Optimal biodiversity loss in multispecies fisheries

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Abstract

As marine ecosystems are under pressure worldwide, many scientists and stakeholders advocate the use of ecosystem-based approaches for fishery management. In particular, management policies are expected to account for the multispecies nature of fisheries. 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 mixed fishery with technical interactions. First, we analytically show how multispecies MSY and MEY can induce overharvesting and extinction of species with low productivity and low monetary value. It implies that multispecies harvesting policies can entail major biodiversity loss. Second, we identify and discuss incentives on effort costs and landing prices, as well as technical regulations, that could promote biodiversity conservation and more globally sustainability. However it turns out that these incentives can be very demanding in economic terms, which significantly questions the bio-economic relevance of MMSY-MMEY strategies for operationalizing the ecosystem approach. Finally, a numerical example based on the coastal fishery in French Guiana illustrates the analytical findings.

Keywords

Multispecies fishery, ecosystem-based fisheries management, maximum sustainable yield, maximum economic yield, overexploitation, technical interaction

1 Introduction

Acceletaring losses in marine biodiversity are affecting the productivity and the resilience of marine and coastal ecosystems worldwide (Worm et al., 2006). These changes are significantly due to increasing fishing pressures (McWhinnie, 2009), and induce severe economic loss in world fisheries (Willmann et al., 2009).

As a consequence, designing management tools and public policies that ensure the long-term bioeconomic sustainability of marine fisheries has become a major challenge (FAO, 2014). In response, many scientists and experts advocate the use of an ecosystem-based fishery management (EBFM) (Pikitch et al., 2004), that aims at integrating the ecological and economic complexities of fisheries, instead of focusing on isolated target species.

However, the way to operationalize the EBFM approach remains challenging (Sanchirico et al., 2008; Doyen et al., 2013), especially from the bioeconomic viewpoint. New models are needed, to integrate the multiple complexities at play (Plagányi, 2007). These models are expected to account for the multispecies nature of fisheries, as well as for the multiple ecosystem services they provide. They should also help evaluating the bioeconomic effectiveness and sustainability of current regulatory instruments such as fishing quotas or financial incentives, and designing relevant ecosystem-based management tools (Patrick and Link, 2015). Our paper intends to give some insights into these EBFM issues through the investigation of multispecies optimum yield policies.

Many fish stocks are currently managed to reach their maximum sustainable yield (MSY), through limitations on fishing quotas or efforts (Mace, 2001). At MSY, catches are maximized at levels where the stock can regenerate. This strategy has been set as the main reference point of many world fisheries, and has been introduced in the US' Magnuson-Stevens Act (NOAA, 2007), and more recently in the European Union's Common Fishery Policy (European Union, 2013). However the sustainability of this monospecific strategy in multispecies contexts is disputed (Larkin, 1977). In particular, applying MSY policies from single-species assessments in multispecies trophic communities has been shown to induce biodiversity losses (Walters et al., 2005).

Instead of MSY, many resource economists advocate the use of maximum economic yield (MEY) targets, at which profits are maximized (Dichmont et al., 2010). Harvesting at MEY is notably known to favor higher biomasses than harvesting at MSY (Clark, 2010). In a single-species context, harvesting at MEY is thus a more profitable and viable strategy than maximizing yield. In that perspective, maximum economic yield has been chosen as a reference point for Australian fisheries, although its implementation remains difficult (Dichmont et al., 2010; Pascoe et al., 2015). However, maximizing profits from a single stock can also induce overexploitation and extinction, provided its price is higher than the cost of depleting the stock (Clark, 1973). Moreover, in a dynamical context, extinction can follow from maximization of present value, whenever discount rates are sufficiently high (Clark, 1973; Clark and Munro, 1975).

To account for the multispecies nature of fisheries, there have been suggestions to set objectives at the level of the fishery, by defining multispecies reference points (Moffitt et al., 2015). However, the potential bioeconomic consequences of such multispecies harvesting policies remain largely unknown. There have been attemps at defining multispecies MSY (MMSY) policies, at which total catches are maximized (Mueter and Megrey, 2006). But in mixed fisheries where technical interactions occur, that is when one fishing fleet harvests different species, maximizing total yields has been suggested to endanger some species (Ricker, 1958; Legović and Geček, 2010; Guillen et al., 2013).

Potential consequences of multispecies MEY (MMEY), at which total profits are maximized, have also been investigated (Anderson, 1975). As in the single-species case, MMEY is found to be more profitable than MMSY (Guillen et al., 2013). However, it has been suggested that a combined MEY is susceptible to induce the overexploitation of stocks with low value (Chaudhuri, 1986; Clark, 2006; Guillen et al., 2013). In other words, if a multispecies fishery is seen as a portfolio of natural assets, maximizing total profits implies to neglect the conservation of inferior assets, thus inducing biodiversity losses (Swanson, 1994).

The aim of this paper is to evaluate and compare the bioeconomic merits of multispecies MSY and MEY policies respectively, as well as to question their relevance for operationalizing ecosystem-based management. We use a bioeconomic model with multiple species and a single fleet, that allows us to derive analytical conditions for sustainable MMSY and MMEY. Thereby, we build a general analytical framework to understand the impacts of MMSY and MMEY in multispecies fisheries with technical interactions. In particular, we determine the biodiversity losses induced by such multispecies strategies. We also describe technical and monetary regulations mitigating or preventing these biodiversity losses, to allow for the sustainable exploitation of species at MMSY and MMEY. These analytical results are used to assess the performances of multispecies strategies on a coastal fishery in French Guiana.

2 Bioeconomic model

2.1 Dynamical model and equilibrium

We consider N species harvested by a single fleet. It is assumed that no ecological interaction occurs between species. The dynamics of every species $i = 1, \dots, N$ is thus described by the following discrete time equation:

$$x_i(t+1) = x_i(t)\big(1 + r_i - s_i x_i(t) - q_i e(t)\big), \tag{1}$$

where $x_i(t)$ denotes the stock of species i at time t, r_i its intrinsic rate of growth, s_i the intraspecific competition term, $q_i > 0$ its catchability and $e(t)$ the fishing effort at time t. In usual models of logistic growth, the intraspecific competition term is $s_i = r_i/K_i$, where K_i is the carrying capacity of the species, or its strictly positive equilibrium stock when unharvested. Equilibrium conditions relating stocks and effort are given by

$$x_i = \frac{r_i - q_i e}{s_i} \tag{2}$$

Stocks at equilibrium thus decrease linearly with the fishing effort, and the stock collapses when the effort reaches r_i/q_i.

2.2 Definition of overharvest

In accordance with (FAO, 2014), we consider that a species is overharvested if its biomass is smaller than MSY levels. In the case of a logistic dynamics given by (1), it is well-known that MSY, where catch at equilibrium is maximal, is characterized by

$$x_i^{MSY} = \frac{r_i}{2s_i} \quad \text{and} \quad e_i^{MSY} = \frac{r_i}{2q_i} \tag{3}$$

The equilibrium condition (2) can then be written

$$x_i = x_i^{MSY}\left(2 - \frac{e}{e_i^{MSY}}\right). \tag{4}$$

Consequently, the equilibrium biomass of species i is smaller than its MSY biomass when the global harvesting effort is larger than the monospecific MSY effort of this species. A species is thus considered overharvested when the harvesting effort is larger than its monospecific MSY effort. On the contrary, if it is smaller than the MSY effort, the species is underharvested. If it is equal to the MSY effort, the species is said to be fully exploited.

2.3 Multispecies maximum sustainable yield

Expanding the concept of MSY to multispecies and ecosystem contexts, we define the multispecies maximum sustainable yield (MMSY) as the situation where the total catches are maximized at equilibrium. The optimisation problem reads as follows:

$$\max_e \sum_{i=1}^{N} x_i q_i e, \tag{5}$$

Replacing x_i with its equilibrium expression (2), and differentiating the resulting formula relatively to e, we obtain the fishing effort at MMSY:

$$e^{MMSY} = \frac{1}{2}\frac{\sum_{i=1}^{N} r_i q_i s_i^{-1}}{\sum_{i=1}^{N} q_i^2 s_i^{-1}}. \tag{6}$$

This expression is a generalization of the formula derived by Legović and Geček (2010).

2.4 Multispecies maximum economic yield

Similarly, extending the concept of MEY to multispecies frameworks, the multispecies maximum economic yield (MMEY) aims at maximizing total profits, defined as the difference between total revenues and total costs. The optimisation problem reads as follows:

$$\max_e \sum_{i=1}^{N} x_i p_i q_i e - ce, \tag{7}$$

where c is the unit fishing cost of effort, and p_i is the price of species i. Replacing again x_i with its equilibrium expression (2), and differentiating the resulting formula relatively to e, we identify the MMEY fishing effort:

$$e^{MMEY} = \frac{1}{2}\frac{\sum_{i=1}^{N} r_i p_i q_i s_i^{-1} - c}{\sum_{i=1}^{N} p_i q_i^2 s_i^{-1}} \tag{8}$$

Introducing the average cost per species, namely the costs per unit effort divided by the number of species $\tilde{c} = c/N$, we obtain

$$e^{MMEY} = \frac{1}{2} \frac{\sum_{i=1}^{N} (r_i p_i q_i s_i^{-1} - \tilde{c})}{\sum_{i=1}^{N} p_i q_i^2 s_i^{-1}}. \tag{9}$$

This expression is similar to the formula derived by (Clark, 2006), with $s_i = r_i/K_i$.

3 Sustainability of MMSY

3.1 Comparing multispecies and monospecies strategies

We now intend to compare the global MMSY effort with monospecific efforts at MSY in order to characterize its sustainability. As captured by the following proposition, it turns out that the global effort at MMSY as defined in (6) directly relates to the different monospecific efforts e_i^{MSY} of equation (3):

Proposition 1. *The effort at MMSY is a convex combination of monospecific MSY efforts:*

$$e^{MMSY} = \sum_{i=1}^{N} \alpha_i e_i^{MSY}, \qquad \textit{with weights} \qquad \alpha_i = \frac{q_i^2 s_i^{-1}}{\sum_{j=1}^{N} q_j^2 s_j^{-1}} \ \ \textit{in} \ \ ]0,1[. \tag{10}$$

In other words, the effort at MMSY is a weighted mean of all monospecific MSY efforts e_i^{MSY} since the sum of α_i is equal to 1. It thus depends on both the monospecific MSY efforts of all harvested species and their respective weights.

Monospecific MSY efforts are positively correlated with the ratios r_i/q_i, called by Clark (2010) the *biotechnical productivities* of the harvested species. Monospecific MSY efforts thus depend positively on the rate of growth r_i and negatively on the catchability q_i of the harvested species. The MMSY effort is expected to be close to the MSY effort of a species if this species is given much weight in the calculation. In particular, the weight α_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 monospecific MSY effort. To simply classify overharvested and underharvested stocks, the species are supposed to be ranked as follows:

$$e_1^{MSY} \leq e_2^{MSY} \leq ... \leq e_N^{MSY}, \tag{11}$$

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. *Species 1 is overharvested at MMSY if the following difference is positive:*

$$\sum_{i=1}^{N} \alpha_i e_i^{MSY} - e_1^{MSY} = \sum_{i=1}^{N} \alpha_i (e_i^{MSY} - e_1^{MSY}), \tag{12}$$

as $\sum_{i=1}^{N} \alpha_i = 1$. From (11), this sum is greater or equal to zero. But if at least two species differ in the sense that $e_i^{MSY} < e_j^{MSY}$, then this sum becomes strictly positive. Species 1 is then overharvested at MMSY. Using a similar proof relying on the ranking (11), it can be shown that species N is always underharvested at MMSY.

It follows that at MMSY, as soon as at least two monospecific MSY efforts do not coincide, the species with the lowest monospecific MSY effort will always be overharvested, while the species with the highest monospecific MSY effort will always be underharvested. The sensitivity of a species to overharvest at MMSY depends on the so-called biotechnical productivity r_i/q_i, species with lower biotechnical productivities being more prone to overharvesting. This is exemplified with two species in Figure 1a: both species display the same catchabilities, but as species 1 displays a lower growth rate than species 2, species 1 is overharvested while species 2 is underharvested.

Furthermore, maximizing total catches leads to the extinction of species i if the effort at MMSY is superior to the effort at which species i goes to extinction, r_i/q_i.

The effort at MMSY then has to be re-calculated with all remaining species. This case is illustrated in Figure 1b, where species 1 disappears at MMSY; the total maximum yield then corresponds to the yield of species 2. The different outcomes in Fig. 1a and Fig. 1b are due to a change in the catchability of species 2. It shows that modifying catchabilities through technical regulations on fishing gears can help regulating fishing patterns. This issue is examined in the next subsection.

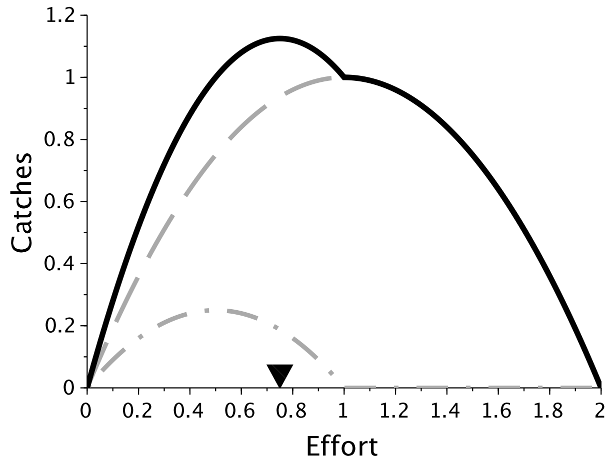
3.3 Selectivity policy for conservation

As pointed out previously, especially by Propositions 1 and 2, overharvesting and extinction at MMSY result from differences between species and more quantitatively between the monospecific MSY efforts e_i^{MSY} of harvested species. Thus, bringing these efforts closer can promote coexistence and sustainability at MMSY. Decision makers can achieve such a sustainability goal by regulating the catchability on the different species through selectivity of gears.

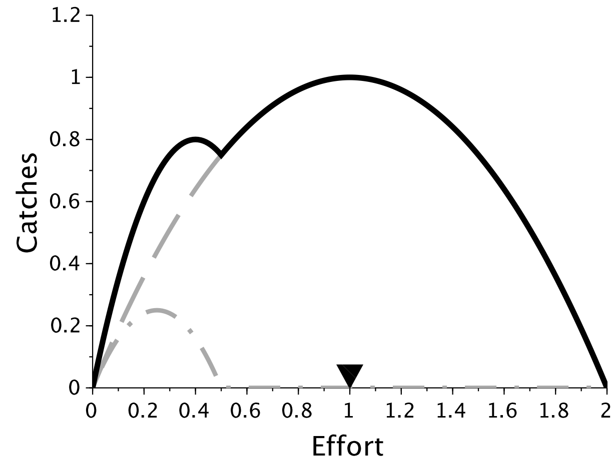
Proposition 3. *Defining new catchabilities* $(q'_1, ..., q'_N)$ *so that for all* i *and* j, $r_i/q'_i = r_j/q'_j$ *makes it possible to sustainably harvest all species at MMSY.*

Proof. *If* $\forall i, j \in \{1, ..., N\}$ $r_i/q'_i = r_j/q'_j$, *then* $e_i^{MSY} = e_j^{MSY}$. *Thus,* $\forall i$, $e^{MMSY} = e_i^{MSY} = e_j^{MSY}$.

Balancing catchabilities with growth rates can thus improve sustainability at MMSY. This idea of harvesting species in relation to their growth rates, known as balanced harvesting, has been suggested as a more sustainable alternative to the selective harvest of groups of species (Zhou et al., 2010). An example of balanced harvest is shown for two species on Figure 1c. In this example, the catchability of the species with the highest growth rate (species 1) is reduced so as to equalize all biotechnical productivities.



(a)



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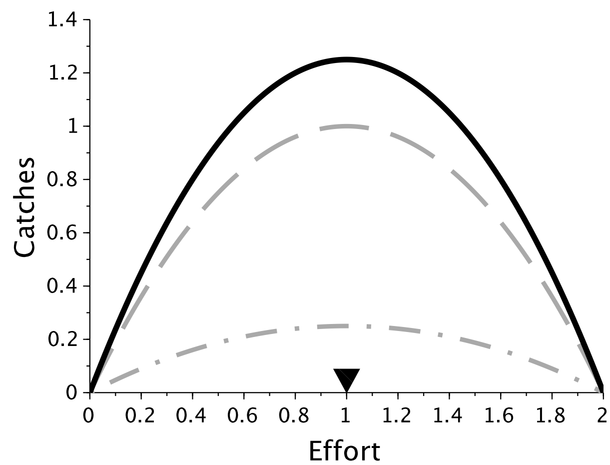

(c)

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

4 Sustainability of MMEY

4.1 Comparing multispecies and monospecies strategies

In the same vein than for MMSY, we now aim at comparing the formulation of the MMEY effort with monospecific efforts at MEY. As shown in (Clark, 2010), monospecific MEY efforts with costs c are equal to

$$e_i^{MEY} = \frac{r_i}{2q_i}(1 - \frac{cs_i}{p_i q_i r_i}). \tag{13}$$

As all species are harvested with a shared cost c, we consider an average cost by species $\tilde{c}$ defined previously and a corresponding MEY effort $\tilde{e}_i^{MEY}$. The following proposition directly derives from this characterization:

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

$$e^{MMEY} = \sum_{i=1}^{N} \beta_i \tilde{e}_i^{MEY} \qquad \textit{with weights} \qquad \beta_i = \frac{p_i q_i^2 s_i^{-1}}{\sum_{j=1}^{N} p_j q_j^2 s_j^{-1}} \ \ \textit{in} \ \ ]0, 1[. \tag{14}$$

Therefore the effort at MMEY is a weighted average of monospecific MEY efforts $\tilde{e}_i^{MEY}$. Again, the effort at MMEY thus depends on the monospecific MEY efforts of all harvested species, and on their respective weights. The weight of a species is high when its catchability and price are high and intraspecific competition is limited. Species with high prices thus display high monospecific MEY efforts and high weights in the MMEY computation.

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. Furthermore, if the effort at MMEY is higher than the effort at which species i goes to extinction, then this species collapses at MMEY. In such a case of extinction, the effort at MMEY has to be re-calculated with all preserved species. As regards overharvesting, Proposition 4 entails that MMEY is more detrimental to species with low monospecific MEY efforts or low weights. This is the case of species with low growth and price, and high intraspecific competition and catchability. For instance in Fig. 2a, species 1 is overharvested as it displays a lower growth and a lower price than species 2.

In single-species equilibrium models, MEY has been shown to be more sustainable than MSY (Clark, 2010), in the sense that it induces higher levels of stocks at equilibrium as compared to MSY. We want to know whether this result still holds in mixed fisheries. Comparing efforts at MMSY and MMEY as designed in Propositions 1 and 4, we obtain the following relationship:

$$e^{MMEY} > e^{MMSY} \Leftrightarrow \sum_{i=1}^{N} \beta_i e_i^{MSY} > \sum_{i=1}^{N} \alpha_i e_i^{MSY} + \frac{c}{2\sum_{i=1}^{N} p_i q_i^2 s_i^{-1}}. \qquad (15)$$

From this expression, we derive the following proposition:

Proposition 5. *It is possible to find systems of prices, catchabilities and costs for which MMEY is less sustainable than MMSY ($e^{MMEY} > e^{MMSY}$). In particular, it can occur when species with high MSY efforts (or high biotechnical productivities) are associated with high prices.*

Proof. *See the following examples.*

Let us consider that $\forall i \neq j$, $q_i = q_j = q$ and $s_i = s_j = s$. Then,

$$e^{MMEY} > e^{MMSY} \Leftrightarrow \sum_{i=1}^{N} \frac{p_i}{\sum_{j=1}^{N} p_j} e_i^{MSY} > \sum_{i=1}^{N} \frac{1}{N} e_i^{MSY} + \frac{c}{2q^2 s^{-1} \sum_{i=1}^{N} p_i}. \qquad (16)$$

Let us now assume that costs are null, $c = 0$. The condition becomes:

$$e^{MMEY} > e^{MMSY} \Leftrightarrow \sum_{i=1}^{N} \frac{p_i}{\sum_{j=1}^{N} p_j} e_i^{MSY} > \sum_{i=1}^{N} \frac{1}{N} e_i^{MSY}. \qquad (17)$$

The effort at MMEY is higher than the effort at MMSY if the price-weighted average of MSY efforts is higher than the simple average of MSY efforts. This occurs if high MSY efforts are associated with high prices. If costs are non-null, then the MMEY effort can also be higher than the MMSY effort as illustrated by Fig. 2b with two species. This is due to the fact that species 1 is characterized by both the highest growth and price, and that costs are relatively low.

4.3 Conservation incentives

As stressed in Proposition 5, maximizing total profits can entail unsustainability in multispecies contexts. Thus, it makes sense to investigate incentives promoting sustainable outcomes. We focus on two economic parameters, namely costs and prices, that significantly influence the intensity of harvest at MMEY.

4.3.1 Incentives on costs

The effort at MMEY depends on the variable costs of harvesting c. In particular, an increased cost decreases all monospecific MEY efforts (13) and reduces the global MMEY effort (14). Thus we can derive a lower bound on effort cost promoting sustainability of the ecosystem. Consider indeed the following threshold

$$c_{sus} = \max_k \sum_{i=1}^{N} \frac{p_i q_i^2}{s_i} \left(\frac{r_i}{q_i} - \frac{r_k}{q_k}\right) \ \ \forall \ k \in \{1, ..., N\} \tag{18}$$

We obtain the following result:

Proposition 6.

$$\textit{If} \ \ c \geq c_{sus}, \tag{19}$$

then the MMEY effort is inferior or equal to the lowest monospecific MSY effort, and no species is overharvested at MMEY.

Proof. *The result directly stems from Proposition 1.*

In other words, if costs are sufficiently high, then no species is overharvested at MMEY. In terms of regulation and public policies, such a situation 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 exemplified 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 cost of conservation is 2 times higher than the initial cost. To facilitate the acceptation of such an increase, it could be associated with incentives on prices.

4.3.2 Incentives on prices

As species with low prices are associated with low monospecific MEY efforts and low weights in the MMEY calculation, risks of their overexploitation and extinction are major. On the contrary, species with high prices display a higher weight, and are less vulnerable in terms of overexploitation. Thus, incentives relying on prices are expected to mitigate extinction risks and improve sustainability at MMEY.

Proposition 7. *For all species i, if $e_i^{MSY} < e^{MMEY}$, subsidizing price to $p_i' = p_i + \tau_i$ reduces the MMEY effort. Likewise if $e_i^{MSY} > e^{MMEY}$, taxing price to $p_i' = p_i - \tau_i$ reduces the MMEY effort. In other words, subsidies on overharvested species and taxes on underharvested species improve sustainability at MMEY.*

Proof. *See Appendix A.2.*

Proposition 7 implies that decreasing prices of species with high monospecific MSY efforts can reduce overharvest at MMEY. In particular, on ecosystems with only two species, it is possible to define a theoretical price at which overharvest vanishes: let us consider two species, 1 and 2, with $r_2/q_2 > r_1/q_1$. We have

$$e^{MMEY} \leq e_1^{MSY} \Leftrightarrow p_2' \leq \frac{q_1}{q_2} \frac{cs_2}{r_2 q_1 - r_1 q_2}, \tag{20}$$

with $p_2' = p_2 - \tau_2$ the new price of species 2. The price of species 2 can thus be reduced to make the MMEY effort reach the lowest MSY effort. An example is shown in Figure 2, where species 1 is overharvested when the price of species 2 is high (Fig. 2a) and fully harvested when the price of species 2 is low (Fig. 2d). In this example, the new price is 2 times lower than the initial price. As fishers can be reluctant to such a sharp decrease, it could turn out to be more efficient to combine subsidies on overharvested species and taxes on underharvested species. This is generalized in the following proposition:

Proposition 8. *A system of subsidies and taxes on species that are respectively overharvested and underharvested at MMEY can be found that allows to avoid overharvesting at MMEY.*

Proof. *See Appendix A.3. We use a corollary of Farkas' lemma to show that it is always possible to find a vector of prices that satisfies inequality (19).*

Consequently, through a fine-tuned system of subsidies and taxes, overharvest can be avoided at MMEY. Such a system could turn out to be more acceptable to fishermen than either increasing costs or reducing prices of underharvested species. Incentives on prices could also be used jointly with incentives on costs to achieve a sustainable MMEY. However, price and cost incentives for a sustainable MMEY are expected to come at a cost for governments and fishers.

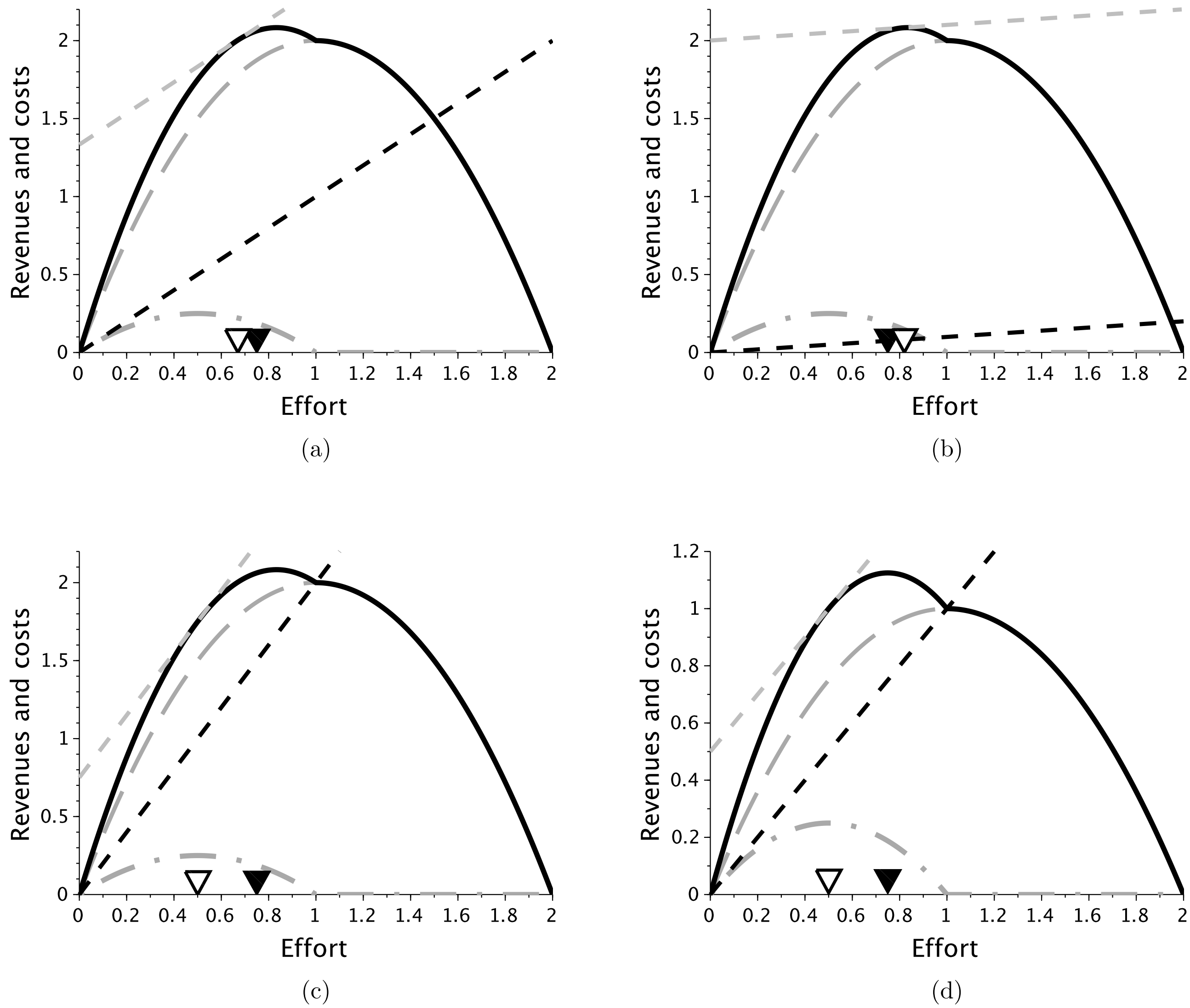

Figure 2: Multispecies maximum economic yield (MMEY) for two species. Revenues and costs are shown for increasing harvesting efforts. Plain black lines represent total revenues, while dashed black lines represent costs of harvesting. Dot-dash dark-grey lines and dashed dark-grey lines respectively represent revenues that arise from catching the species with the lowest growth rate (species 1), and the species with the highest growth rate (species 2). Black triangles indicate MMSY efforts at which total catches are maximized. White triangles indicate MMEY efforts at which total profits are maximized. At this effort, the slope of the tangent to the revenue curve (the dashed light-grey line) is equal to the slope of the cost curve. (a) Parameters are set to $r_1 = 1$, $r_2 = 2$, $s_1 = s_2 = 1$, $q_1 = 1$, $q_2 = 1$, $p_1 = 1$, $p_2 = 2$, $c = 1$. (b) Idem, except $c = 0.1$. (c) Same as (a), except $c = 2$. (d) Same as (a), except $p_2 = 1$.

5 Case study: coastal fishery in French Guiana

5.1 Calibration

We apply our analytical results to 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 thirty 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 simplifying assumptions. 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. 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 the proportion of each fleet remains constant. As in Guillen et al. (2013), a global effort multiplier is thus applied. This is equivalent to considering that all species are harvested by a single aggregate fleet, and that the catchability of species i is $q_i = \sum_{j=1}^4 e_j q_{ij} / \sum_{j=1}^4 e_j$, its price is $p_i = \sum_{j=1}^4 p_{ij} q_{ij} e_j / \sum_{j=1}^4 q_{ij} e_j$, and the associated cost is $c = \sum_{j=1}^4 e_j c_j / \sum_{j=1}^4 e_j$, where e_j is the mean effort of fleet j between 2006 and 2010, q_{ij} is the catchability of species i by fleet j, p_{ij} is the price of species i when harvested by fleet j, and c_j is the cost associated with fleet j. 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 i	Abbreviations	Growth rate r_i (10^{-2}) (/month)	Intraspecific competition s_i (10^{-8}) (/kg /month)	Catchability q_i (10^{-7}) (/h)	Landing price p_i (EURO)
Acoupa weakfish	A.w.	2.08	0.033	2	2.30
Crucifix sea catfish	C.s.c.	5.95	0.41	0.79	1.11
Green weakfish	G.w.	0.17	0.0057	2	1.56
Common snooks	C.s.	2.47	1.46	9	2.60
Smalltooth weakfish	S.w.	0.64	0.069	1	2.55
South American silver croaker	S.A.s.c.	3.44	4.15	4	2.47
Tripletail	T.	9.34	18.34	8	1.44
Gillbacker sea catfish	G.s.c.	1.94	5.77	32	2.12
Bressou sea catfish	B.s.c.	4.52	18.02	5	1.54
Flathead grey mullet	F.g.m.	5.31	16.90	3	2.85
Parassi mullet	P.m.	6.71	31.08	4	2.68

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 harvesting strategies, we compute the deviation from the MSY biomass (see Eq. 3) 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 (see Table 1). At MMSY, Smalltooth weakfish is also extinct, while only overharvested at MMEY. This results from the (relatively) high price of this species. 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.

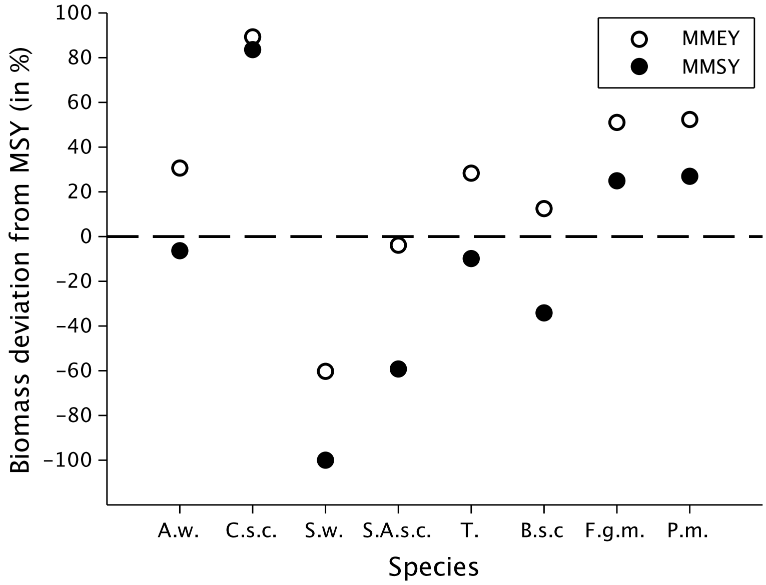

Figure 3: Sustainability of MMSY and MMEY policies in the coastal fishery in French Guiana. Deviation of the harvested species' biomasses from their MSY levels are shown. A −100% deviation indicates that the species is extinct. As the Green weakfish, the Common snooks and the Gillbacker sea catfish are 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 as an ecological objective. Biodiversity is measured with a Shannon index, equal to

$$SI = -\sum_{i=1}^{N} u_i log(u_i), \tag{21}$$

where $u_i = x_i / \sum_{i=1}^{N} x_i$ 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. It is thus more informative than the mere number of surviving 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 a sustainable MMEY strategy, at which there is no overharvested species. To reach this point, we increased costs according to Proposition 6. As sustainable strategies based on price incentives yield similar results (as they fulfill the same sustainability conditions), we choose not to represent them here.

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 increase by more than 60% at MMEY, but the biodiversity is negatively impacted. In fact at MMEY, a supplementary extinction occurs, namely that of Common snooks, compared to the status quo situation. In that respect, we compute the cost at which MMEY is completely sustainable. Initially, mean variable costs are equal to approximately 7.55 euros per fishing hour. The calculated sustainable cost is approximately equal to $c_{sus} = 36.13$ euros per fishing hour. Thus, the sustainable cost is almost five times as high as the initial cost. Although there are ecological gains, profits at the sustainable MMEY are more than 30 times lower than profits at the initial MMEY. In the MMEY perspective, there is thus a clear trade-off between conserving biodiversity and generating profits in the fishery.

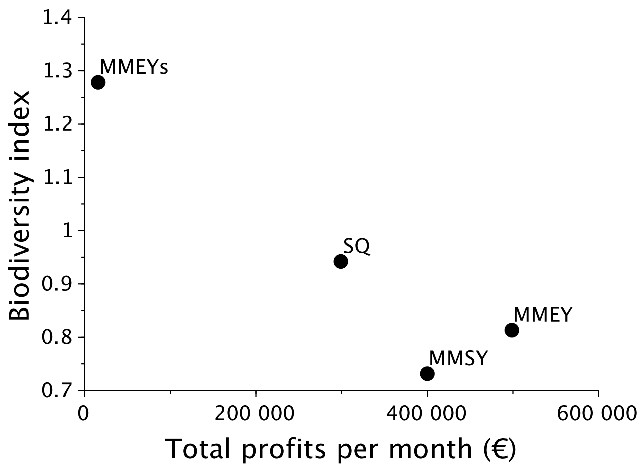

Figure 4: Ecological and economic efficiency of different harvesting policies in the coastal fishery in French Guiana. For each harvesting strategy, the Shannon index of biodiversity and the total profits per month are shown. Strategies shown are the status quo (SQ), the multispecies maximum sustainable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

6 Conclusion

In this paper, we address the question of optimal harvest for mixed fisheries involving technical interactions. Using a bioeconomic model of multiple species harvested by a single fleet, we derive the expression of the fishing effort that maximizes total catches (MMSY) and total profits (MMEY). These expressions are generalizations of those found by (Legović and Geček, 2010) and (Clark, 2006). Moreover, we show how the efforts at MMSY and MMEY are respectively weighted averages of monospecific efforts at MSY and MEY. The interpretation of these weighted averages allows to easily identify conditions for overharvest and extinction. These results thus provide a general framework that brings novel insights into the potentially deleterious consequences of MSY and MEY policies in mixed fisheries.

First, we show to what extent MMSY threatens low-productivity species. More precisely, we prove that overharvest at MMSY is induced by a combination of biological (low growth rate, high intraspecific competition) and technical (high catchabilities) parameters. These general conditions concur with previous results based on more specific models (Ricker, 1958; Larkin, 1977; Legović and Geček, 2010) and can help to interpret results from data-based models (Guillen et al., 2013). We also show that reducing the overharvest of species at risk implies to balance growth rates with catchabilities. The idea of balancing harvest relatively to the productivities of harvested stocks has been suggested as a more sustainable alternative to the selective harvest of age-classes or species (Zhou et al., 2010; Garcia et al., 2012). However the balanced harvesting approach also faces criticism for lack of practical evidences and for difficulties of implementation (Froese et al., 2015; Burgess et al., 2015).

Second, we show that MMEY endangers low-value species. In fact, populations with low biotechnical productivity and low value are expected to have also low monospecific MEY efforts and low weight in the MMEY calculation, and thus be overharvested or even extinct at MMEY. These findings provide a general framework to understand previous results from the literature. With a model of two harvested independent populations, Clark (2010) concluded that "populations with relatively low biotechnical productivity are subject to elimination under joint harvesting conditions provided that the cost-price ratio of the other species is relatively low". A similar conclusion has been drawn by Chaudhuri (1986) with a model involving ecological interactions. Likewise, Matsuda and Abrams (2006) suggested that if two valuable species were harvested by a single fleet, the optimal effort would be driven towards the most valuable of the two. Our results also indicate that in multispecies contexts, targeting MMEY can be less sustainable than reaching MMSY, although single-species models show inverse outcomes (see for instance (Clark, 2010)). This result had been hypothesized by Guillen et al. (2013), who suggest that depending on the relative prices of the different species, the MMEY effort could also be higher than the MMSY effort, especially if the most productive species are given higher prices. Our results ascertain this conjecture and offer it an analytical foundation.

Third, we identify economic incentives that promote conservation at MMEY. We show that taxing highly-productive underharvested species and subsidizing lowly-productive overharvested species improves sustainability at MMEY. Landing fees have already been proved an efficient instrument for managing uncertain stocks (Weitzman, 2002). Subsidies on prices are ranked by Sumaila et al. (2010) as *capacity-enhancing*, or even *bad* subsidies, as they are supposed to increase pressure on stocks. On the contrary, our results indicate that when total profits are maximized, subsidizing low-value species can be beneficial to their stocks. In accordance with Sumaila et al. (2010), we suggest that subsidies on variable costs increase pressure on stocks, and we derive the expression of a sustainable cost that precludes overharvest at MMEY. Subsidies on variable costs are for the most part subsidies on fuel, as shown in (Sumaila et al., 2008, 2010). Phasing out fuel subsidies could thus be an efficient incentive to foster biodiversity conservation at MMEY. But as shown with our case study, this conservation measure can also yield significant economic losses to the fishery and reduce fish food supply. Such outcomes strongly question the relevance of MMSY and MMEY strategies for operationalizing the ecosystem approach to fisheries management.

In this study, we assumed that all species are ecologically independent, while harvesting certain species is known to have cascading effects in trophic networks (Finnoff and Tschirhart, 2003). For instance, Voss et al. (2014) found that maximizing profits in the Baltic Sea reduces the stock of sprat below precautionary limits, due to predation by cods. However, we argue that our findings are general enough to explain results of models with ecological interactions, as for instance in (Chaudhuri, 1986; Matsuda and Abrams, 2006; Legović et al., 2010). We also considered that all species are harvested by a single fleet, while most fisheries involve multiple fleets that may interfere with each others (Ulrich et al., 2001). As shown in (Guillen et al., 2013), multiple fleets can also complement to reach more profitable and sustainable multispecies yields. Reaching MMSY and MMEY then requires to define an optimal allocation of efforts between fleets, that can lead to the exclusion of less efficient fleets.

Optimal extinction of harvested species has mainly been discussed with single-species dynamic models (Clark and Munro, 1975, 1978). In line with Swanson (1994), our results suggest that even in a static framework, optimizing for multiple species can induce severe depletions in harvested ecosystems. Moreover, potential economic incentives to promote sustainability would likely incur heavy costs and reductions in landings. Overall, these results highlight the potential bioecononmic unsustainability of multispecies MSY and MEY and challenge the relevance of multispecies optimum yields in implementing an ecosystem approach to fisheries management.

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A Appendix

A.1 Proof of Proposition 7

Let $p_k' = p_k + \tau_k$ be the subsidized price of species k, with τ_k positive. Then,

$$e^{MMEY'} = \frac{1}{2}\frac{\sum_{i=1}^{N} r_i p_i q_i s_i^{-1} - c + r_k q_k s_k^{-1}\tau_k}{\sum_{i=1}^{N} p_i q_i^2 s_i^{-1} + q_k^2 s_k^{-1}\tau_k} = \frac{1}{2}\frac{\gamma + \delta\tau_k}{\rho + \phi\tau_k}, \tag{22}$$

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 $\phi = q_k^2 s_k^{-1}\tau_k$. The effect of subsidy τ_k is given by differentiating this expression relatively to τ_k:

$$\frac{\partial(e^{MMEY'})}{\partial\tau_k} = \frac{1}{2}\frac{\delta\rho - \gamma\phi}{(\rho + \phi\tau_k)^2} \tag{23}$$

This derivative is negative if

$$\frac{\gamma}{\rho} > \frac{\delta}{\phi} \;\Leftrightarrow\; \frac{\sum_{i=1}^{N} r_i p_i q_i s_i^{-1} - c}{\sum_{i=1}^{N} p_i q_i^2 s_i^{-1}} > \frac{r_k}{q_k} \;\Leftrightarrow\; e^{MMEY} > e_k^{MSY}. \tag{24}$$

It means that if species k is overharvested at MMEY ($e^{MMEY} > e_k^{MSY}$), subsidies on species k reduce the effort at MMEY and thus improve sustainability. Likewise, by considering that $p_k' = p_k - \tau_k$ is the taxed price of species k, it can be found that taxing species that are underharvested at MMEY also reduces the effort at MMEY.

A.2 Proof of Proposition 8

It is equivalent to proving that a vector of prices can be found that avoids overharvesting at MMEY. From Proposition 6, we know that if $\forall k \in \big[1, ..., N\big], c \geq \sum_{i=1}^{N} \frac{p_i q_i^2}{s_i}(\frac{r_i}{q_i} - \frac{r_k}{q_k})$, then all species are either underharvested or fully harvested at

MMEY. In matrix form, it is equivalent to $MP \leq \mathcal{C}$, with $P = \begin{pmatrix} p_1 \\ \vdots \\ p_N \end{pmatrix}$, $\mathcal{C} = \begin{pmatrix} c \\ \vdots \\ c \end{pmatrix}$ and

$$M = \begin{pmatrix} 0 & \dots & \frac{q_N^2}{s_N}(\frac{r_N}{q_N} - \frac{r_1}{q_1}) \\ \vdots & \ddots & \vdots \\ \frac{q_1^2}{s_1}(\frac{r_1}{q_1} - \frac{r_N}{q_N}) & \dots & 0 \end{pmatrix}.$$

Following a corollary to Farkas' lemma described in (Border, 2013), only one of the following alternatives holds: either $\exists\ P \in \mathbb{R}^N$ so that $MP \leq \mathcal{C}$ and $P \geq 0$, or else $\exists\ \mu \in \mathbb{R}^N$ so that $\mu' M \geq 0$, $\mu'\mathcal{C} < 0$ and $\mu > 0$ (μ' being the transpose of vector μ). As $\mathcal{C} > 0$, only the first alternative holds. It is thus always possible to find a system of prices that avoids overharvesting at MMEY, by reducing the effort at MMEY. As reducing the MMEY efforts amounts to subsidizing overharvested species and taxing underharvested species (Proposition 7), it is always possible to find a system of taxes and subsidies that precludes overharvesting at MMEY.