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1 **Balancing yield with resilience and conservation objectives in harvested**
2 **predator-prey communities**

3

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15 **Abstract**

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

34 Introduction

35 The overexploitation of fish stocks is a global phenomenon that has major impacts on
36 the structure and the functioning of marine ecosystems (Pauly et al. 1998, Worm et al.
37 2009). It has been shown to reduce the numbers of top predators such as sharks
38 (Myers et al. 2007), thus triggering trophic cascades that compromise the
39 conservation of marine biodiversity (Pauly et al. 1998, Estes et al. 2011) and affect its
40 global functioning. Resulting biodiversity losses impair the delivery of ocean
41 ecosystem services, altering the resilience and the productivity of fisheries (Worm et
42 al. 2006). As a consequence, scientists are now calling for a consistent ecosystem-
43 based fisheries management (EBFM), able to tackle the complexity of multispecies
44 fisheries, and to balance multiple ecosystem services (Pikitch et al. 2004, Bennett et
45 al. 2009).

46 However, many fisheries only focus on a single service, namely the
47 productivity of the fishery. As a result, the maximum sustainable yield (hereafter
48 MSY), has become the most common management target in world fisheries (Mace
49 2001). This reference point corresponds to the maximum level of catches that can be
50 harvested from a fish stock while allowing the stock to regenerate. However, MSY
51 targets generally rely on single-species assessments (Larkin 1977), which in
52 multispecies contexts has been found to deteriorate the structure of marine ecosystems
53 (Walters et al. 2005). This may in turn have far-reaching consequences on other
54 ecosystem services such as ecosystem regulation and biomass preservation (Bennett
55 et al. 2009). The compatibility of yield-maximizing strategies with the principles of
56 ecosystem-based management is thus in question. This issue is particularly pressing
57 given ecological network structures, where harvesting a species can affect other
58 interacting species.

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

68 Accordingly, former theoretical studies suggested that maximizing prey yield
69 requires culling predators (May et al. 1979, Beddington and Cooke 1982, Legović et
70 al. 2010, Kar and Ghosh 2013), except if the predator can rely on other resources or if
71 the trophic interaction is ratio-dependent (Larkin 1966, Kar and Ghosh 2013). On the
72 contrary, if the predator is the only harvested species, harvesting it at MSY enables
73 the coexistence of prey and predator species (Legović et al. 2010, Kar and Ghosh
74 2013). Harvesting both prey and predator species to reach a multispecies MSY can
75 enable the coexistence of the two species if the predator species is productive enough
76 and can sustain sufficient harvesting levels (Larkin 1966, May et al. 1979, Matsuda
77 and Abrams 2006, Kar and Ghosh 2013).

78 Second, yield-maximizing strategies can impact the resilience of the harvested
79 food webs. Resilience is generally construed as the ability of food webs to recover
80 from disturbances (McCann 2000). Empirical evidence usually suggests that
81 harvesting reduces the resilience of marine ecosystems. Hsieh et al. (2006) found for
82 instance that fishing increases variability in the abundance of harvested species. This
83 effect has been interpreted as the result of changes in the size structure of fish

84 populations (Anderson et al. 2008, Kuparinen et al. 2016). In predator-prey
85 communities, harvesting predators has also been shown to promote regime shifts
86 towards persistently low predator populations (Estes et al. 2011), as shown with cod
87 in the Baltic Sea (Gardmark et al. 2014). Likewise, the resilience of coral
88 communities can be affected by the harvest of herbivorous fish (Mumby et al. 2013,
89 2016). A local stability analysis of a coastal fish community based on empirical data
90 also revealed a destabilizing effect of predator decline over time (Britten et al. 2014).

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

103 In the present work, we intend to discuss management from a simple point of
104 view, accounting for multiple ecosystem services. We not only assess the productivity
105 of the fishery (resource supply ecosystem service), a classical target of MSY models,
106 but also the integrity of the community (maintenance of all species, a conservation
107 target) and its resilience. To allow for a more thorough mathematical analysis,
108 resilience is measured as the time it takes for the system to come back to equilibrium

109 after a small disturbance. We investigate the effects of maximizing yield on one of the
110 two interacting species and on the whole community. We explore synergies and trade-
111 offs between yield, conservation and resilience that arise from different harvesting
112 strategies. More specifically, we predict: (1) from a conservation point of view, as
113 predator populations limit potential prey yields, yield-maximizing strategies can be
114 expected to deplete predator populations, resulting in a trade-off between yield and
115 conservation objectives. (2) This in turn could affect resilience; in particular,
116 increased prey harvests can be expected to reduce resilience, while the effects of
117 predator harvest remain unclear. Thus, trade-offs are also likely to arise between
118 resilience and yield and to depend on the relative intensities of prey and predator
119 harvest. (3) That given these two trade-off axes, one may only need to sacrifice a little
120 yield compared to MSY targets, to allow a better and more integrative management of
121 marine ecosystems (in line with Pretty Good Yield concepts (Hilborn 2010)).

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

126

127 **Methods**

128 *Model*

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

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

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

140

141 *Equilibrium*

142 At the equilibrium, the variations of densities in time (Eq. (1)) are set to zero. A trivial
 143 equilibrium exists where the two populations are extinct. This trivial equilibrium is
 144 stable provided the effort remains below the growth rate of the prey species, given its
 145 catchability ($E < r/q_N$, see Appendix 1 in Supplementary Material). Otherwise, prey
 146 population increases when rare. In the single-species equilibrium, the density of the
 147 prey is equal to $N^* = K(1 - q_N E/r)$, while the predator remains extinct. This
 148 equilibrium is feasible and stable if the harvesting effort is smaller than the maximum
 149 effort the prey can sustain ($E < r/q_N$) and larger than the maximum effort the
 150 predator can sustain ($E > r(e\gamma K - m)/(r q_P + e\gamma K q_N)$). This latter limit decreases
 151 with predator and prey catchabilities and predator mortality as these parameters
 152 undermine predator growth, and increases with the growth rate of the prey. If
 153 $e\gamma K < m$, the predator is extinct even in a unharvested system. Finally, a coexistence
 154 equilibrium also exists:

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

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

162

163 *Maximum sustainable yield*

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

$$\max_E (q_N E N^* + q_P E P^*) \quad (3)$$

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

171

172 *Resilience*

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

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

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

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

181

182 **Results**

183 *Prey harvest*

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

195 For low to intermediate harvesting efforts, the resilience of the community
196 remains unaffected (Fig. 1b). However, close to predator extinction, the resilience of
197 the community shrinks abruptly as the return time to the equilibrium soars. As shown
198 in Appendix 1, this is due to a spiral-to-node bifurcation of the stable equilibrium.
199 Here, resilience and conservation objectives are then aligned. Right after the shift in

200 dynamics, yield can only be increased at the expense of resilience, indicating a trade-
201 off between these two objectives.

202

203 *Predator harvest*

204 We now consider the case in which the predator is the only harvested species.

205 Increasing harvesting efforts on predator leads to a decrease in predator density and to
206 an increase in prey density due to diminished top-down control (Eq. (2), Fig. 2a).

207 Catches can be maximized for efforts twice as small as the effort leading to predator
208 extinction (see Appendix 1). In that case, maximization of fishery productivity is thus
209 a sustainable strategy as it enables the coexistence of the two interacting species.

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

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

223 The yield-maximizing policy is more likely to be destabilizing if the predator
224 has a low recovery potential and if its prey is subject to intense intraspecific

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

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

240

241 *Simultaneous harvest of predators and prey*

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

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

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

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

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

273 Effects of varying prey and predator catchabilities on system resilience are
274 however not monotonic. Increasing prey catchability from low values first increases

275 resilience. Likewise, starting from high values, decreasing predator catchability
276 increases resilience. Thus, in a predator-oriented fishery with high predator
277 catchabilities and low prey catchabilities, turning towards a more prey-oriented
278 harvest both increases yield and resilience: there is a synergy between yield and
279 resilience at MSY. For higher prey catchabilities and lower predator catchabilities, the
280 situation is reversed, and a trade-off appears between yield and resilience at MSY:
281 focusing on prey at the expense of predator harvest leads to small increases in yield
282 and strong decreases in resilience. Conversely, in a prey-oriented fishery with high
283 yield and low resilience at MSY, turning towards a more predator-oriented harvest
284 might increase resilience at the expense of yield.

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

294 We now move from this view, centered on MSY strategies, to a more global
295 set of strategies that consider all possibilities from MSY to RMY. That is, from a
296 management primarily directed at productivity to one devoted to maintaining system
297 stability. We have shown in Figure 2 that the yield-maximizing and the resilience-
298 maximizing equilibria are generally reached for different efforts. In between, it is
299 impossible to increase yield without decreasing resilience, and vice versa. All

300 equilibria between MSY and RMY strategies thus denote a trade-off between yield
301 and resilience. In Figure 5, we compute all these equilibria for different prey (Fig. 5a)
302 and predator (Fig. 5b) catchabilities, thereby illustrating the set of possible states. For
303 each catchability value (i.e., each shade of grey), the dotted line traces out the
304 equilibria between MSY and RMY, with effort varying along the line. Thus, MSY
305 equilibria in Figure 5 trace out the same curves as in Figure 4. From any state among
306 these dotted lines, it is possible to reach any other state, by changing the catchabilities
307 or the fishing effort. In particular, both yield and resilience can be improved, until we
308 reach the external part of the set (thick dark-gray line in Fig. 5), where yield cannot be
309 increased without decreasing resilience and vice versa. This border part of the set, on
310 which no further improvement of yield or resilience is possible, is called a Pareto
311 frontier.

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

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

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

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

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

350 functional responses. In both models, balancing harvest between predator and prey
351 thus allows for a simultaneous management of the two objectives.

352

353

354 **Discussion**

355 *Focusing harvest on predator favors conservation at MSY*

356 Our results stress potential conservation issues of yield-maximizing policies in trophic
357 communities. We find that maximizing prey yield results in the extinction of predator
358 populations, in agreement with previous studies (May et al. 1979, Beddington and
359 Cooke 1982, Legović et al. 2010, Kar and Ghosh 2013). On the contrary, maximizing
360 predator yield is compatible with species coexistence, as shown in Legović et al.
361 (2010), Kar and Ghosh (2013). In more complex communities however, single-
362 species MSY policies may induce many indirect effects that deteriorate the structure
363 of harvested communities (Walters et al. 2005). Maximizing total yields, or reaching
364 multispecies MSY, has thus been suggested as a potential ecosystem-based alternative
365 to single-species MSY (Mueter and Megrey 2006).

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

375 oriented harvest than with a prey-oriented harvest, as the predator extinction risk is
376 lower.

377

378 *Focusing harvest on prey increases maximum yields*

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

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

400 supposed to preferentially target species with high productivity and value. In that
401 sense, our results already partly reflect the consequences of a differential valuation of
402 prey and predator species.

403

404 *Moderate predator harvesting favors resilience*

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

420 Yet, defining and measuring resilience remains challenging (McCann 2000).
421 Our measure of resilience as a return time to equilibrium is simple enough to allow a
422 complete mathematical analysis. It can however be difficult to assess empirically
423 (Donohue et al. 2016). Nevertheless, Britten et al. (2014) did evaluate the return time
424 to equilibrium of a coastal fish community by using the approach developed by Ives

425 et al. (2003). But such an assessment is not relevant in unstable systems characterized
426 by transient or oscillatory dynamics. A broader definition of resilience as the ability to
427 absorb changes and still persist is then needed (Holling 1973). Such other measures
428 include variability (coefficient of variation over time) and persistence (maintenance of
429 the structure of the system after a specified amount of time) (Donohue et al. 2016).

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

437 On the other hand, we show that when harvesting at MSY brings the predator
438 species close to extinction, the system abruptly becomes less resilient. Thus, when the
439 predator population is reduced to low levels, then the principle of energy flux does not
440 hold anymore and harvesting the predator species becomes destabilizing. This is
441 coherent with the assumption that predator species are stabilizing (Christensen 1996,
442 Rooney et al. 2006), and with the finding by (Britten et al. 2014) based on empirical
443 data that predator declines reduce the stability of coastal fish communities. The
444 sudden decrease in resilience close to the collapse of the predator population implies a
445 critical slowing down in the recovery ability of the disturbed system (Scheffer et al.
446 2009). Slow return times to equilibrium, in addition to low predator densities, could
447 make the predator population particularly vulnerable to an accumulation of
448 perturbations.

449

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

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

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

469

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

471 Our results show the existence of a global trade-off between yield and
472 resilience in mixed predator-prey fisheries, represented by a Pareto-optimality frontier
473 between these services. Different parts of this frontier can be reached by changing
474 prey and predator catchabilities, but also the intensity of harvest. Thus, the trade-off

475 between yield and resilience is indicative of a trade-off between a predator-oriented
476 harvest with low yields but high resilience and a prey-oriented harvest with high
477 yields but potentially low resilience.

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

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

500

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

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

522

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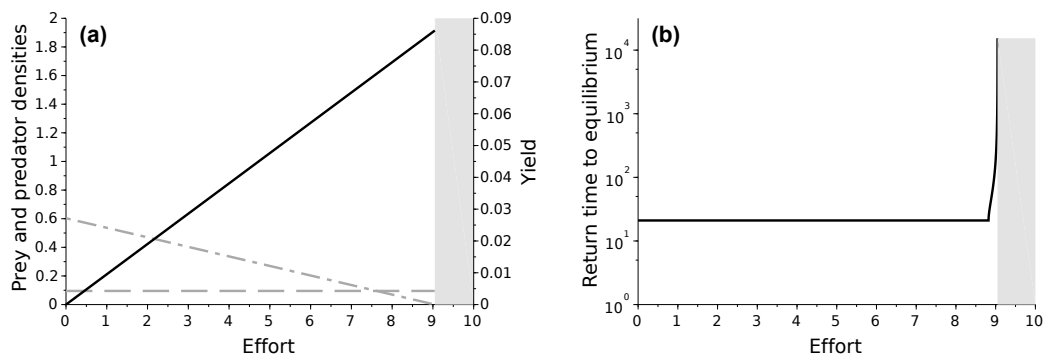
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640 selective fishing philosophy. - *Proc. Natl. Acad. Sci.* 107: 9485–9489.
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643 **Figure legends**

644

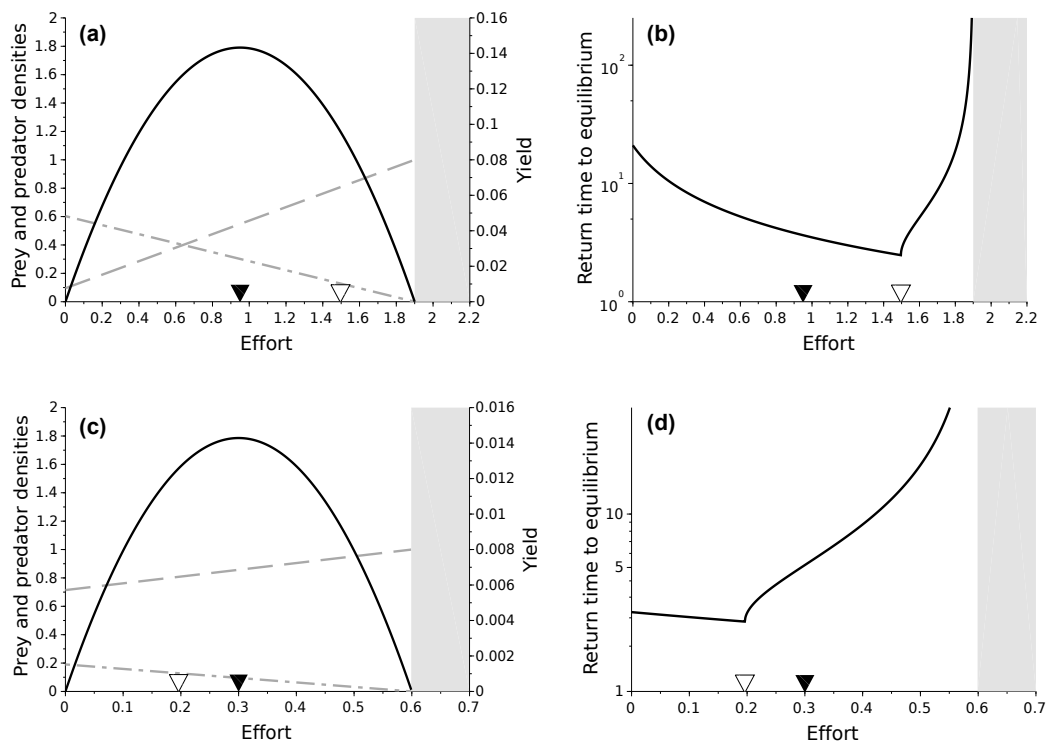
645 Figure 1: Effects of prey harvesting. (a) Prey (gray dashed line) and predator (gray
 646 dash-dotted line) densities at the equilibrium, and total catches (black line). (b) Return
 647 time to the equilibrium after a perturbation. Shaded areas indicate that predators are
 648 extinct. Parameters: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



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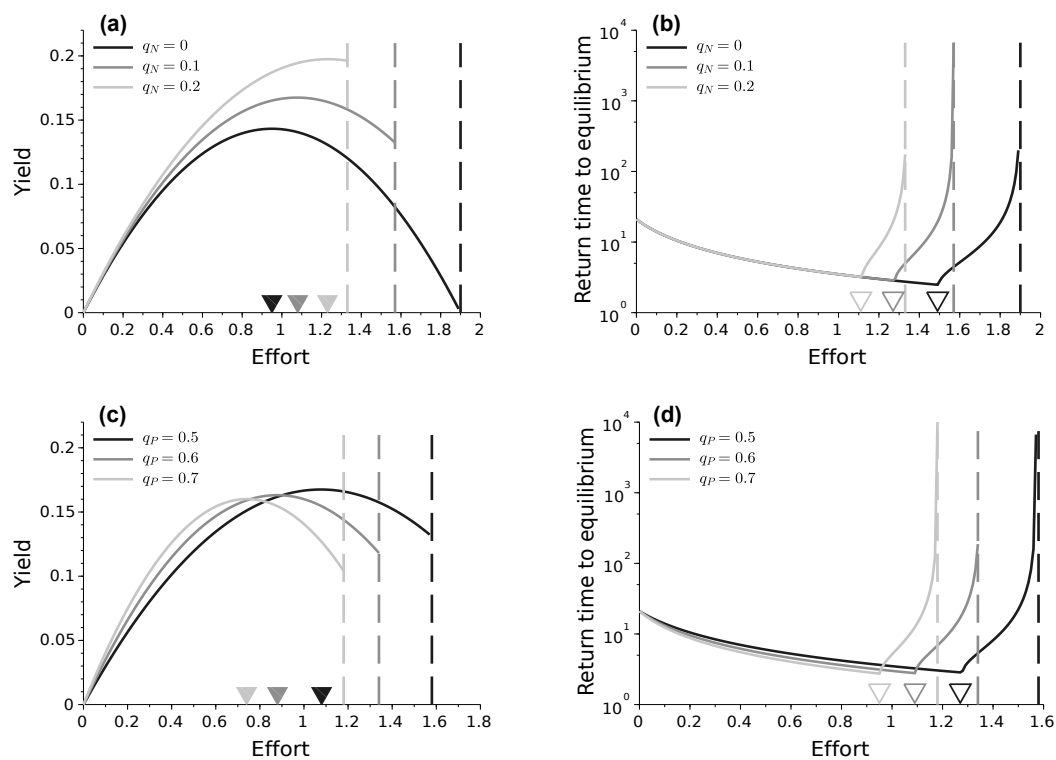
651 Figure 2: Effects of predator harvesting. (a,c) Prey (gray dashed line) and predator
 652 (gray dash-dotted line) densities at the equilibrium, and total catches (black line).
 653 (b,d) Return time to the equilibrium after perturbation. Shaded areas indicate that
 654 predators are extinct. Filled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



657

658

659 Figure 3: Effects of a simultaneous harvesting of predators and prey. (a,c) Total
 660 catches for different (a) prey and (c) predator catchabilities. (b,d) Return time to
 661 equilibrium after a perturbation for different (b) prey and (d) predator catchabilities.
 662 Vertical lines indicate efforts at which the predator species goes to extinction. Filled
 663 triangles indicate MSY efforts while empty triangles indicate RMY efforts. (a,b)
 664 Same parameters as Figure 1, except: $q_N = (0, 0.1, 0.2)$, $q_P = 0.5$. (c,d) Idem, except:
 665 $q_N = 0.1$, $q_P = (0.5, 0.6, 0.7)$.

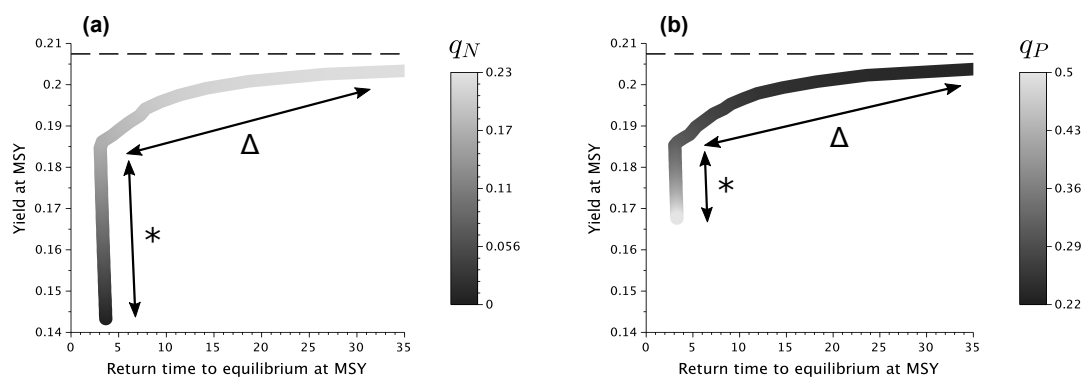


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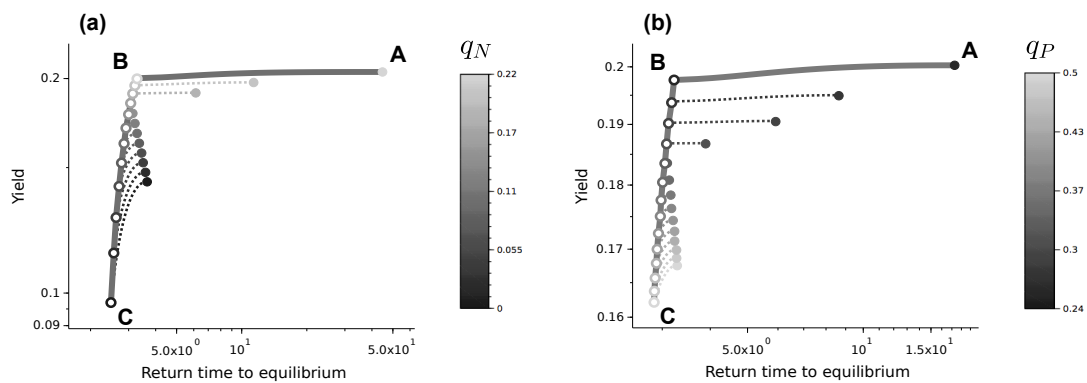
669 Figure 4: Trade-offs and synergies between productivity and resilience objectives at
 670 MSY when varying prey (a) and predator (b) catchabilities. Low to high catchabilities
 671 values are represented with colors ranging from black to light gray. As return times
 672 tend towards infinity close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



681

682

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



694