

# Optimal biodiversity loss in multispecies fisheries

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## Abstract

Marine ecosystems and biodiversity are under pressure worldwide. In that context, many scientists and stakeholders advocate the use of ecosystem-based approaches for fishery management. In particular, management plans are expected to account for the multispecies nature of fisheries. This is especially important as species are linked together by biological and technical interactions, the latter being due to the unselectivity of fishing gear. However, numerous fisheries management plans remain based on single-species concepts such as Maximum Sustainable Yield (MSY) and Maximum Economic Yield (MEY), that respectively aim at maximizing catches or profits of single species or stocks. In this study, we assess the sustainability and profitability of multispecies MSY and MEY in a multispecies fishery with technical interactions. We analytically show how multispecies MSY and MEY can be detrimental to biodiversity, as they lead to the extinction of the less productive and the less valuable species. Technical regulations, as well as incentives on costs and prices that promote biodiversity conservation are identified. The economic efficiency of these incentives is discussed. An example of the coastal fishery in French Guiana illustrates the analytical findings.

## Keywords

Maximum sustainable yield, maximum economic yield, ecosystem-based fisheries management, overexploitation, technical interactions

## 1 Introduction

Marine and coastal ecosystems are experiencing accelerating changes affecting species and communities at different biotic scales, sometimes with alarming trends and largely unknown consequences (Butchart et al., 2010). These changes are partially due to past and current fishing pressures, thus questioning the sustainability of current fishing activities and food production systems, and raise key questions in terms of food security, especially for developing countries with high demographic growth (FAO, 2014).

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27 As a consequence, ensuring the long-term ecological-economic sustainability of ma-  
28 rine fisheries systems, and preserving the marine biodiversity and ecosystems that sup-  
29 port them, have become a major issue for national and international agencies (FAO,  
30 2014). In response, an increasing number of marine scientists and experts advocate  
31 the use of ecosystem-based fishery management (EBFM) accounting for the various  
32 ecological and economic complexities at play. Pikitch et al. (2004) for instance claim  
33 that EBFM is a new direction for fishery management, essentially reversing the order  
34 of management priorities so that management starts with the ecosystem rather than  
35 a target species. In particular, an ecosystem approach to fisheries management is ex-  
36 pected to account for the multispecies nature of fisheries, as harvested species are linked  
37 by numerous biological and technical interactions (most fishing fleets harvesting several  
38 species).

39 The way to operationalize this EBFM approach, however, remains challenging (Sanchirico  
40 et al., 2008; Doyen et al., 2013), along with the identification of methods, approaches  
41 and tools to support its implementation. Hence, there is a need to develop new models,  
42 indicators and scenarios in this domain (Plagányi, 2007). In particular, the effective-  
43 ness of current regulatory instruments including fishing quotas or financial incentives  
44 needs to be reconsidered in the light of this new multi-functional, cross-sectoral and in-  
45 terdisciplinary context, accounting for the multiple commodities and services provided  
46 by marine biodiversity and ecosystems. In this regard, Patrick and Link (2015) claim  
47 that defining optimum harvesting yields -a hitherto predominant fisheries management  
48 instrument- can be useful to operationalize ecosystem-based fisheries management.

49 So far, the most common regulatory approach is to set limitations on fishing quotas  
50 or efforts (Stefansson and Rosenberg, 2005). The definition of these limits often aims  
51 at reaching the maximum sustainable yield (MSY) of each harvested stock. At MSY,  
52 catches are maximized at densities at which the stock can regenerate from year to  
53 year. This strategy has been set as the main reference point of many world fisheries,  
54 and has been introduced in the US' Magnuson-Stevens Act (NOAA, 2007), and more  
55 recently in the European Union's Common Fishery Policy (European Union, 2013). Yet  
56 the sustainability of this strategy in multispecies contexts is disputed (Larkin, 1977).  
57 In particular, applying MSY policies from single-species assessments in multispecies  
58 trophic communities has been shown to induce biodiversity losses (Walters et al., 2005).

59 There have been attempts at setting objectives at the level of the fishery, by defining  
60 multispecies maximum sustainable yields (MMSY) (Mueter and Megrey, 2006; Moffitt  
61 et al., 2015). Yet in the presence of technical interactions, that is when one fishing fleet  
62 harvests different species, maximizing total yields has been shown to endanger some  
63 species (Ricker, 1958; Legovic and Gecek, 2010). In the Bay of Biscay mixed fishery,  
64 Guillen et al. (2013) showed for instance that maximizing total catches leads to the  
65 overharvest of hake.

66 Moreover, as fishing also incurs costs to fishermen, MSY is not an economically  
67 efficient reference point. Instead, many resource economists advocate the maximization  
68 of profits and thus targeting the maximum economic yield (MEY) of each harvested  
69 stock (Dichmont et al., 2010). Furthermore, harvesting at MEY is notably known to  
70 favor higher biomasses than harvesting at MSY (Grafton et al., 2010). In a single-species  
71 context, harvesting at MEY is thus more profitable and sustainable than maximizing  
72 yield. In that perspective, maximum economic yield has been chosen as a reference  
73 point for Australian fisheries, although its concrete implementation remains complex  
74 (Dichmont et al., 2010; Pascoe et al., 2015).

75 However, maximizing profits from a single stock can also induce overexploitation  
76 and extinction, provided its price is higher than the cost of depleting the stock (Clark,  
77 1973). Moreover, in a dynamical context, extinction can follow from maximization of  
78 present value, whenever discount rates are sufficiently high (Clark, 1973; Clark and  
79 Munro, 1975).

80 In multispecies contexts, maximizing revenues implies to reach a global multispecies  
81 MEY (MMEY) (Anderson, 1975). As in the single-species case, multispecies MEY is  
82 more profitable than multispecies MSY (Guillen et al., 2013). However, it has been  
83 suggested that a combined MEY is susceptible to induce the overexploitation of some  
84 harvested stocks (Chaudhuri, 1986; Clark, 2006). Guillen et al. (2013) argue that this  
85 situation is likely to occur when the most productive species also display higher prices.  
86 In other words, if a multispecies fishery is seen as a portfolio of assets, maximizing total  
87 profits will exclude inferior assets and thus induce species losses (Swanson, 1994).

88 The aim of this paper is to evaluate the respective bio-economic merits of multi-  
89 species MSY and MEY policies. We use a bioeconomic model with multiple species  
90 and a single fleet, that allows us to derive analytical conditions for sustainable MMSY  
91 and MMEY. Thereby, we build an analytical framework to understand the impacts of  
92 MMSY and MMEY in multispecies fisheries with technical interactions. In particular,  
93 we determine the biodiversity loss induced by such ecosystem-based strategies. We also  
94 describe technical and economic regulations to allow for the optimal exploitation of  
95 species at MMSY and MMEY. These results are used to evaluate the consequences of  
96 multispecies strategies on a coastal fishery in French Guiana.

## 97 2 Bio-economic model

### 98 2.1 Dynamical model and equilibrium

99 We consider  $N$  independent species that are harvested by a single fleet. The dynamics  
100 of every species  $i$  is described by the following equation:

$$x_i(t+1) = x_i(t)(1 + r_i - s_i x_i(t) - q_i e(t)), \quad (1)$$

101 where  $x_i(t)$  denotes the stock of species  $i$  at time  $t$ ,  $r_i$  its intrinsic rate of growth,  $s_i$   
102 the intraspecific competition term,  $q_i$  its catchability and  $e(t)$  the fishing effort at time  
103  $t$ . In usual models of logistic growth, the intraspecific competition term is  $s_i = r_i/K_i$ ,  
104 where  $K_i$  is the carrying capacity of the species, or its strictly positive equilibrium

105 stock when unharvested. It is convenient to define the vectors  $X = \begin{pmatrix} x_1 \\ \vdots \\ x_N \end{pmatrix}$ ,  $R = \begin{pmatrix} r_1 \\ \vdots \\ r_N \end{pmatrix}$ ,

106  $Q = \begin{pmatrix} q_1 \\ \vdots \\ q_N \end{pmatrix}$ , and the matrix  $S = \begin{pmatrix} s_1 & & 0 \\ & \ddots & \\ 0 & & s_N \end{pmatrix}$ . Then, as we assume that for every

107 species  $\forall i$   $s_i > 0$ , the matrix  $S$  is invertible and equilibrium densities are given by

$$X^* = S^{-1}(R - Qe) \quad (2)$$

## 2.2 Definition of overharvest

In accordance we (FAO, 2014), we consider that a species is overharvested if its biomass is smaller than MSY levels. As we know that the equilibrium biomass from species  $i$  is  $x_i^* = (r_i - q_i e)/s_i$ , that its MSY biomass is  $x_i^{MSY} = r_i/(2s_i)$  and that its effort at MSY is  $e_i^{MSY} = r_i/(2q_i)$  (Clark, 2010), we find that the equilibrium biomass of species  $i$  can be written

$$x_i^* = x_i^{MSY} \left( 2 - \frac{e}{e_i^{MSY}} \right). \quad (3)$$

The equilibrium biomass of species  $i$  is smaller than its MSY biomass when the global harvesting effort is larger than the individual MSY effort of this species. A species is thus considered as overharvested when the harvesting effort is superior to its individual MSY effort. On the contrary, if it is inferior to the MSY effort, the species is underharvested, and if it is equal to the MSY effort, the species is fully exploited. The harvested species directly collapses when the harvesting effort becomes twice as big as its individual MSY effort, namely when it reaches  $r_i/q_i$  (see (Clark, 2010)).

## 2.3 Multispecies maximum sustainable yield

Expanding the concept of MSY to multi-species and ecosystem contexts, we define the multispecies maximum sustainable yield (MMSY) as the situation where the total catches are maximized at equilibrium. In matrix form, total catches read as follows:

$$H = \sum_{i=1}^N x_i q_i e = X' Q e, \quad (4)$$

At equilibrium, total catches can be written as a function of effort as follows:

$$X' Q e = (R - Q e)' S^{-1} Q e = R' S^{-1} Q e - e Q' S^{-1} Q e. \quad (5)$$

This expression is equivalent to

$$X' Q e = A e - e B e, \quad (6)$$

with  $A = R' S^{-1} Q$  and  $B = Q' S^{-1} Q$ . Using first order optimality conditions and differentiating this expression relatively to  $e$ , we obtain the expression of the fishing effort at MMSY:

$$e^{MMSY} = A(B + B')^{-1}, \quad (7)$$

or equivalently

$$e^{MMSY} = \frac{1}{2} \frac{\sum_{i=1}^N r_i q_i s_i^{-1}}{\sum_{i=1}^N q_i^2 s_i^{-1}}. \quad (8)$$

This expression is similar to the one derived by Legovic and Gecek (2010), though more general.

## 2.4 Multispecies maximum economic yield

Similarly, extending the concept of MEY to multi-species frameworks, at the multi-species maximum economic yield (MMEY), total profits, defined as the difference between total revenues and total costs, are maximized. The total rent induced by the

137 catches of the  $N$  species corresponds to:

$$\Pi = \sum_{i=1}^N x_i p_i q_i e = X' \tilde{P} e - ce, \quad (9)$$

138 where  $X'$  is the transpose of  $X$ ,  $c$  is the unit fishing cost of effort, and  $\tilde{P}$  is the Hadamard  
139 product of the vectors of catchabilities  $Q$  and prices  $P$ , that is their element-by-element

140 multiplication:  $\tilde{P} = Q \circ P$ , with  $P = \begin{pmatrix} p_1 \\ \vdots \\ p_N \end{pmatrix}$ . At equilibrium, the total rent as described

141 in (8) becomes a function of effort

$$X' \tilde{P} e - ce = (R - Qe)' S^{-1} \tilde{P} e - ce = Ce - eDe, \quad (10)$$

142 with matrices  $C$  and  $D$  defined by  $C = R' S^{-1} \tilde{P} - c$  and  $D = Q' S^{-1} \tilde{P}$ . Using again  
143 first order optimality conditions and differentiating this expression relatively to  $e$ , we  
144 identify the MMEY fishing effort:

$$e^{MMEY} = C(D + D')^{-1}, \quad (11)$$

145 that is

$$e^{MMEY} = \frac{1}{2} \frac{\sum_{i=1}^N (r_i p_i q_i s_i^{-1}) - c}{\sum_{i=1}^N p_i q_i^2 s_i^{-1}} \quad (12)$$

146 or

$$e^{MMEY} = \frac{1}{2} \frac{\sum_{i=1}^N (r_i p_i q_i s_i^{-1} - \tilde{c})}{\sum_{i=1}^N p_i q_i^2 s_i^{-1}}, \quad (13)$$

147 with  $\tilde{c} = c/N$ , the costs per unit effort divided by the number of species. This expression  
148 is equivalent to the one derived by Clark (2006), with  $s_i = r_i/K_i$ .

## 149 3 Sustainability of MMSY

### 150 3.1 Comparing multispecies and monospecies strategies

151 We intend to compare the global MMSY effort with individual efforts at MSY in order  
152 to characterize their sustainability. As proved in (Clark, 2010), individual MSY efforts  
153 are equal to  $e_i^{MSY} = r_i/(2q_i)$ . The following proposition directly stems from this value  
154 together with the characterization of  $e^{MMSY}$  the effort at MMSY displayed in (8):

155 **Proposition 1.** *The effort at MMSY is a convex combination of individual MSY ef-*  
156 *forts:*

$$e^{MMSY} = \sum_{i=1}^N \alpha_i e_i^{MSY}, \quad \text{with} \quad \alpha_i = \frac{q_i^2 s_i^{-1}}{\sum_{j=1}^N q_j^2 s_j^{-1}}. \quad (14)$$

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158 In other words, the effort at MMSY is a weighted average of all individual MSY  
159 efforts  $e_i^{MSY}$  since the sum of  $\alpha_i$  is equal to 1. It thus depends on both the individual  
160 MSY efforts of all harvested species, and their respective weights.

Individual MSY efforts are positively correlated with the ratios  $r_i/q_i$ , called by Clark (2010) the *biotechnical productivities* of the harvested species. Individual MSY efforts thus depend positively on the rate of growth and negatively on the catchability of the harvested species. This arises from the fact that high growth can sustain higher efforts, while at high catchabilities catches are maximized for low efforts.

The MMSY effort is expected to be close to its individual MSY effort if a species is given much weight. In particular, the weight  $\alpha_i$  of a species is high when its catchability is high and intraspecific competition is low.

## 3.2 Overharvest and extinction

Hereafter, a species is considered to be overharvested if the MMSY effort is superior to its individual MSY effort. To simply classify overharvested and underharvested stocks, the species are supposed to be ranked as follows:  $e_1^{MSY} \leq e_2^{MSY} \leq \dots \leq e_N^{MSY}$  (all efforts being positive). The following proposition, claiming that at least one species will be overharvested at MMSY, can be derived:

**Proposition 2.** *If at least two species differ in the sense that  $e_i^{MSY} < e_j^{MSY}$ , then at least species 1 is overharvested and at least species  $N$  is underharvested.*

**Proof.** *If  $\exists i, j \in [1, \dots, N]$  so that  $e_i^{MSY} < e_j^{MSY}$ , then  $e_1^{MSY} < e^{MMSY} < e_N^{MSY}$ , as  $e^{MMSY}$  is a convex combination belonging to the interval  $]e_1, e_N[$ . Then, species  $i$  is overharvested and species  $j$  is underharvested.*

It follows that at MMSY, if at least two individual MSY efforts are different, the species with the lowest individual MSY effort will always be overharvested, while the species with the highest individual MSY effort will always be underharvested. In other words in most cases, maximizing total catches in a multispecies fishery implies the depletion of at least one stock (see for instance Fig.1a).

As  $e_i^{MSY} = r_i/(2q_i)$ , the sensitivity of a species to overharvest at MMSY depends on the ratio  $r_i/q_i$ . This is shown with two species in Figure 1a: both species display the same catchabilities, yet as their growth rates differ, the species with the highest growth rate is underharvested at MMSY while the species with the lowest growth rate is overharvested.

Now if the effort at MMSY is superior to the effort at which species  $i$  goes to extinction,  $r_i/q_i$ , then maximizing total catches leads to the extinction of species  $i$ . The effort at MMSY then has to be re-calculated with all remaining species. This case is illustrated in Figure 1b, where one of the two harvested species disappears at MMSY; the total maximum yield then corresponds to the yield of the other harvested species.

In these examples, we only considered changes in the catchability of the harvested species, as this parameter can be potentially modified by regulations on fishing gears. The effect of changes in catchability are complex as it modifies both the individual MSY effort and its weight in the MMSY calculation. By contrast, increasing the rate of growth only increases the individual MSY effort, while decreasing the intraspecific competition only increases the weight in the MMSY calculation.

## 3.3 Selectivity policy for conservation

Overharvesting and extinction result from differences between species and more quantitatively between the individual MSY efforts of harvested species. Thus, bringing these

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efforts closer can promote coexistence and sustainability at MMSY:

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**Proposition 3.** *As  $e_i^{MSY} = r_i/q_i$ , if  $\forall i, j \in [1, \dots, N]$   $r_i/q_i = r_j/q_j$ , then all species are optimally exploited at MMSY. Balancing catchabilities with growth rates can thus improve sustainability at MMSY.*

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**Proof.** *If  $\forall i, j \in [1, \dots, N]$   $r_i/q_i = r_j/q_j$ , then  $\forall i, j \in [1, \dots, N]$   $e_i^{MSY} = e_j^{MSY}$ . Thus,  $\forall i, e^{MMSY} = e_i^{MSY}$ .*

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An example of balanced harvest is shown for two species on Figure 1c. This can be achieved by balancing the growth rate of each species with its catchability, that is by associating high catchabilities to high growth rates, and lower catchabilities to lower growth rates. In this case, all biotechnical productivities are equal. Such a balanced harvest can improve the sustainability of MMSY and limit the overexploitation of susceptible species.

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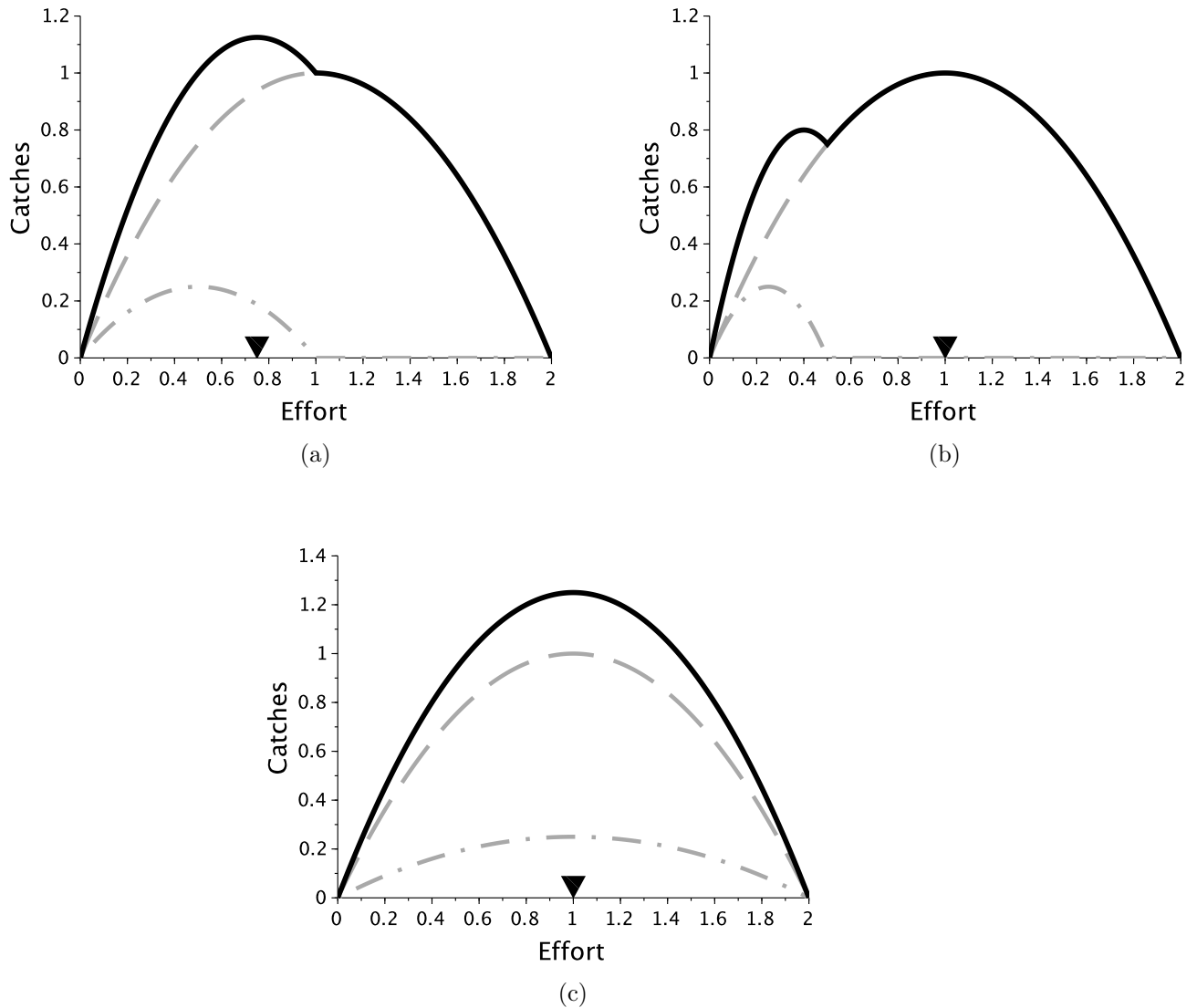


Figure 1: Multispecies maximum sustainable yield for two independent species. Catches are shown for increasing harvesting efforts. Black lines represent total catches. Dashed grey lines and dot-dash grey lines respectively represent catches of the species with the highest growth rate (species 1), and of the species with the lowest growth rate (species 2). Black triangles indicate efforts at which total catches are maximized. (a) Parameters:  $r_1 = 2$ ,  $r_2 = 1$ ,  $s_1 = s_2 = 1$ ,  $q_1 = 1$ ,  $q_2 = 1$ . (b) Parameters:  $r_1 = 2$ ,  $r_2 = 1$ ,  $s_1 = s_2 = 1$ ,  $q_1 = 1$ ,  $q_2 = 2$ . (c) Parameters:  $r_1 = 2$ ,  $r_2 = 1$ ,  $s_1 = s_2 = 1$ ,  $q_1 = 1$ ,  $q_2 = 0.5$ .



## 4 Sustainability of MMEY

### 4.1 Comparing multispecies and monospecies strategies

In the same vein than for MMSY, we aim at comparing the formulation of the MMEY effort with individual efforts at MEY. As shown in (Clark, 2010), individual MEY efforts with average costs by species  $\tilde{c} = c/N$  are equal to  $\tilde{e}_i^{MEY} = (r_i/(2q_i))(1 - \tilde{c}s_i/(p_iq_i r_i))$ . The following proposition directly derives from this characterization:

**Proposition 4.** *The effort at MMEY can be written as a convex combination of individual MEY efforts with costs  $\tilde{c}$ :*

$$e^{MMEY} = \sum_{i=1}^N \beta_i \tilde{e}_i^{MEY} \quad \text{with} \quad \beta_i = \frac{p_i q_i^2 s_i^{-1}}{\sum_{j=1}^N p_j q_j^2 s_j^{-1}}. \quad (15)$$

The effort at MMEY is a weighted average of individual MEY efforts  $\tilde{e}_i^{MEY}$ . Again, the effort at MMEY thus depends on the individual MEY efforts of all harvested species, and on their respective weights.

Individual MEY efforts depend positively on the rate of growth and on the price of the species, and negatively on the cost of harvesting and on intraspecific competition. This stems from the fact that for species with high growth and high value, it will take higher efforts for costs to counterbalance increasing revenues. On the contrary, for high intraspecific competition and high costs, profits begin to falter for lower efforts. The effect of catchabilities on individual MEY efforts depend on the value of catchabilities. For a species  $i$ , if  $q_i$  is lower than  $2cs_i/p_i$  (but still higher than  $cs_i/p_i$ , so that the MEY effort is positive), then individual MEY efforts depend positively on catchabilities. But if  $q_i$  is higher than  $2cs_i/p_i$ , then the relation between catchability and the individual MEY effort is negative.

The MMEY effort is expected to be close to its individual MEY effort if a species is given much weight. In particular, the weight of a species is high when its catchability and price are high and intraspecific competition is low.

### 4.2 Overharvest and extinction

As previously, we consider that if the MMEY effort is superior to the MSY effort of a species, this species is overharvested at MMEY. Further, if the effort at MMEY is higher than the effort at which species  $i$  goes to extinction, then this species collapses at MMEY. After the extinction of a species, the new effort at MMEY has to be recalculated with all preserved species. As regards overhasting, the Proposition 4 entails that MMEY is more detrimental to species with low individual MEY efforts or low weights. This is the case of species with low growth and price, and high intraspecific competition and catchability.

Comparing efforts at MMSY and MMEY, we obtain the following proposition:

**Proposition 5.** *If  $c = 0$ ,  $\forall i \neq j$   $q_i = q_j$  and  $s_i = s_j$ ,*

$$e^{MMEY} > e^{MMSY} \Leftrightarrow \sum_{i=1}^N \frac{p_i}{\sum_{j=1}^N p_j} e_i^{MSY} > \sum_{i=1}^N \frac{1}{N} e_i^{MSY} \quad (16)$$

251 The effort at MMEY is higher than the effort at MMSY, if the price-weighted average  
 252 of MSY efforts is higher than the simple average of MSY efforts. This is verified if high  
 253 MSY efforts are associated with high prices. Thus, maximizing total profits can be less  
 254 sustainable than maximizing total catches.

255 **Proof.** From the equations above, we find that

$$e^{MMEY} > e^{MMSY} \Leftrightarrow \sum_{i=1}^N \beta_i e_i^{MSY} > \sum_{i=1}^N \alpha_i e_i^{MSY} + \frac{c}{2 \sum_{i=1}^N p_i q_i^2 s_i^{-1}} \quad (17)$$

256 If  $c = 0$ ,  $\forall i \neq j$   $q_i = q_j$  and  $s_i = s_j$ , we directly derive the proposition.

257 If costs are non-null, then the MMEY effort can also be higher than the MMSY  
 258 effort. For instance, the effort at MMEY shown in Fig. 2a is higher than the effort at  
 259 MMSY shown in Fig. 1a, although with the same biological and technical parameters.  
 260 This is due to the species with the highest growth also displaying the highest price.

### 261 4.3 Conservation incentives

262 As maximizing total profits can exhibit unsustainability in multispecies contexts, we  
 263 investigate incentives promoting sustainable outcomes. We focus on two economic pa-  
 264 rameters, namely cost and prices, that influence the intensity of harvest at MMEY.

#### 265 4.3.1 Incentives on prices

266 As species with low prices are associated with a low individual MEY effort and a low  
 267 weight in the MMEY calculation, risks of their overexploitation and extinction are  
 268 major. Thus, incentives relying on prices can improve their sustainability at MMEY.

269 **Proposition 6.** At MMEY, subsidizing the price of overharvested species improves  
 270 sustainability.

271 **Proof.** Let  $p'_k = p_k + \tau_k$  the subsidized price of species  $k$ . Then,

$$e^{MMEY'} = \frac{1}{2} \frac{\sum_{i=1}^N r_i p_i q_i s_i^{-1} - c + r_k q_k s_k^{-1} \tau_k}{\sum_{i=1}^N p_i q_i^2 s_i^{-1} + q_k^2 s_k \tau_k} = \frac{1}{2} \frac{\gamma + \delta \tau_k}{\rho + \phi \tau_k}, \quad (18)$$

272 with  $\gamma = \sum_{i=1}^N r_i p_i q_i s_i^{-1} - c$ ,  $\delta = r_k q_k s_k^{-1} \tau_k$ ,  $\rho = \sum_{i=1}^N p_i q_i^2 s_i^{-1}$  and  $\phi = q_k^2 s_k \tau_k$ . The effect of  
 273 subsidy  $\tau_k$  is given by differentiating this expression relatively to  $\tau_k$ :

$$\frac{\partial \left( \frac{\gamma + \delta \tau_k}{\rho + \phi \tau_k} \right)}{\partial \tau_k} = \frac{\delta \rho - \gamma \phi}{(\rho + \phi \tau_k)^2} \quad (19)$$

274 If  $e_k^{MSY} < e^{MMEY}$ , this derivative is negative. Subsidizing species  $k$  reduces the MMEY  
 275 effort, thus improving sustainability.

276 In particular, increasing the price of the species with the lowest individual MSY  
 277 effort is susceptible to improve sustainability at MMEY. This is exemplified in the  
 278 following Lemma:

279 **Lemma 1.** *Let  $i$  be the species with the lowest  $e_i^{MSY}$ . If  $p_i \rightarrow \infty$ , then  $e^{MMEY} \rightarrow e_i^{MSY}$ .  
 280 *If the price of the species with the lowest effort at MEY infinitely increases, the effort at  
 281 MMEY tends towards the lowest effort at MSY, at which level there is no overharvested  
 282 anymore.**

283 **Proof.** *If  $p_i \rightarrow \infty$ , then  $e_i^{MEY} \rightarrow e_i^{MSY}$  and  $\beta_i \rightarrow \infty$ . Then, as the weight of species  $i$   
 284 becomes predominant in the MMSY effort calculation,  $e^{MMEY} \rightarrow e_i^{MSY}$ .*

285 Although infinitely increasing the price of a species is impossible, this proposition  
 286 indicates that increasing the price of the species with the lowest  $r/q$  ratio can attenuate  
 287 overharvest at MMEY.

288 Likewise, decreasing prices of species with high individual MEY efforts can reduce  
 289 overharvest at MMEY.

290 **Proposition 7.** *At MMEY, taxing underharvested species improves sustainability.*

291 **Proof.** *See proof of Proposition 6.*

292 On systems with only two species, it is possible to define a price at which there is  
 293 no overharvest anymore:

294 **Lemma 2.** *Let us consider two species,  $i$  and  $j$ , with  $r_i/q_i > r_j/q_j$ . We have*

$$e^{MMEY} \geq e_j^{MSY} \Leftrightarrow p_i \geq \frac{q_j}{q_i} \frac{cs_i}{r_i q_j - r_j q_i} \quad (20)$$

295 *The price of species  $i$  can thus be reduced to make the MMEY effort reach the lowest  
 296 MSY effort.*

297 An example is shown in Figure 2, where species 2 is overharvested when the price  
 298 of species 1 is high (Fig. 2a) and fully harvested when the price of species 1 is low (Fig.  
 299 2b). Now when more than two species are harvested, it will generally be necessary to  
 300 reduce the price of several species with high  $r/q$  ratios to decrease the MMEY effort  
 301 down to the lowest MSY effort.

302 In the previous example, the new price is 20 times lower than the initial price. As  
 303 fishers are not likely to welcome such a sharp decrease, it could reveal more efficient  
 304 to combine subsidies on overharvested species and taxes on underharvested species.  
 305 Consequently, through a system of well-defined subsidies on overharvested species and  
 306 taxes on underharvested species, the overharvest of susceptible species can be avoided  
 307 at MMEY.

### 308 4.3.2 Incentives on costs

309 The effort at MMEY is also dependent on the variable costs of harvesting. In particular,  
 310 an increased cost decreases all individual MEY efforts and reduces the global MMEY  
 311 effort. Thus,

**Proposition 8.**

$$\text{If } \forall k \in [1, \dots, N], c \geq \sum_{i=1}^N \frac{p_i q_i^2}{s_i} \left( \frac{r_i}{q_i} - \frac{r_k}{q_k} \right), \quad (21)$$

312 *then the MMEY effort is equal to the lowest individual MSY effort, and no species is  
 313 overharvested at MMEY.*

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**Proof.** *It follows from Proposition 1.*

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If costs are sufficiently high, then no species is overharvested at MMEY. This can be obtained for instance by introducing taxes on fuel or on the amount of time spent at sea. An example of such a tax is shown in Figure 2, where species 2 is overharvested when the cost is low (Fig. 2a) and fully harvested when the cost is high (Fig. 2c). In this example, the "corrected" cost is 20 times higher than the initial cost. As such a sharp increase in costs is not socially acceptable, it could be associated with subsidies on overharvested species.

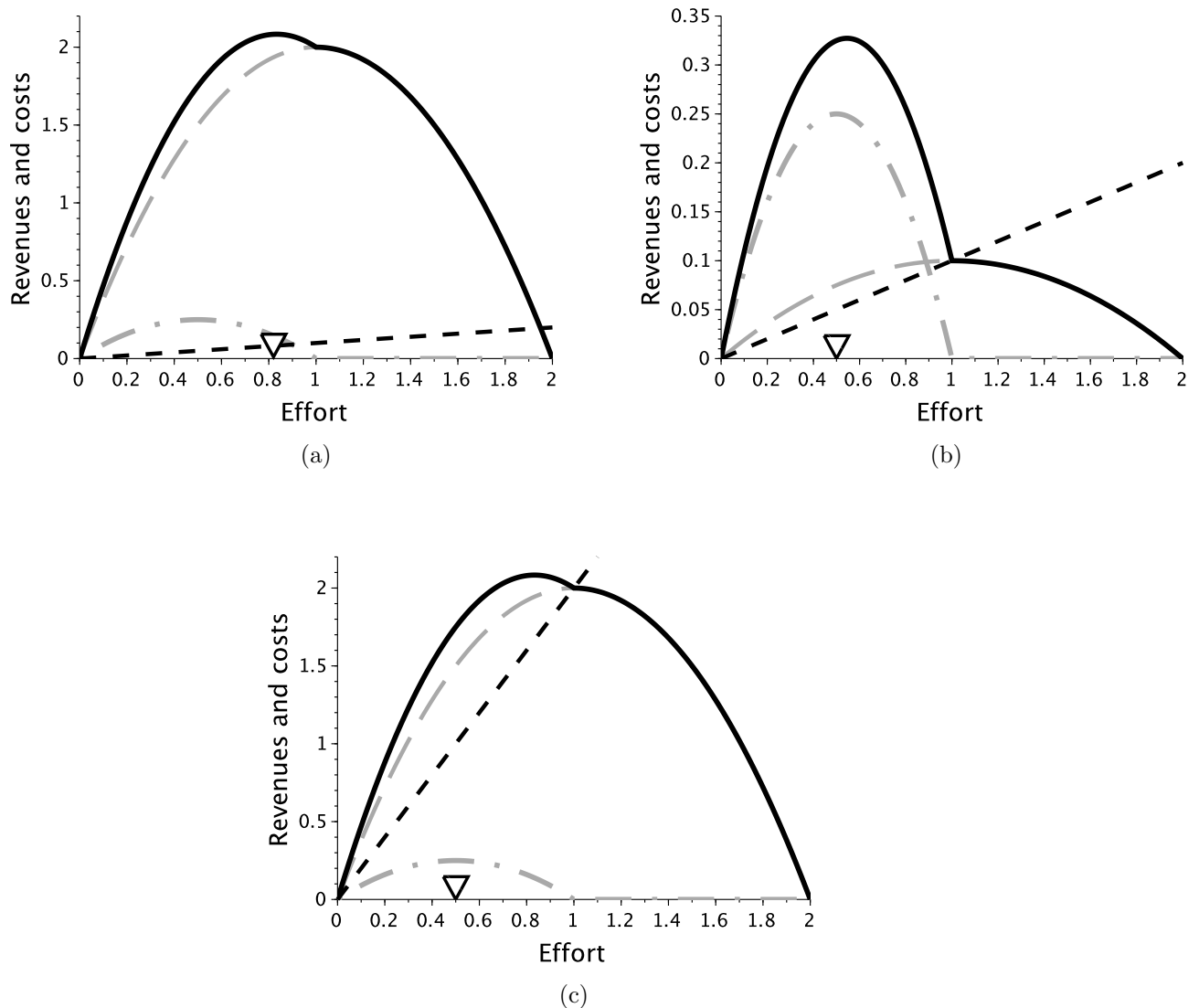


Figure 2: Multispecies maximum economic yield for two independent species. Revenues and costs are shown for increasing harvesting efforts. Plain black lines represent total revenues, while dashed black lines represent costs of harvesting. Dashed grey lines and dot-dash grey lines respectively represent revenues that arise from catching the species with the highest growth rate (species 1), and the species with the lowest growth rate (species 2). White triangles indicate efforts at which total profits (or the difference between revenues and costs) are maximized. (a) Parameters:  $r_1 = 2$ ,  $r_2 = 1$ ,  $s_1 = s_2 = 1$ ,  $q_1 = 1$ ,  $q_2 = 1$ ,  $p_1 = 2$ ,  $p_2 = 1$ ,  $c = 0.1$ . (b) Idem, except  $p_1 = 0.1$ . (c) Same as (a), except  $c = 2$ .

## 5 Case study: coastal fishery in French Guiana

### 5.1 Calibration

We apply our analytical results to the case study of the coastal artisanal fishery in French Guiana, which has been studied by Cissé et al. (2013) and Cissé et al. (2015). This small-scale fishery involves four fleets and 30 species. Cissé et al. (2013) only consider 13 species that capture an important part of the catches (88% between 2006 and 2009). This fishery is modeled by a Lotka-Volterra model in discrete time, and parameters are calibrated with monthly catch data from 2006 to 2010.

To apply this calibration to our results, we use two simplifications. First, we consider that ecological interactions are negligible, as in the calibration from (Cissé et al., 2015), trophic interactions coefficients are at least  $10^5$  times lower than intraspecific competition coefficients. Then, as in this calibration two top predator species (sharks and groupers) display negative rates of growth, we do not take them into account in this study. We thus focus our analysis on 11 harvested species.

Second, we consider that these 11 species are harvested by a single fleet, which catchabilities are a weighted mean of those of the four fleets. This assumption is similar to the one made by Guillen et al. (2013) with the Bay of Biscay case study. The mean effort of each fleet between 2006 and 2010 is used as a weight. The catchability of species  $i$  is then  $q_i = \sum_{k=1}^4 e^k q_i^k / \sum_{k=1}^4 e^k$ , where  $e_k$  is the mean effort of fleet  $k$  between 2006 and 2010 and  $q_i^k$  is the catchability of species  $i$  by fleet  $k$ . Likewise, costs are weighted means of those of the four fleets  $c = \sum_{k=1}^4 e^k c^k / \sum_{k=1}^4 e^k$ . We also consider average prices for each species:  $p_i = \sum_{k=1}^4 p_i^k / 4$ . With this assumption, an increased fishing effort implies that all efforts are increased while keeping the historical share in the total effort constant. Calibrated parameters used for the analyses are shown in Table 1.

Table 1: Calibrated parameters from the coastal fishery in French Guiana, adapted from (Cissé et al., 2015). The growth rate, intraspecific competition term, catchability and price of each considered species is indicated. The average effort between 2006 and 2010 is equal to 182 hours per day (as several fleets are active in parallel), and the average cost is approximately equal to 7.5 euros per fishing hour.

Species	Abbreviations	Growth rate	Intraspecific competition	Catchability	Price
		$r$ ( $10^{-2}$ ) (/month)	$s$ ( $10^{-8}$ ) (/kg /month)	$q$ ( $10^{-7}$ ) (/h)	$p$ (EURO)
Acoupa weakfish	A.w.	2.08	0.033	2	2.66
Crucifix sea catfish	C.s.c.	5.95	0.41	0.79	1.11
Green weakfish	G.w.	0.17	0.0057	2	2.05
Common snooks	C.s.	2.47	1.46	9	2.61
Smalltooth weakfish	S.w.	0.64	0.069	1	2.76
South American silver croaker	S.A.s.c.	3.44	4.15	4	2.36
Tripletail	T.	9.34	18.34	8	1.73
Gillbacker sea catfish	G.s.c.	1.94	5.77	32	2.36
Bressou sea catfish	B.s.c.	4.52	18.02	5	1.42
Flathead grey mullet	F.g.m.	5.31	16.90	3	3.03
Parassi mullet	P.m.	6.71	31.08	4	2.50

## 5.2 Results

We use the calibration from Cissé et al. (2013) to compute the impacts of multispecies strategies on the sustainability and the profitability of the fishery. To assess the sustainability of multispecies harvesting strategies, we compute the deviation from the MSY biomass of each of the harvested species. If the deviation is positive, the biomass is higher than the biomass at MSY, indicating that the species is underharvested. On the contrary, if the deviation is negative, the species is overharvested and if it reaches  $-100\%$ , the species is extinct.

Results are shown in Figure 3. Both MMSY and MMEY strategies lead to the extinction of Green weakfish, Common snooks and Gillbacker sea catfish. This can be explained by the relatively low growth rates of Green weakfish and Gillbacker sea catfish, and the high catchabilities of Common snooks and Gillbacker sea catfish. At MMSY, Smalltooth weakfish are also extinct, while only overharvested at MMEY. This can be the result of Smalltooth weakfish having relatively high prices. More species are thus extinct at MMSY than at MMEY. The state of remaining species is also better at MMEY than at MMSY. In particular, while Acoupa weakfish, Tripletail and Bressou sea catfish are overharvested at MMSY, they become underharvested at MMEY. In this example, maximizing total profits is thus more sustainable than maximizing total catches.

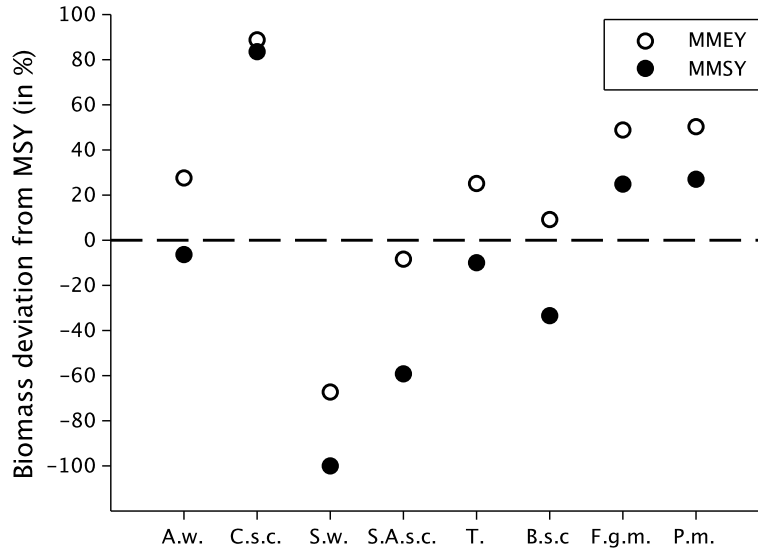


Figure 3: Sustainability of MMSY and MMEY policies in the coastal fishery in French Guiana. Deviation of the harvested species' biomasses from their MSY levels are shown. A  $-100\%$  deviation indicates that the species is extinct. As the Green weakfish, the Common snooks and the Gillbacker sea catfish are extinct at MMSY and MMEY, their corresponding deviations are not shown on this figure. Abbreviations are explained in Table 1.

We next assess the impact of harvesting strategies on ecological and economic objectives. We use the total profits per month as an economic objective and the biodiversity

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as an ecological objective. Biodiversity is measured with a Shannon index, equal to  $-\sum_{i=1}^N u_i \log(u_i)$ , where  $u_i$  is the proportion of biomass from species  $i$  in the system (see for instance (Zhang et al., 2016)). This index is low if the number of species is low, but also if a great part of total biomass is represented by a single or a few species. We compare four different strategies: the status quo situation, where the harvesting effort corresponds to the mean effort between 2006 and 2010, the MMSY strategy, the MMEY strategy and the "cost-corrected" MMEY strategy, at which there is no overharvested species.

As illustrated by Figure 4, both profits and biodiversity are higher at MMEY than at MMSY. Moreover, as compared to the status quo situation, profits are doubled at MMEY, but the biodiversity is negatively impacted. In that respect, we compute the optimal cost at which MMEY is completely sustainable. Initially, mean variable costs are equal to approximately 7.5 euros per fishing hour. The calculated optimal cost is approximately equal to 36.9 euros per fishing hour. Thus, the optimal cost is almost five times as high as the initial cost. Although there are ecological gains, profits at the corrected MMEY are more than 30 times lower than profits at the initial MMEY. There is thus a clear trade-off between conserving biodiversity and generating profits in the fishery.

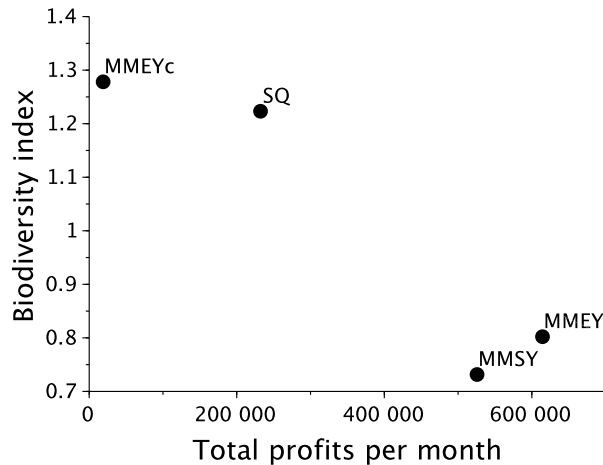


Figure 4: Ecological and economic efficiency of different harvesting policies in the coastal fishery in French Guiana. For each harvesting strategy, the Shannon index of biodiversity and the total profits per month are shown. Strategies shown are the status quo (SQ), the multispecies maximum sustainable yield (MMSY), the multispecies maximum economic yield (MMEY), and the MMEY with optimal cost at which no species is overharvested (MMEYc). In the status quo case, the applied harvesting effort corresponds to the mean effort between 2006 and 2010.

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## 6 Discussion and conclusion

In this paper, we address the question of optimally harvesting multiple species in a context of technical interactions. By technical interactions between species is meant



388 the simultaneous catch of different species (Punt et al., 2010). The joint harvest of  
389 multiple species is a common feature of many fisheries involving unselective fishing gear  
390 (see for instance (Gourguet et al., 2013)), and induces problems for defining optimal  
391 yield policies in multispecies fisheries (Anderson, 1975). It is thus an important feature  
392 to account for in operationalizing ecosystem-based fisheries management (Patrick and  
393 Link, 2015).

394 We derived an analytical expression for the effort at MMSY in a mixed fishery  
395 with independent stocks and technical interactions. We show that it is a weighted  
396 average of all individual MSY efforts. By comparing the expression of the MMSY ef-  
397 fort with individual MSY efforts, we find conditions for under- and overexploitation  
398 at MMSY. In particular, we show that overharvest at MMSY is the result of biological  
399 (low growth rate, high intraspecific competition) and technical (high catchabilities)  
400 parameters. These general conditions concur with previous results based on more spe-  
401 cific models. On the joint harvest of two independent stocks, Ricker (1958) suggested  
402 that "the achievement of maximum average yield may find one of the two originally  
403 equal stocks as abundant or even more abundant than before the fishery began, while  
404 the other may persist only at a low level or even be exterminated completely." Larkin  
405 (1977) added that in mixed fisheries, the less productive species will be eliminated or  
406 reduced below their MSY. Further, Legovic and Gecek (2010) derived an analytical  
407 expression of the effort at MMSY on multiple species and concluded that populations  
408 with small biotic potentials could be extinct at MMSY. The expression we obtain is  
409 very similar to that of Legovic and Gecek (2010), though more general, as we spec-  
410 ify different catchabilities for all species. This allows us to discuss the importance of  
411 technical parameters, namely catchabilities, in the sustainability of MMSY.

412 Our findings also can help to interpret results from data-based models. For instance  
413 Guillen et al. (2013) found that in the multispecies and multi-fleet Bay of Biscay fishery,  
414 maximizing total landings with fixed proportional allocation by fleet would lead to a  
415 slight overexploitation of hake, and to the underexploitation of nephrops and sole. This  
416 could be explained by the fact that in this case, the catchability of hake is high compared  
417 with the other catchabilities: the species is overharvested as its individual MSY effort  
418 is the lowest, but as its weight in the MMSY calculation is high, the overexploitation  
419 is relatively limited.

420 We discuss potential regulation measures to promote conservation and biodiversity  
421 at MMSY. In particular, we show that reducing the overharvest of species at stake  
422 implies to balance growth rates with catchabilities. The idea of balancing harvest  
423 relatively to the productivities of harvested stocks has been suggested as an alternative  
424 to the selective harvest of age-classes or species (Zhou et al., 2010). A balanced harvest  
425 is expected to preserve the age-structure as well as the ecosystem structure of harvested  
426 communities. In accordance with our results, Garcia et al. (2012) further found that a  
427 balanced harvest could turn out to be more sustainable and productive than a selective  
428 harvest. However the balanced harvesting approach also faces criticism for lack of  
429 practical evidences and for difficulties of implementation (Froese et al., 2015; Burgess  
430 et al., 2015).

431 We also derived an analytical expression for the effort at MMEY in a mixed fishery  
432 with independent stocks and technical interactions. We show that it is a weighted  
433 average of all individual MEY efforts with costs divided by the number of species. As  
434 previously, comparison with individual MSY efforts allows us to find conditions for  
435 under- and overharvest. Populations with low biotechnical productivity and low value

436 are expected to have also low individual MEY efforts and low weight in the MMEY  
437 calculation, and thus be overharvested or even extinct at MMEY. Although impacts of  
438 a multispecies MEY have mainly been studied on models involving both biological and  
439 technical interactions, and although many of these studies are based on a dynamical  
440 framework, our findings accords well with previous results from the literature. Anderson  
441 (1975) derived analytical conditions for reaching MMEY and proved that they do not  
442 hold if each stock is managed at its individual MEY. Accordingly, our results suggest  
443 that the multispecies optimal solution generally does not coincide with individual MEY,  
444 inducing under- and overharvest. Further, with a model of two harvested independent  
445 populations, Clark (2010) concluded that "populations with relatively low biotechnical  
446 productivity are subject to elimination under joint harvesting conditions provided that  
447 the cost-price ratio of the other species is relatively low". A similar conclusion has been  
448 drawn by Chaudhuri (1986) with a model involving ecological interactions. Likewise,  
449 Matsuda and Abrams (2006) suggested that if two valuable species were harvested by  
450 a single fleet, the optimal effort would be driven towards the most valuable of the two.  
451 Our results provide a more general framework to these assertions.

452 Our results also indicate that in multispecies contexts, reaching MMEY can be  
453 less sustainable than reaching MMSY, although single-species models show an inverse  
454 trend (see for instance (Clark, 2010)). This result had been hypothesized by Guillen  
455 et al. (2013), who suggest that depending on the relative prices of the different species,  
456 the MMEY effort could also be higher than the MMSY effort, especially if the most  
457 productive species are given higher prices. Our results verify this suggestion and offer  
458 it an analytical formulation.

459 As reaching MMEY can be detrimental to biodiversity, we discuss economic in-  
460 centives for preserving stocks at MMEY. As species with low productivity and value  
461 are more prone to overharvest, we show that reducing the price of highly productive  
462 species and increasing the price of lowly productive species can improve sustainability  
463 at MMEY. The value of a species can be reduced by imposing landing fees, which has  
464 been proved an efficient instrument for managing uncertain stocks (Weitzman, 2002).  
465 Subsidies on prices are ranked by Sumaila et al. (2010) as *capacity-enhancing*, or even  
466 *bad* subsidies, as they are supposed to increase pressure on stocks. On the contrary,  
467 our results indicate that when total profits are maximized, subsidizing low-value species  
468 can be beneficial to their stocks, as the global effort gets closer to the individual MSY  
469 effort of the subsidized species.

470 Further, we find that increasing variable harvesting costs can improve sustainability  
471 at MMEY, and we derive the expression of the optimal cost at which all stocks are  
472 underharvested or fully harvested. In accordance with Sumaila et al. (2010), we thus  
473 suggest that subsidies on variable costs increase pressure on stocks and reduce the  
474 sustainability of management policies. Subsidies on variable costs are for the most  
475 part subsidies on fuel, as shown in (Sumaila et al., 2008, 2010). Phasing out fuel  
476 subsidies could thus be a efficient incentive to foster biodiversity conservation at MMEY.  
477 Nevertheless our case study of a coastal fishery in French Guiana shows that optimal  
478 variable costs would be 5 times as high a current costs, that profits at MMEY would be  
479 more than 30 times lower than profits at the initial MMEY, and total landings would  
480 also be significantly reduced. This conservation measure would then incur significant  
481 losses to the fishery and greatly reduce local fish food supply. These losses are damped  
482 if technical regulations (to adjust catchabilities to growth rates for instance) enable to  
483 increase the lowest individual MSY effort. In this case, economic incentives should then

484 be used in addition to technical regulations.

485 Instead of economic incentives, biologically-based efforts regulations can also im-  
486 prove the sustainability of multispecies fisheries with technical interactions. As sug-  
487 gested by Guillen et al. (2013), the most conservative strategy is to set the multispecies  
488 fishing effort to the lowest individual MSY effort. As the catches of the species with the  
489 minimum individual MSY effort are then maximized, we call this a *maximin* strategy  
490 (Doyen and Martinet, 2012). At this reference point, the most susceptible species are  
491 fully exploited while all other species are underharvested. Yet this may also lead to  
492 strong reductions in profitability.

493 We did not include ecological interactions into our modelling approach, while in-  
494 creasing or decreasing harvest on certain species is known to have cascading effects on  
495 other species (Pauly, 1998). For instance, Voss et al. (2014) found that maximizing  
496 profits in the Baltic Sea reduces the stock of sprat below precautionary limits, due to  
497 the predation by cods. However, we argue that our main findings remain valid in a  
498 trophic network, as they agree with results from models with ecological interactions  
499 (Chaudhuri, 1986; Matsuda and Abrams, 2006; Legović et al., 2010). In particular, our  
500 results can serve as a basis for developing and interpreting models integrating ecological  
501 interactions.

502 We also considered that all species are harvested by a single fleet, while most fisheries  
503 involve multiple fleets that may interfere with each others (Ulrich et al., 2001). As shown  
504 in (Guillen et al., 2013), multiple fleets can also complement to reach more profitable  
505 and sustainable multispecies yields. Reaching MMSY and MMEY then requires to  
506 define an optimal allocation of efforts between fleets, that can lead to the exclusion of  
507 less efficient fleets.

508 Finally our study gives indications of the best management options in the coastal  
509 fishery in French Guiana. We find that at MMEY, the profits per month can be more  
510 than doubled compared with the status quo situation. But this would imply to bring  
511 several lowly productive and lowly valuable stocks to extinction. On the contrary,  
512 promoting biodiversity would come at the expense of productivity, in a context of  
513 increasing demand and needs for food security (Cissé et al., 2013). This case study  
514 is illustrative of a strong trade-off between economic and ecological efficiency. In this  
515 context, an efficient allocation of efforts between the multiple fleets involved could allow  
516 for improvements in sustainability and profitability.

517 Optimal extinction of harvested species has mainly been discussed with single-  
518 species dynamic models (Clark and Munro, 1975, 1978). Our results suggest that even  
519 in a static framework, optimizing for multiple species can induce severe depletions in  
520 harvested ecosystems. In particular, without adequate economic incentives and techni-  
521 cal regulations, multispecies optimum yields imply the extinction of the less productive  
522 and valuable species. Multispecies MSY and MEY concepts should thus be used with  
523 caution in implementing an ecosystem-based fisheries management.

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