

Results

Prey harvest

We first consider the case in which the prey species is the only harvested species. Increasing harvesting efforts then leads to a decrease in predator density while prey density remains (Eq (2), Fig. 1a). As predation pressure decreases with reduced predator densities, higher prey yields can be harvested with increased efforts. Prey catches increase linearly until the predator goes to extinction. It follows that to maximize prey yields, it is necessary to first cull predator populations, by increasing the harvesting effort up to the point at which the predator goes extinct. After the extinction of the predator, the effort must be readjusted to $r/(2q_N)$ to reach the monospecific prey MSY (see Appendix 1). As reaching MSY implies to cull the predator, there is a clear trade-off between maximizing yields and promoting community conservation.

For low to intermediate harvesting efforts, the resilience of the community remains unaffected (Fig. 1b). However, close to predator extinction, the resilience of the community shrinks abruptly as the return time to the equilibrium soars. As shown in Appendix 1, this is due to a spiral-to-node bifurcation of the stable equilibrium. Here, resilience and conservation objectives are then aligned. Right after the shift in dynamics, yield can only be increased at the expense of resilience, indicating a trade-off between these two objectives.

Predator harvest

We now consider the case in which the predator is the only harvested species. Increasing harvesting efforts on predator leads to a decrease in predator density and to an increase in prey density due to diminished top-down control (Eq. (2), Fig. 2a). Catches can be maximized for efforts twice as small as the effort leading to predator extinction (see Appendix 1). In that case, maximization of fishery productivity is thus a sustainable strategy as it enables the coexistence of the two interacting species.

The return time to equilibrium first decreases with increasing efforts, indicating a stabilization of the system (Fig. 2b). Then after a spiral-to-node bifurcation, the return time rises close to the extinction of the predator, indicating a reduced resilience. Given the resilience profile, an effort exists that maximizes the resilience of the community, hereafter called *resilience maximizing yield* (RMY).

The harvesting effort at RMY can be above (Fig. 2a-b) or below (Fig. 2c-d) the effort at MSY. When the yield-maximizing effort is below the resilience-maximizing effort (Fig. 2a-b), the resilience at MSY is always higher than the resilience of an unharvested system. On the other hand, when the yield-maximizing effort is above the resilience-maximizing effort (Fig. 2c-d), then the MSY-harvested system can be less resilient than the unharvested system (Fig. 2d). Thus, while MSY harvesting is always sustainable in this case (in the sense that it guarantees coexistence), it can still induce resilience losses.

The yield-maximizing policy is more likely to be destabilizing if the predator has a low recovery potential and if its prey is subject to intense intraspecific competition. In fact, as shown in Appendix 1, the effort at MSY is above the effort at RMY if $m > (4e\gamma K - r)/(4 + r/e\gamma K)$. This expression tells us that harvesting at MSY a predator with a low maximum growth rate $e\gamma K$ and a high mortality m is more likely to destabilize the system. Note also that when the prey growth rate r is high, harvesting at MSY is also more likely to be destabilizing. The opposite effects of prey growth rate r and prey carrying capacity K indicate that if prey populations are subject to intense intraspecific competition (defined by the rate r/K), MSY likely destabilizes the system. Understanding the implications of MSY for resilience thereby requires a simultaneous study of predator and prey life-histories.

As long as the efforts at MSY and RMY do not coincide, between these efforts, yield cannot be increased without reducing resilience and vice versa. A trade-off between yield and resilience therefore exists. Managers that desire more resilient yields may thus choose to depart from the classical MSY strategy and give up some yield to gain resilience, effectively making a compromise between MSY and RMY strategies.

Simultaneous harvest of predators and prey

We now consider the full system as described by Eq. (2). In this case, it is possible to find parameter sets for which maximizing the total yield is compatible with coexistence (Fig. 3, see also Appendix 1 for detailed analytical explanations).

For increasing prey catchabilities, the total maximum yield rises (Fig. 3a, see analytical demonstration in Appendix 1). However, the MSY effort also gets closer to the effort at which the predator population collapses. This underlines the fact that MSY strategies in this multispecies context become increasingly risky from a conservation point of view for high prey catchabilities.

On the contrary, for increasing predator catchabilities, the total maximum yield is reduced (Fig. 3c, see analytical demonstration in Appendix 1). Thus, a prey-oriented effort is more likely to bring higher maximum yields than a predator-oriented effort. The distances between the MSY effort and the effort at which the predator population collapses are not affected by predator catchabilities. As demonstrated in Appendix 1, increasing predator catchabilities actually decreases extinction risk at MSY. Thus, while a predator-oriented harvest is less productive than a prey-oriented harvest at MSY, it appears to lower the risk of breaking community coexistence, facilitating the conservation objective. There is then a trade-off between a prey-oriented harvest with high yields but high risks in terms of conservation and a predator-oriented harvest with lower yields but higher sustainability.

When increasing prey catchabilities, the minimum return time to equilibrium is also increased (Fig. 3b). On the contrary, for increasing predator catchabilities, the minimum return time to equilibrium is slightly reduced (Fig. 3d). Thus, a predator-oriented effort is potentially more resilient than a prey-oriented effort. As a result, a prey-oriented harvest is more likely to be more productive and less resilient than a predator-oriented harvest, which can be less productive but more resilient to perturbations.

The relationship between yield and resilience at MSY is illustrated for varying prey and predator catchabilities in Figure 4. Increasing prey catchability augments the total yield at MSY (Fig. 4a), while increasing predator catchability reduces the total yield at MSY (Fig. 4b). As pointed out before, prey-oriented systems are thus more productive than predator-oriented systems at MSY.

Effects of varying prey and predator catchabilities on system resilience are however not monotonic. Increasing prey catchability from low values first increases resilience. Likewise, starting from high values, decreasing predator catchability increases resilience. Thus, in a predator-oriented fishery with high predator catchabilities and low prey catchabilities, turning towards a more prey-oriented harvest both increases yield and resilience: there is a synergy between yield and resilience at MSY. For higher prey catchabilities and lower predator catchabilities, the situation is reversed, and a trade-off appears between yield and resilience at MSY: focusing on prey at the expense of predator harvest leads to small increases in yield and strong decreases in resilience. Conversely, in a prey-oriented fishery with high yield and low resilience at MSY, turning towards a more predator-oriented harvest might increase resilience at the expense of yield.

These results have direct implications in terms of management. Let us for instance consider a predator-oriented harvest, with a low prey-to-predator catchability ratio. As increasing this ratio can bring higher yield and resilience at MSY, it can be expected to increase up to the point at which the trade-off between yield and resilience appears. The manager then has to decide whether to increase yield at the expense of resilience or not. Note that the trade-off front is quite sharp on Figure 4. Therefore, past the breaking point, a small increase in yield would induce an important decrease in resilience. A prudent manager could be expected to choose an intermediate ratio, that is a balanced harvesting between prey and predator species.

We now move from this view, centered on MSY strategies, to a more global set of strategies that consider all possibilities from MSY to RMY. That is, from a management primarily directed at productivity to one devoted to maintaining system stability. We have shown in Figure 2 that the yield-maximizing and the resilience-maximizing equilibria are generally reached for different efforts. In between, it is impossible to increase yield without decreasing resilience, and vice versa. All equilibria between MSY and RMY strategies thus denote a trade-off between yield and resilience. In Figure 5, we compute all these equilibria for different prey (Fig. 5a) and predator (Fig. 5b) catchabilities, thereby illustrating the set of possible states. For each catchability value (i.e., each shade of grey), the dotted line traces out the equilibria between MSY and RMY, with effort varying along the line. Thus, MSY equilibria in Figure 5 trace out the same curves as in Figure 4. From any state among these dotted lines, it is possible to reach any other state, by changing the catchabilities or the fishing effort. In particular, both yield and resilience can be improved, until we reach the external part of the set (thick dark-gray line in Fig. 5), where yield cannot be increased without decreasing resilience and vice versa. This border part of the set, on which no further improvement of yield or resilience is possible, is called a Pareto frontier.

This Pareto frontier denotes a global trade-off between yield and resilience, that is associated with a trade-off between a prey-oriented harvest and a predator-oriented harvest: for low prey catchabilities or high predator catchabilities, a small yield is associated with a high resilience, while for higher prey catchabilities or lower predator catchabilities, resilience is decreased as the total yield is increased. As this trade-off is concave, at high yields resilience can be highly increased without losing much yield, while at high resilience yields can be highly increased without losing much resilience.

Analysis of the Pareto frontier may help to guide the management of the harvested system. Without knowing the preferences of the managers however, it is impossible to define a single optimal strategy. If a manager is only interested in yield, the optimal state would be to maximize catches at the expense of resilience and then put the predator population at risk. This strategy is denoted by the letter A in Figure 5.

This can be done by focusing harvest on prey and harvesting the system at MSY. Now if a manager is only interested in resilience, the best target is a focus on predator to reach RMY (letter C in Figure 5). But as the manager can be expected to seek a balance between resilience and yield, he may want to increase yield until resilience losses are acceptable. The breaking point of the Pareto frontier (letter B in Figure 5) can then be an optimal solution, which corresponds to focusing harvest on prey and reaching RMY.

Most MSY points are not situated on the global Pareto frontier, while all RMY points are. Thus, if we include resilience among the objectives of a fishery, MSY does not appear to be the best-suited harvesting strategy. Consider for instance a system where only the predator is harvested at MSY (Fig. 5a): to improve both yield and resilience and reach the Pareto frontier, one may slightly increase harvesting pressure on prey and adjust the effort to maximize resilience. But as the point at which MSY and RMY coincide is situated on the frontier, balancing harvest between trophic levels can in any case be considered an optimal strategy.

As we show in Appendix 2, our main results are not specific to the linear functional response we use here. We investigated a Rosenzweig-MacArthur model characterized by a non-linear (Holling type II) functional response. Our conclusions regarding the impact of predator harvest or joint prey and predator harvest on resilience are similar in both models (compare Fig. A2b and A2c with Fig. 2 and 3). Note however that contrary to the linear case, prey harvest can increase resilience (Fig A2a). We also observe similar relationships between yield and resilience (compare Fig. A3 with Fig. 5), regardless of the functional response. Particularly, the trade-off between a prey-oriented fishery with high yield and low resilience and a predator-oriented fishery with low yield and high resilience remains when using non-linear functional responses. In both models, balancing harvest between predator and prey thus allows for a simultaneous management of the two objectives.

Discussion

Focusing harvest on predator favors conservation at MSY

Our results stress potential conservation issues of yield-maximizing policies in trophic communities. We find that maximizing prey yield results in the extinction of predator populations, in agreement with previous studies (May et al. 1979, Beddington and Cooke 1982, Legović et al. 2010, Kar and Ghosh 2013). On the contrary, maximizing predator yield is compatible with species coexistence, as shown in Legović et al. (2010), Kar and Ghosh (2013). In more complex communities however, single-species MSY policies may induce many indirect effects that deteriorate the structure of harvested communities (Walters et al. 2005). Maximizing total yields, or reaching multispecies MSY, has thus been suggested as a potential ecosystem-based alternative to single-species MSY (Mueter and Megrey 2006).

Along these lines, we show that when both prey and predator species are harvested, it is possible to implement strategies that conciliate both productivity objectives and the conservation of predators and prey, thus reconciling "resource supply" with ecosystem services that are directly linked with the maintenance of biodiversity (Costanza et al. 1997). Such management strategies are consistent with other theoretical analyzes (May et al. 1979, Kar and Ghosh 2013). Yet depending on parameters, the MSY effort can still be very close to the extinction effort, so that harvesting becomes risky and any implementation error could lead to species loss. We argue in particular that maximizing total yield is more sustainable with a predator-oriented harvest than with a prey-oriented harvest, as the predator extinction risk is lower.

Focusing harvest on prey increases maximum yields

Our results also show that multispecies maximum yields are higher with a prey-oriented harvest than with a predator-oriented harvest, consistently with findings from Beddington and Cooke (1982). This also is coherent with the assumption that catches decrease with the trophic level (Christensen 1996). If maintaining all populations is not considered a priority, the solution is again to cull down predator species to maximize prey yields (Yodzis 1994). Yet this culling strategy is not considered in depth here as we assume that maintaining coexistence is a prerequisite to any ecosystem-based management strategy.

Our results hinge on the assumption that individuals of each species are valued equivalently. A common hypothesis in multispecies MSY studies is that each species has the same value per unit biomass (Mueter and Megrey 2006, Kar and Ghosh 2013). In such conditions, predatory fish usually having larger body sizes may be expected to have a higher value than prey individuals. A straightforward way to consider differential valuation in our model could be to weight equation (3) by introducing the prices of predators and prey explicitly. If predators have higher prices than prey, maximizing profits instead of yield, to reach what is usually called a *maximum economic yield* policy (Clark 2006), would then imply a larger focus on predators. In general, maximizing aggregate profits is likely to lead to a dominant harvesting of the most productive and valuable species (as suggested in Clark 2006). While we do not capture this explicitly, note that we analyze differences in catchabilities of the two species that can be expected to reflect differential valuations. Indeed, fishermen are supposed to preferentially target species with high productivity and value. In that sense, our results already partly reflect the consequences of a differential valuation of prey and predator species.

Moderate predator harvesting favors resilience

Next to the maintenance of the community and the productivity of the fishery, our analysis also focuses on resilience criteria. Indeed, given current global changes and generalized human impacts, marine ecosystems face many disturbances (Lejeusne et al. 2010) and their ability to sustain such disturbances (resistance) and to get back to their initial state (resilience) has become an important focus in ecosystem management in general (Côté and Darling 2010) and in fisheries in particular (Hsieh et al. 2006, Barnett and Baskett 2015). Resilience is especially important to fishermen, whose activity may then rely on stable catches and profits in time (Armsworth and Roughgarden 2003). Given a fast pace of disturbances, a non resilient system that would take a long time to go back to equilibrium would undergo a new perturbation before it can get back to its state. This accumulation of disturbances could maintain the system in a transient state, possibly threatening the overall ecosystem functioning and associated ecosystem services. Incorporating resilience-oriented objectives in fisheries management is therefore highly needed given this global context.

Yet, defining and measuring resilience remains challenging (McCann 2000). Our measure of resilience as a return time to equilibrium is simple enough to allow a complete mathematical analysis. It can however be difficult to assess empirically (Donohue et al. 2016). Nevertheless, Britten et al. (2014) did evaluate the return time to equilibrium of a coastal fish community by using the approach developed by Ives et al. (2003). But such an assessment is not relevant in unstable systems characterized by transient or oscillatory dynamics. A broader definition of resilience as the ability to absorb changes and still persist is then needed (Holling 1973). Such other measures include variability (coefficient of variation over time) and persistence (maintenance of the structure of the system after a specified amount of time) (Donohue et al. 2016).

Our analysis brings together contrasting views regarding the effects of predator harvesting on resilience. On the one hand, we show that for low harvesting pressures, harvesting the predator as a sole or joint target can bring resilience to the system. This is coherent with the *principle of energy flux* (Rosenzweig 1971, Rip and McCann 2011), which states that decreased energy fluxes, relative to the consumer loss rate, makes consumer-resource interactions more stable. A similar result has been found in marine ecosystems by (Plank and Law 2012).

On the other hand, we show that when harvesting at MSY brings the predator species close to extinction, the system abruptly becomes less resilient. Thus, when the predator population is reduced to low levels, then the principle of energy flux does not hold anymore and harvesting the predator species becomes destabilizing. This is coherent with the assumption that predator species are stabilizing (Christensen 1996, Rooney et al. 2006), and with the finding by (Britten et al. 2014) based on empirical data that predator declines reduce the stability of coastal fish communities. The sudden decrease in resilience close to the collapse of the predator population implies a critical slowing down in the recovery ability of the disturbed system (Scheffer et al. 2009). Slow return times to equilibrium, in addition to low predator densities, could make the predator population particulary vulnerable to an accumulation of perturbations.

Managing yield and resilience at MSY by balancing predator and prey exploitation

By comparing yield and resilience at MSY, we uncover synergies and trade-offs between these two services, with important consequences in terms of management. We show that in a predator-oriented mixed fishery, turning towards a more prey-oriented harvest can first increase both yield and resilience at MSY. However, such a strategy eventually leads to increased yield at the expense of resilience, implying a trade-off between these two services. As giving up small yields can bring much resilience, managers can be expected to choose intermediate prey and predator catchabilities, resulting in a balanced harvest between trophic levels.

Balancing harvest between trophic levels has recently been advanced as an alternative to the classical selective paradigm in fisheries (Zhou et al. 2010). It has notably been shown to improve maximum yields in multispecies fisheries (Garcia et al. 2012, Jacobsen et al. 2013) . The consequences of balanced harvesting for the stability of size-structured fish populations have also been assessed (Rochet and Benoit 2012, Law et al. 2012). These studies suggest that a balanced harvest could be more productive and stabilizing than selectively harvesting either small fish (mostly prey fish) or big fish (mostly predator fish). Our results offer a more nuanced view by showing that balancing harvest is not always a win-win solution, but rather an optimal strategy along a trade-off that balances yield and resilience.

Beyond MSY: trading off yield and resilience in harvested trophic communities

Our results show the existence of a global trade-off between yield and resilience in mixed predator-prey fisheries, represented by a Pareto-optimality frontier between these services. Different parts of this frontier can be reached by changing prey and predator catchabilities, but also the intensity of harvest. Thus, the trade-off between yield and resilience is indicative of a trade-off between a predator-oriented harvest with low yields but high resilience and a prey-oriented harvest with high yields but potentially low resilience.

Interestingly, yield-maximizing strategies are almost never found on the optimality frontier and thus often revealed to be suboptimal when considering multiple objectives. This concurs with Beddington and Cooke (1982), who argue that maximum yields should be reduced to account for the stability of harvested systems. It is also coherent with empirical claims that harvest reduces the resilience of fish stocks (Hsieh et al. 2006, Anderson et al. 2008). As a result, strict MSY policies do not seem to fit into the multi-objective framework of ecosystem-based management (Bennett et al. 2009). This is especially true in multispecies communities in which emergent properties such as resilience are highly constrained by interactions between species.

On the contrary, resilience-maximizing policies are always found to be optimal in this multi-objective context. To improve yield without losing much resilience, managers can be expected to focus harvest on prey with low efforts, in order to maximize resilience. In that case, balancing yield and resilience would imply to focus harvest on prey with a low harvesting intensity. This strategy could bring higher yields than a balanced harvesting, without losing much resilience. Therefore, some level of selectivity can also be beneficial if harvesting pressures are reduced. This is coherent with the claim that favoring a targeted exploitation of fish stocks below maximum sustainable yields could be more efficient than a balanced harvest (Froese et al. 2015). In that sense, maximum sustainable yields can still serve as useful reference points to implement ecosystem-based fisheries management, as long as other objectives are taken into account (Hilborn 2010).

For the sake of a complete analysis, we proposed here the study of a simple model. We notably assumed a linear functional response for predators, which typically leads to stable equilibria. Other functional responses are however possible, and may involve unstable and oscillatory states. To check whether our results can be extended to such dynamics, we numerically investigated a Rosenzweig-MacArthur model, characterized by a type-II functional response (see Appendix 2). Consistent with other studies (e.g., Ghosh et al. 2014), maximizing predator-only or aggregate prey and predator catches decreases oscillations and often leads the system to a stable state. Investigation of these stable states shows consistent relationships between yield and resilience. In particular, the existence of a general trade-off between yield and resilience turns out to be robust when considering a non-linear functional response.

Further complexities such as age- or size-structure of the harvested populations could also affect the generality of our conclusions. Resilience losses are for instance known to occur in the context of fisheries-induced disruption of size-structure (Rochet and Benoit 2012). Also in complex food webs with many direct and indirect interactions between species (Bascompte et al. 2005), the relationship between yield and resilience may be strongly dependent on the structure of the food web. Investigating the relevance of our results for more complex systems such as structured populations or food webs is an interesting challenge for future research. This concerns in particular our finding that a balanced harvesting between predator and prey can reconcile resilience maximization with high yields.

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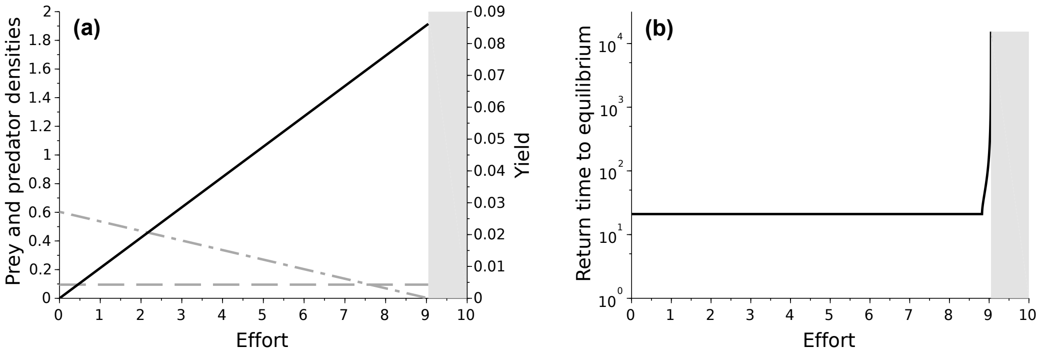
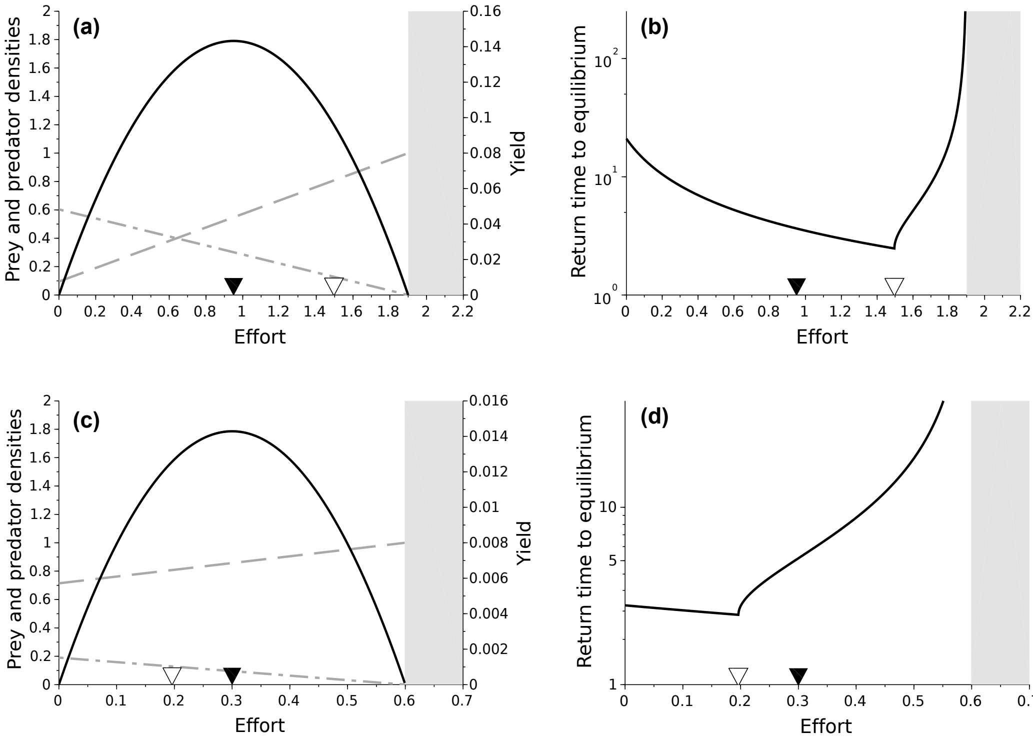
Figure legends

Figure 1: Effects of prey harvesting. (a) Prey (gray dashed line) and predator (gray dash-dotted line) densities at the equilibrium, and total catches (black line). (b) Return time to the equilibrium after a perturbation. Shaded areas indicate that predators are extinct. Parameters: $r = 1$, $K = 1$, $m = 0.1$, $e = 0.7$, $\gamma = 1.5$, $q_N = 0.1$, $q_P = 0$.



 DOI: 10.1111/oik.03985

Figure 2: Effects of predator harvesting. (a,c) Prey (gray dashed line) and predator (gray dash-dotted line) densities at the equilibrium, and total catches (black line). (b,d) Return time to the equilibrium after perturbation. Shaded areas indicate that predators are extinct. Filled triangles indicate efforts that maximize catches (MSY) while empty triangles indicate efforts that maximize resilience (RMY). (a,b) Same parameters as Figure 1, except $q_N = 0$ and $q_P = 0.5$. (c,d) Idem, except $m = 0.75$.



 DOI: 10.1111/oik.03985

Figure 3: Effects of a simultaneous harvesting of predators and prey. (a,c) Total catches for different (a) prey and (c) predator catchabilities. (b,d) Return time to equilibrium after a perturbation for different (b) prey and (d) predator catchabilities. Vertical lines indicate efforts at which the predator species goes to extinction. Filled triangles indicate MSY efforts while empty triangles indicate RMY efforts. (a,b) Same parameters as Figure 1, except: $q_N = (0, 0.1, 0.2)$, $q_P = 0.5$. (c,d) Idem, except: $q_N = 0.1$, $q_P = (0.5, 0.6, 0.7)$.

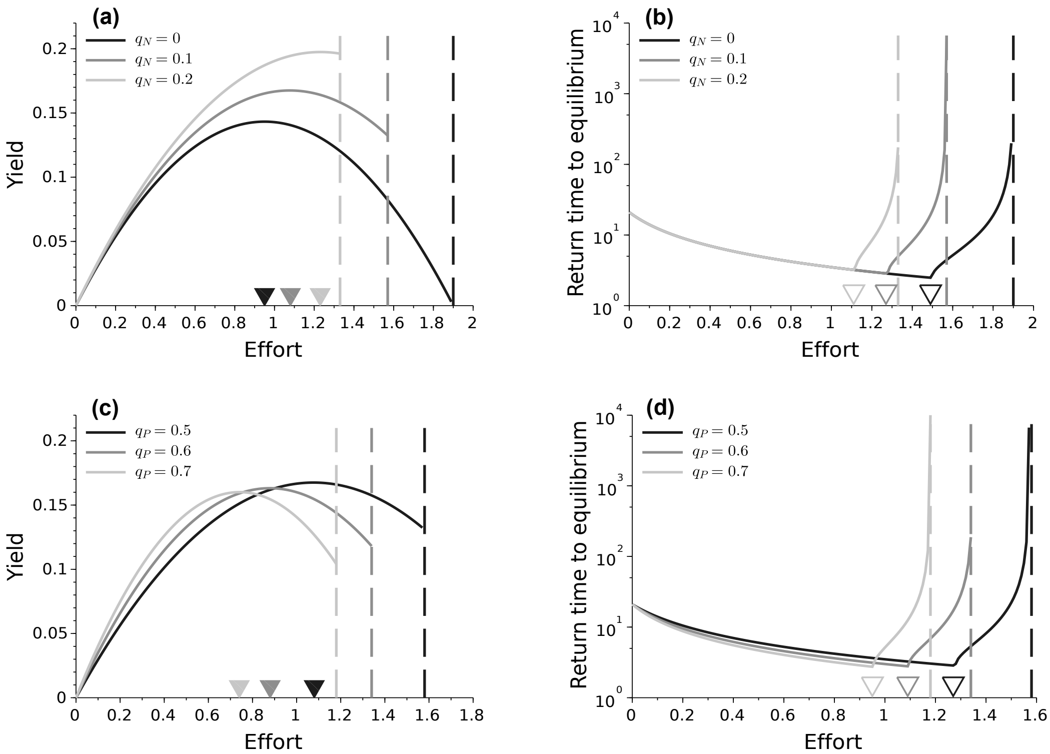


Figure 4: Trade-offs and synergies between productivity and resilience objectives at MSY when varying prey (a) and predator (b) catchabilities. Low to high catchabilities values are represented with colors ranging from black to light gray. As return times tend towards infinity close to predator extinction, only equilibria with return times below 35 are shown. Close to predator extinction, yields at MSY tend asymptotically towards a maximum value indicated by a dashed line. Arrows indicate synergy (*) and trade-off (Δ) zones between yield and resilience. (a) The predator catchability is fixed, and the prey catchability varies between 0 and the maximum value at which predators collapse. Parameters are similar to Figure 1, except: $q_P = 0.5$. (b) The prey catchability is fixed, and the predator catchability varies between 0.5 and the minimum value at which the MSY effort is focused on prey and predator populations collapse. Parameters are similar to (a), except: $q_N = 0.1$.

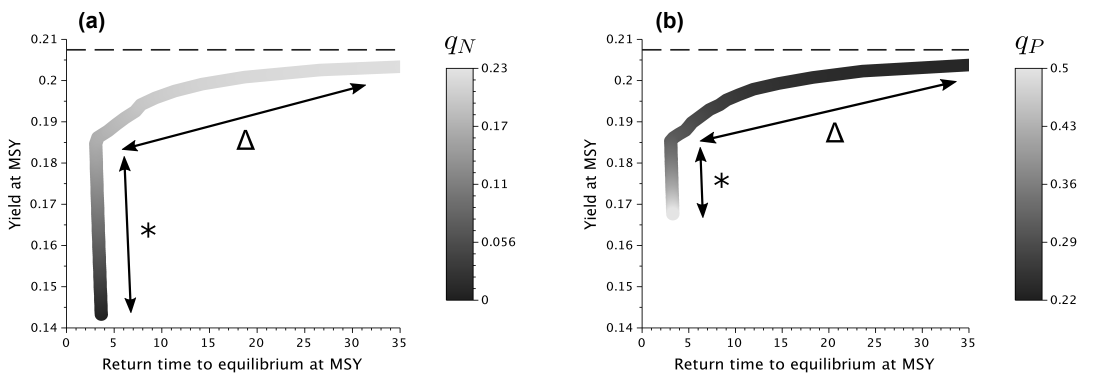


Figure 5: Relationship between yield and return time to equilibrium for varying prey (a) and predator (b) catchabilities (log scale). Low to high catchabilities values are represented with colors ranging from black to light gray and applied to circles and dotted lines. For each pair of catchabilities, MSY equilibria are shown with filled circles and RMY equilibria are shown with empty circles. For each catchability value, the dotted line traces out the equilibria between MSY and RMY, with effort varying along the line. Thus, each pair of circles and associated lines represent a different catchability parameter value. The thick dark-gray line shows the global Pareto frontier between yield and resilience. Letters A, B and C respectively indicate global yield-maximizing, balanced and resilience-maximizing strategies. Parameters are similar to Figure 4.