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► To cite this version:

Florence Briton, Lynne Shannon, Nicolas Barrier, Philippe Verley, Yunne-Jai Shin. Reference levels of ecosystem indicators at multispecies maximum sustainable yield. ICES Journal of Marine Science, 2019, 76 (7), pp.2070-2081. 10.1093/icesjms/fsz104. hal-02170169

HAL Id: hal-02170169 https://hal.science/hal-02170169

Submitted on 22 Jul 2021

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Reference levels of ecosystem indicators at multispecies maximum sustainable yield

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Abstract :

We investigate reference points for ecosystem indicators in support of an Ecosystem Approach to Fishery. In particular, we assess indicator capacity to detect when the Multispecies Maximum Sustainable Yield (MMSY) is reached, under a wide range of multispecies fishing strategies. The analysis was carried out using a simulation approach based on the ecosystem model OSMOSE in the southern Benguela. We show that the 13 ecosystem indicators have reference points at MMSY that are highly variable across fishing strategies. The state of the ecosystem at MMSY is so variable across fishing strategies that it is not possible to set reference points without considering the fishing strategy. However, strategy-specific reference points were found to constitute robust proxies for MMSY in more than 90% of the simulated fishing strategies. For instance, under the current fishing strategy in the southern Benguela, robust reference points at MMSY could be identified for the following indicators: mean length of fish, mean lifespan, biomass over catch ratio, trophic level of the surveys, mean trophic index, proportion of predatory fish, intrinsic vulnerability index, and mean maximum length.

Keywords: ecosystem-based fishery management, fishing strategy, indicator reference point, multispecies MSY, southern Benguela

1 **Introduction**

² Ecological indicators for an Ecosystem Approach to Fisheries

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The early 2000's featured as a turning point in the way fisheries management should be considered. The limits of the dominant single-species approach opened 5 the way to the concept of a more integrative Ecosystem Approach to Fisheries (EAF 6 or EBFM- Ecosystem Based Fisheries Management) (Marasco et al., 2007; Ruckelshaus 7 et al., 2008). Most importantly, EBFM embodies a desire to reconcile sometimes con-8 tradictory expectations from society regarding the ecosystem and the services it pro-9 vides. EBFM also aims at moving beyond mono-specific approaches to fisheries. Some 10 species cannot be evaluated or managed independently from others (by-catches, trophic 11 interactions, competition for habitats), hence the necessity to establish management 12 policies at the scale of an ecosystem rather than of a stock (Hall and Mainprize, 2004; 13 Shannon et al., 2004; Mackinson et al., 2009). Finally, the transition towards an ecosys-14 tem approach to fisheries is particularly crucial as the mono-specific approach can be 15 too lenient when applied to multiple species in parallel, potentially leading to the col-16 lapse of certain stocks (Ghosh and Kar, 2013; Voss et al., 2014). 17

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To make progress in the implementation of EBFM, the status of the ecosystem 19 needs to be assessed and its key properties characterized (e.g. resilience, biodiversity, 20 structure or functioning). Numerous ecosystem indicators were developed to provide 21 relevant information on the health of an ecosystem, commonly defined in terms of 22 preserving the following 4 attributes: (1) biodiversity, (2) stability and resilience, (3) 23 structure and functioning, and (4) the productive potential (Shin et al., 2010b). Aside 24 from giving insight into the state of an ecosystem, an indicator should fulfil various 25 criteria suggested by Rice and Rochet (2005): namely a suitable candidate indicator 26 should (1) have ecological meaning regarding a perturbation, (2) be sensitive to such 27 perturbation, (3) be easily measurable, and (4) be widely understood by non-experts. 28 Many indicators were proposed at the onset of the EAF worldwide, and eventually the 29

time came to evaluate their usefulness and performance and select the ones best meeting the afore-mentioned requirements (Shin et al., 2012; Coll et al., 2016; Shin et al.,
2018).

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Values and trends of indicators are intended not only to assess the state of an 34 ecosystem, but also how far it is from reaching one or several objectives. This can 35 be accomplished by means of reference points. A reference point for an indicator may 36 either be a value one aims at reaching (which will be referred to as a "target" reference 37 point) or a threshold that should not be crossed (referred to as "limit" or "precau-38 tionary" reference points) (Jennings and Dulvy, 2005). Target reference points may 39 be more suitable if one aims at maximizing the yield for instance, whereas limit ref-40 erence points may be more closely associated with conservation objectives (Hall and 41 Mainprize, 2004). Indicators are usually selected with regard to one specific driver of 42 change. In the case of EBFM, indicators should respond in a predictable way to the 43 fishing driver in its diverse forms (e.g., fishing effort, mortality, spatial allocation). If 44 target reference points can be determined, the corresponding range of desirable fish-45 ing efforts can be estimated. When reference points cannot be determined due to the 46 lack of sufficiently precise information on the ecosystem, the knowledge of reference 47 directions can help to guide management measures, although there is no indication of 48 whether success or failure to reach an objective is to be expected (Jennings and Dulvy, 49 2005). The difficulties faced when addressing reference points should not dissuade 50 perseverance in that direction. The study led by (Shin et al., 2010a) showed that some 51 consensus emerged in the estimation of reference points based on expert elicitation 52 across various ecosystems. This consensus is particularly encouraging as it reinforces 53 the ecological meaning of the indicators and suggests that very different ecosystems 54 could be compared on the basis of simple indicators. 55

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Multispecies Maximum Sustainable Yield and fishing strategies

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Indicator reference points aim to reflect simultaneously a specific state of the ecosystem and whether some precise management objectives have been/can be met. By analogy to the mono-specific Maximum Sustainable Yield (MSY), which is a common target for fisheries agencies worldwide, we investigate reference points for ecosystem indicators for an ecosystem equivalent, namely Multispecies Maximum Sustainable Yield (MMSY) (Worm et al., 2009; Rindorf et al., 2016; Link, 2018).

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So far, the regulation of fishing effort has been the primary lever of action to en-66 sure the sustainability of a commercially exploited stock. Most often, when the state 67 of a stock is evaluated, an estimate of the MSY is provided (and the associated fishing 68 mortality F_{MSY}) and translated into direct or indirect management decisions such as 69 catch quotas until the next evaluation. Similar management procedures could be en-70 visaged at the ecosystem scale by estimating the ecosystem exploitation rate allowing 71 maximisation of the total catches, also referred to as Multispecies Yield (MY) (Worm 72 et al., 2009; Jennings and Collingridge, 2015). 73

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At the level of the ecosystem, the expected MMSY and the response of *MY* to fish-75 ing effort depend on how the latter is allocated between the different exploited stocks, 76 hereafter referred to as the "fishing strategy". Recently, the fishing strategy has been 77 shown to influence the performance of the fishing sector both in terms of production 78 and conservation (Voss et al., 2014; Kolding et al., 2016). Because both the structure 79 and productivity of an ecosystem largely depend on how it is exploited (Travers et al., 80 2006, 2010), it can be anticipated that, given the large range of potential harvesting 81 strategies, a given management objective (e.g. MMSY) may be reached under differ-82 ent states of an ecosystem reflected by different values of ecosystem indicators. This 83 potential variability of indicator reference points implies that they may not be consid-84 ered as intrinsic values of an ecosystem, disregarding how it is exploited. However, 85 rather than an obstacle to the practical use of ecosystem reference points to guide man-86 agement decisions, their potential dependence on the fishing strategy could provide 87

⁸⁸ more flexibility in the appropriate management options and some mitigation oppor-⁸⁹ tunities. If an objective can be reached under different states of the ecosystem and ⁹⁰ fishing strategies, it opens the possibility to choose the best management option re-⁹¹ garding other societal needs, such as conservation issues.

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The Southern Benguela case study

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Here, we were interested in the productive upwelling ecosystem of the Southern 95 Benguela that has provided a pioneer case study on how to implement EBFM since 96 the early 2000's (Shannon et al., 2004) and has been successfully implementing partic-97 ipatory approaches with various stakeholder groups (Jarre et al., 2018). The present 98 work was designed more as an exploratory study on reference points rather than a 99 concrete management plan for the Southern Benguela fisheries, and thus the choice of 100 the objectives was not the core issue. The reference points considered hereafter refer 101 to the values of a selection of ecosystem indicators when MMSY is reached. In order to 102 quantify the variability of indicator reference points in a systematic way, we adopted 103 a simulation approach to generate a large number of fishing scenarios. We used the 104 individual-based model (IBM) OSMOSE (Shin and Cury, 2004) applied to the Southern 105 Benguela ecosystem (Travers-Trolet et al., 2014a) to simulate 200 randomly-generated 106 fishing strategies. The simulation plan aims at testing the existence of reference points 107 which would be robust to a variety of fishing strategies. 108

109 2 Material and methods

110 2.1 OSMOSE model



Figure 1: Schematic of the OSMOSE - ROMS- $N_2P_2Z_2D_2$ coupling. "One-way" coupling: the plankton represented by the Low Trophic Level (LTL) model ROMS- $N_2P_2Z_2D_2$ forces the High Trophic Level (HTL) model OSMOSE by providing prey fields to fishes. Source: http://www.osmose-model.org/

The 2D individual-based model OSMOSE ("Object oriented Simulator of Marine 111 Ecosystems") is a multispecies fish model relying on size-based opportunistic preda-112 tion. Consequently, fish diets are solely the result of local prey availability and preda-113 tor/prey size ratios (Shin and Cury, 2004). The modeled super-individuals represent 114 fish schools sharing the same following characteristics: taxonomy, species-dependent 115 life history traits, size, weight, age and geographical position on the horizontal grid. 116 At each time step (every 15 days in our configuration), the characteristics of a super-117 individual evolve according to its life cycle (growth, predation, natural and starvation 118 mortalities, reproduction, migration), to inter-individual interactions, and the fishing 119 pressure exerted on its recruits. The fishing pressure for each species was implemented 120 as a mortality rate for which the distribution within a year followed the observed sea-121 sonality of the different fleets in the Southern Benguela. At each time step, the number 122 of fish removed by the fishery is: $N_{dead_fishing}(t) = N(t)(1 - e^{-F \times s(t)})$, N(t) being the 123 number of individuals at time t and s(t) the fraction of the annual fishing mortality 124 exerted at time t. In order to resolve simultaneous mortality caused from different 125 sources (fishing, predation, starvation, diverse additional), a stochastic algorithm was 126

¹²⁷ applied (www.osmose-model.org, Grüss et al. (2016)).

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OSMOSE can be coupled "one way" or "two-ways" to a ROMS $N_2P_2Z_2D_2$ model 129 simulating the dynamics of the lower trophic levels (Dinoflagellates, Diatoms, Cili-130 ates and Copepods) (Koné et al., 2005; Travers et al., 2009; Travers-Trolet et al., 2014a). 131 In the "one-way" coupling, the plankton represented by the LTL (low-trophic level) 132 model ROMS- $N_2P_2Z_2D_2$ forces the HTL (high-trophic level) model OSMOSE by pro-133 viding prey fields to fishes (Figure 1). The "two-way" coupling considers the feedback 134 from the HTL model to the LTL model in the form of predation mortality on plankton 135 groups by predation from higher trophic levels. For this particular study, the model 136 was coupled "one-way" as running the two-ways coupled model for hundreds of sce-137 narios would not have been tractable. Bi-weekly intra-annual variability in LTL forc-138 ing was incorporated. Ten key species or groups of species of the Southern Benguela 139 ecosystem chosen for their importance in terms of biomass, catches or trophic role 140 were represented in the high trophic level model OSMOSE (Shin et al., 2004): anchovy 141 (Engraulis capensis), round herring, also commonly called "redeye" (Etrumeus white-142 headi), horse mackerel (Trachurus trachurus capensis), shallow water hake (Merluccius 143 capensis), deep water hake (Merluccius paradoxus), snoek (Thyrsites atun), the remain-144 ing large pelagic species (e.g. kob, yellowtail, yellowfin tuna, albacore, carpenter) 145 grouped in one functional group because they share similar life traits, the mesopelagic 146 fish species Lampanyctodes hectoris and Maurolicus muelleri also grouped together, and 147 euphausids (Euphausiacea). The spatial distribution of each species, accounting for pos-148 sible ontogenic migrations, was documented by age-specific presence-absence maps 149 found in the literature (maps from Travers-Trolet et al. (2014a) and updated with re-150 spect to the changes in distribution observed in the early 2000's documented in Water-151 meyer et al. (2016)). 152

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¹⁵⁴ Most species parameters of the model are common life history traits (reproduction, ¹⁵⁵ growth parameters, etc...) that were easily found in the literature (Table S1 in Online

Supplementary Material, and Travers et al. (2009)). Nevertheless, some parameters 156 remain largely unknown and were estimated using a heuristic optimization algorithm 157 particularly suited to the calibration of stochastic models like OSMOSE (Duboz et al., 158 2010; Oliveros-Ramos and Shin, 2016). This was the case of the plankton accessibility 159 factor (i.e. the fraction of the plankton biomass available to the higher trophic lev-160 els) and the larval mortality rate of the different species. Their estimation was done 161 through the multi-phases minimization of an objective function (here, a log-likelihood 162 objective function measuring the deviation between the outputs of the model and the 163 historical biomass and catch data for the period 2000-2003) in the following order: 164 1) estimation of the plankton accessibility only, 2) estimation of the larval mortali-165 ties (one for each species or taxonomic group), and the plankton accessibility, and 3) 166 estimation of the fishing mortality rates, along with the two previous sets of parame-167 ters. The configuration of the model running with those estimated parameters reached 168 equilibrium after a spin-up time of circa 40 years. Because the time that the model 169 takes to reach equilibrium can depend on the configuration, and the latter changed 170 depending on the different scenarios of fishing strategies, the "spin-up" phase was 171 extended to 60 years. All the ecosystem indicators addressed in this study were cal-172 culated from model state variables (biomass or yield outputs structured, or not, by 173 age or size classes or trophic levels), averaged over the period 60-80 years. Moreover, 174 because OSMOSE is a stochastic model, 30 replicates of each configuration were run, 175 over which the output state variables were averaged. 176

177 2.2 Ecosystem Indicators

Since landings data are known to be biased due to illegal, unreported and unregulated (IUU) fishing, which may represent up to one third of the global reported catches (Agnew et al., 2009), complementary indicator reference points other than those based solely on reported catches have the potential to improve the assessment of fishing impacts and to operationalize EBFM.The existence of reference points was tested for the set of ecological indicators selected by the working group IndiSeas (Coll et al., 2016; Table 1: Summary of the various ecosystem indicators tested in the present study. Only surveyed species were considered to calculate survey-based indicators and only harvested species were considered for the calculation of catch-based indicators. Whether a species is surveyed, harvested or considered as a predator is documented in Table S1 (Online Supplementary Material). *N* refers to number of individuals, *B* to biomass in the ecosystem, *Y* to yield, *MY* to multispecies yield, *IVI* to the intrinsic vulnerability index, *max age* to species life span, *max size* to species maximal size, and *TL* to trophic level. Subset *sp* stands for species, and *size_{lim}* and *TL_{lim}* are the size and TL thresholds used in the calculation of some indicators.

Indicator	Abbreviation	Calculation	Туре	Unit
Total Biomass	ТВ	$\sum_{sp} B_{sp}$	survey-based	MT
Inverse of fishing pressure	B_Y	TB/MY	survey-based	Ø
Intrinsic Vulnerability Index of the landings	IVI	$\frac{\sum\limits_{sp} IV I_{sp} \times Y_{sp}}{MY}$	catch-based	Ø
Large Fish Indicator	$LFI(size_{lim})$	$\frac{\sum\limits_{size>size_{lim}}B_{size}}{TB}$	survey-based	Ø
Mean Size	LG	$rac{\sum size}{N}$	survey-based	ст
Mean Life Span	LS	$\frac{\sum_{sp} max age_{sp} \times B_{sp}}{TB}$	survey-based	year
Mean Maximal Size	MML	$\frac{\sum\limits_{sp} maxsize_{sp} \times B_{sp}}{TB}$	survey-based	ст
Marine Trophic Index	$MTI(TL_{lim})$	$\frac{\sum\limits_{TL>TL_{lim}}TL\times Y_{TL}}{MY}$	catch-based	Ø
Proportion of predatory fish	PF	$\frac{B_{predators}}{TB}$	survey-based	Ø
Size spectrum slope	SSS	opposite slope of log(abundance) = f(log(size))	survey-based	Ø
Trophic level of landings	TLL	$\frac{\sum\limits_{sp} TL_{sp} \times Y_{sp}}{MY}$	catch-based	Ø
Trophic level of surveyed community	TLS	$\frac{\sum\limits_{sp} TL_{sp} \times B_{sp}}{TB}$	survey-based	Ø

Shin et al., 2010b). Three indicators commonly used for the European Marine Strategy
Framework Directive were added to this list: the large fish indicator *LFI* (Greenstreet
et al., 2011), the mean maximum length *MML* (Jennings et al., 1999), and the slope of

the size spectrum SSS (Shin et al., 2005). A summary of their calculation is presented
in Table 1 and additional information in Table S2 (Online Supplementary Material).

Further refinements of indicators like the large fish indicator LFI, the marine trophic 189 index MTI or size spectrum slope SSS are possible by considering different size or 190 trophic level thresholds or ranges. Because an indicator calculated at different thresh-191 olds can give complementary insights on the dynamics of a community (Shannon 192 et al., 2014), we deemed it important to assess whether the choice of the threshold 193 influenced the sensitivity of the associated reference points to the harvesting strat-194 egy. The large fish indicator was calculated by considering fishes larger than 20 cm 195 (LFI20) and 30 cm (LFI30). The marine trophic index was calculated at 4 thresholds, 196 i.e. considering fish of which the trophic level (TL) is higher than 3.25 (the reference 197 threshold), 3.5, 3.75, and 4.0 (threshold suggested by Shannon et al. (2014) and Coll 198 et al. (2016) for upwelling ecosystems like the Southern Benguela). Finally, the size 199 spectrum slope was calculated by considering fish between 10 and 60 cm (SSS60) and 200 10 and 100cm (SSS100) (Shin et al., 2005). 201

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203 2.3 Testing the sensitivity of ecosystem-based reference points to

²⁰⁴ the fishing strategy

205 2.3.1 Reference points at MMSY

The aim of the first part of the study was to explore the variability of reference points for ecosystem indicators across a wide range of fishing strategies. The hypothesis tested is that a variety of fishing strategies leads to variable MMSYs that potentially underlie contrasted statuses of fish stocks as reflected by different values of indicator reference points.

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In our simulations, a fishing strategy *S* reflected a given distribution of the fishing effort among the different exploited species (i.e. all species except euphausids and

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mesopelagic fish). Formally, it was defined as a vector of fishing mortality rates, one 214 for each species. In order to assess the sensitivity of the indicators' reference levels 215 to the fishing strategy, 200 randomly generated fishing strategies were simulated. For 216 each fishing strategy, the fishing mortality rate S[sp] of the species *sp* was drawn be-217 tween $0.05 yr^{-1}$ and $F_{collapse}[sp]$, the latter being the fishing mortality rate at which the 218 species sp collapsed (i.e. reached 10% of its virgin biomass) while all other species 219 remained fished at their estimated levels for the period 2000-2003 (Table S1). The re-220 sponse of each species to the fishing pressure was determined with the function *F_msy* 221 from the R package osmose2R (www.osmose-model.org). The lower bound of $0.05 yr^{-1}$ 222 referred to the minimal fishing rate among the exploited species obtained after cali-223 bration for the period 2000-2003, and was imposed in order to reach the MMSY for 224 reasonable values of the multiplier λ of fishing mortality rates (defined hereunder). 225 226

For each strategy, we increased the fishing pressure on all species by multiplying 227 the vector S by a factor λ . The vector of fishing mortality rates corresponding to a 228 fishing multiplier λ was thus defined as: $F = \lambda \times S$. Fishing pressure kept increasing 229 until MMSY was reached for each strategy. Because the fishing multiplier λ at which 230 the MMSY was reached strongly varied between strategies, it was not relevant to fix 231 a priori the values taken by λ . They were thus determined for each strategy inde-232 pendently according to the following algorithm (Figure S1 - Online Supplementary 233 Material): 234

²³⁵ 1. A first estimate of λ_{MMSY} (the value of λ at which the MMSY was reached) was ²³⁶ made through a coarse screening of the fishing multipliers at a step $\Delta\lambda_1 = 10$ ²³⁷ between $\lambda = 0$ and $\lambda = 500$.

238 2. This first estimate of λ_{MMSY} set the upper bound of a second screening of λ with 239 20 λ values equally distributed between $\lambda = 0$ and $\lambda = \lambda_{MMSY} + 2 \times \Delta \lambda_1$. So 240 the finer second step applied is $\Delta \lambda_2 = \frac{\lambda_{MMSY} + 2 \times \Delta \lambda_1}{20}$.

3. Finally, λ steps were further refined at the beginning of the *MY* curve (between

 $\lambda = 0 \text{ and } \Delta\lambda_2$) and around λ_{MMSY} (between $\lambda_{MMSY} - \Delta\lambda_2$ and $\lambda_{MMSY} + \Delta\lambda_2$) with a step $\Delta\lambda_3 = \frac{\Delta\lambda_2}{10}$. These refinements were made to improve the curve fittings described hereunder.

Simulated values of multispecies yield (*MY*) as well as other ecosystem indicators 245 were then generalized so that: (1) MMSY and the reference points of ecosystem indi-246 cators at MMSY could be better approached, and (2) the evolution of the indicators 247 with the fishing multiplier could be reconstructed at regular intervals. As we were not 248 interested in the actual parameters from a model fitting the data, we chose to general-249 ize the data based on local polynomial regressions (loess function from the R package 250 *stats*) as it allowed to fit the data more closely especially in the presence of plateau or 251 abrupt changes in slope. In 10% of the simulated scenarios, total catches would reach 252 a plateau at MMSY and not display the typical bell-shaped curve. Because increasing 253 fishing effort once total catches have reached a plateau would cause economic losses 254 for the fisheries, we deemed it relevant to estimate MMSY as the beginning of the 255 plateau. The beginning of the plateau was generally observed at 98% of MMSY. Esti-256 mating MMSY as 98% of the real MY maximum was therefore a satisfying option to 257 similarly treat both bell-shaped and plateau curves. The curve fitting of MY allowed 258 estimation of λ_{MMSY} as the abscissa at which 98% of the *MY* maximum was reached. 259 Finally, the reference points of the various indicators were determined as the values of 260 the fitted indicators at $\lambda = \lambda_{MMSY}$. 261

²⁶² 2.3.2 Testing the robustness of reference points across fishing strategies

For each indicator, the set of reference points at MMSY for the 200 simulated fishing strategies defined what we called its *reference distribution* (200 values per indicator), and the interdecile range [Q10; Q90] of this distribution defined its *reference interval*. The *total distribution* of an indicator referred to the whole set of values the latter could take, independently of the strategy or fishing intensity λ . It was reconstructed by extracting 100 values of the indicator (equally distributed between $\lambda = 0$ and λ_{MMSY} (20 000 values per indicator)) for each strategy from the fitted indicator's curves for that 270 strategy.

Whether an indicator displayed typical values at MMSY that could be used as alternative target reference points, or proxies, for MMSY was investigated by calculating the proportion of its total distribution contained in its reference interval. An indicator was considered as useful to detect when MMSY was reached regardless of the fishing strategy when less than 10% of its total distribution fell within its reference interval.

For visualization purposes, and comparison between indicators, standardized in dicators were calculated as: value - mean of the total distribution
 standard deviation of the total distribution.

279 2.3.3 Testing the robustness of reference points within fishing strategies

If our hypothesis is confirmed, ecosystem indicators may be too sensitive to the fishing 280 strategy for their reference points at MMSY to be set regardless of fishing strategy. In 281 this case, strategy-specific reference values are likely to provide more robust proxies 282 for MMSY. Still, because of the stochastic nature of the model (cf 2.1), a single set of 283 inputs (of particular interest in this work: the fishing strategy S and fishing intensity λ) 284 will result in different outputs (the ecosystem indicators). As a consequence, strategy-285 specific reference levels should be expressed in terms of confidence intervals rather 286 than single values. For each strategy, robust indicators at MMSY were identified as the 287 ones for which less than 10% of the total distribution of the indicator in the strategy 288 was contained in the 95% Student based confidence interval of the mean of the mean 289 reference point across the 30 replicates. This allowed us to identify the indicators that 290 were the most likely to provide robust strategy-specific proxies for MMSY. 291

²⁹² 2.4 Focus on realistic fishing strategies in the Southern Benguela

In addition to these exploratory analyses, we gave special attention to more realistic fishing strategies in the Southern Benguela. These strategies explicitly accounted for technical interactions among species simultaneously caught by a fishing fleet. Indeed, the various fishing fleets in the Southern Benguela are not species-specific (i.e. they do not target a single species but catch many species in various proportions), and it is thus not realistic to apply uncorrelated fishing pressures on the various species. The same methodology as described in 2.3.3 was used to determine which indicators could be used as robust proxies for MMSY.

³⁰¹ 2.4.1 Reaching MMSY by increasing the fishing effort on all species

³⁰² The first scenario simulated an increase of the fishing effort on all species proportion-³⁰³ ally to their exploitation levels for the period 2000-2003. This was done by multiplying ³⁰⁴ the vector of fishing mortality rates $F_{2000-2003}$ estimated by the calibration algorithm ³⁰⁵ to fit the mean annual catches for the period 2000-2003 (Table S1) by a fishing multi-³⁰⁶ plier λ until MMSY was reached. This scenario would correspond to simultaneously ³⁰⁷ developing all South African sectors from their 2000-2003 levels.

³⁰⁸ 2.4.2 Reaching MMSY by developing only some fishing sectors

Rather than increasing the fishing effort of all fleets, one could also imagine reach-309 ing MMSY by developing only some fishing sectors. This could be done to preserve 310 the most vulnerable stocks for instance. We successively explored the development of 311 two fishing sectors, namely the purse seine fishery catching mostly the small pelagic 312 species such as sardine, anchovy and redeye, and the hake trawl fishery targeting both 313 hake species but also catching large pelagic species and horse mackerel. We chose to 314 focus on those 2 sectors as they account for most of the reported catches (the purse 315 seine and hake trawl sectors respectively accounted for 70% and 25% of the total land-316 ings between 2003 and 2014). For each modelled species, the proportion of its an-317 nual catches attributed to each sector was calculated from official annual catch data by 318 sector (data records of the Department of Agriculture, Forestry and Fisheries, South 319 Africa). Annual landings of each species of each sector were averaged between 2003 320 and 2014, which is the period for which data was available. The contribution of each 321 sector to the catches of each species is reported in Figure 2. For each sector separately, 322 we multiplied the fishing effort by a factor λ . The resulting fishing mortality rate for 323

the species *sp* for which a proportion p[sp] is caught by the developing fishing fleet was calculated as : $F[sp] = F_{2000-2003}[sp] \times ((1 - p[sp]) + \lambda \times p[sp])$. In this way, only the proportion of the fishing mortality rate attributed to the selected developing fishing sector increased by a factor λ .



Figure 2: Mean contribution of each fishing sector to the landings of the modeled commercial species between 2003 and 2014

328 **3 Results**

329 3.1 High sensitivity of the reference points to the fishing strategy

By looking at the tails of indicator density functions (Figure 3), it appeared that the 330 reference distributions of all indicators were narrower than their total distributions. 331 However, the proportion of the total distribution that fell within the reference interval 332 was much higher than 10% for all indicators (Figure 3). This means that, without 333 specification on how MMSY is expected to be reached (i.e. the fishing strategy), the 334 ranges of values taken by the tested ecosystem indicators at MMSY were too wide 335 to constitute robust signals that MMSY had been reached. In other words, there is 336 no "one size fits all" value for those indicators that could help track MMSY: they are 337 dependent on the fishing strategy. 338



Figure 3: Distributions of the standardized indicators and their reference points (all randomly generated fishing strategies included). Refer to Table 1 for the indicators' definition. In black: the total distribution of all indicator values across all strategies (n=20000), in gray: the reference distribution, i.e. the distribution of the reference points at MMSY across all strategies (n=200). Numbers indicate the percentage of the total distribution of the indicator that fell within the interdecile range of its reference distribution.

339 3.2 Strategy-specific reference points at MMSY

As shown on Figure 4-A, all indicators were not equally useful in detecting when 340 MMSY had been reached. The indicators *B*_*Y*, *LS*, *TB*, *MML* and *LFI*20 appeared 341 as the most likely to provide robust proxies for MMSY, as their confidence interval at 342 MMSY had less than 10% overlap with the total distribution of the indicator in more 343 than 60% of the simulated strategies. It is worth noting that the thresholds used for 344 calculating indicators such as the marine trophic index MTI, the large fish indicator 345 LFI or the size spectrum slope SSS influenced their robustness. This is especially strik-346 ing for the large fish indicator which could be used as a proxy in 60% of the strategies 347 when calculated at a threshold of 20cm, but was only useful in 25% (respectively 16%) 348 of the strategies when calculated at a threshold of 40cm (respectively 30cm). The size 349 spectrum slope was in general more useful when calculated at a threshold of 60cm 350 (40% of the strategies) than when calculated at a threshold of 100cm (15% of the strate-351 gies). The mean trophic index appeared slightly more likely to provide a robust proxy 352 for MMSY when calculated at thresholds of 3.5 or 3.75 cm (respectively 38 and 34% 353 of the strategies) than when using the commonly used threshold of 3.25 (31% of the 354 strategies). 355



Figure 4: A- Percentage of strategies in which the indicator was a useful proxy for MMSY (i.e. less than 10% of the total distribution of the indicator fell within the 95% confidence interval of its reference point at MMSY)

B- Histogram of robust proxies for MMSY across the 200 simuated strategies (in %). For example, 7% of strategies did not have a robust proxy for MMSY, in 5% of them, one indicator could be used as a robust proxy, in 2% of them 2 indicators could be used, etc...

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As shown on Figure 4-B, only 7% of strategies did not have a robust proxy indicator for MMSY which means that at least one indicator among the proposed list provided a robust proxy for MMSY in more than 93% of the strategies. MMSY could be detected by more than one indicator in 88% of the strategies (bins 0 and 1 account for 12% of the strategies). In those cases, monitoring the ecosystem with a suite of indicators rather than a single one could increase the reliability of the assessment.



Figure 5: Cumulated yield and biomass of the modelled species when fishing pressure increases proportionally to the 2000-2003 configuration. The response of the community to the increase of fishing effort on all species could be divided in 3 parts delimited by vertical black lines. The vertical dashed line indicates 98% of MMSY

363 3.3 Focus on more realistic fishing strategies

When fishing pressure increased on all species proportionally to the 2000-2003 levels, the response of the ecosystem could be divided into 3 main phases as illustrated by Figure 5:

Phase 1: The strong decrease in anchovy biomass released competition pressure
 for large zooplankton (euphausids), which largely benefited horse mackerel and
 redeye, the biomass of which increased despite increasing fishing pressure (start ing from current fishing mortalities almost three times lower than that of an chovy, Table S1). However, it did not benefit sardine, which feeds on smaller
 plankton (mainly copepods and diatoms) and which decreased in biomass in

this first phase. Biomass of both hake species also declined, and the large pelagics collapsed quickly.

• Phase 2: Even though the biomass of anchovy kept decreasing, we observed a 375 shift in the ecosystem's dynamics. For sardine and hakes on one hand and redeve 376 and horse mackerel on the other hand, the dynamics in this second phase was 377 opposite to the one observed during the first phase. In this 2nd phase, the release 378 of competition for zooplankton was not sufficient to counter the still increasing 379 fishing pressure, and biomasses of both redeye and horse mackerel started de-380 clining. In the meantime, the biomass of sardine and hakes increased as a re-381 sult of predation and/or competition interactions. It is during this hypothetical 382 phase that multispecies yield reached its maximum value around 5,200,000 tons, 383 which is around 7 times the mean annual total catch between 2000 and 2003 384 $(\lambda = 1)$. At the end of the 2nd phase, anchovy collapsed. 385

386 387 • Phase 3: After the collapse of anchovy, the ecosystem reached an equilibrium with age classes accessible to the fishery completely depleted for all species.



Figure 6: Standardized reference points at MMSY for realistic fishing scenarios in the Southern Benguela and their 95% confidence interval. To be compared with the indicator's value when fishing effort is maintained at 2000-2003 levels (in grey).

³⁸⁸ The reference points at MMSY of the various ecosystem indicators as well as their

95% confidence interval are presented in Figure 6. As expected, the values of the refer-389 ence points depended on the fishing strategy under which MMSY was reached. More-390 over, for some indicators, we could not even provide a reference direction from the 391 2000-2003 situation (i.e. $\lambda = 1$) towards MMSY that would be common to all scenarios. 392 For instance, the reference point at MMSY for the mean maximum length (MML) was 393 lower than its 2000-2003 value when only the hake trawl fishery developed, whereas 394 it was greater than the 2000-2003 value for the other scenarios. This highlights the fact 395 that, even though those indicators were originally designed to decrease when fish-396 ing pressure increases, they do not always behave that way. The only indicators that 397 showed a common reference direction in all three strategies were LG, B_Y, MTI3.75, 398 *MTI*4.0, *TLS*, and *SSS*100. 399

400

Again, the indicators that provided robust proxies for MMSY depended on the strategy. The indicators that could be useful to detect MMSY in each scenario are highlighted in Table 2. The only indicator that provided robust reference levels in all three strategies was the mean life span indicator *LS*.

405 4 Discussion

Just like the single species MSY is attached to a fishing strategy (for example, depend-406 ing on size of recruitment, seasonality, spatial distribution of effort, etc...), results pre-407 sented here confirmed our assumption that MMSY is particular to a multispecies fish-408 ing strategy (i.e. how fishing effort is distributed across species). As a consequence, 409 we showed that robust proxies for MMSY based on ecosystem indicators could not be 410 set without considering the context under which MMSY is reached. However, in more 411 than 93% of the simulated strategies, strategy-specific reference levels for ecosystem 412 indicators could be used to detect when MMSY had been reached. In more than 88% 413 of the cases, there were at least two indicators that could be used as proxies for MMSY. 414 In these cases, a monitoring process based on several indicators could increase the re-415

Table 2: Indicators that provide robust proxies for MMSY under realistic fishing scenarios (i.e.
the ones for which less than 10% of the values taken in the scenario is contained in the 95%
confidence interval of the reference point at MMSY) are highlighted in gray

	All	Purse Seine	Hake trawl
B_Y			
IVI			
LFI20			
LFI30			
LFI40			
LG			
LS			
MML			
MTI3.25			
MTI3.5			
MTI3.75			
MTI4.0			
PF			
SSS100			
SSS60			
ТВ			
TLL			
TLS			

⁴¹⁶ liability of the assessment of the ecosystem relative to MMSY.

417

Two approaches can be used to estimate reference points based on the maximiza-418 tion of some utility function: constrained or unconstrained optimization. Whereas 419 the unconstrained approach only seeks to maximize a utility function, constrained 420 optimization methods look at maximizing a utility function while respecting other 421 constraints. These other constraints can express other objectives not accounted for 422 in the utility function (e.g. maintaining all stocks above a limit biomass, maintain-423 ing biodiversity, ensuring minimum profits for the fishery...) or reflect inflexibilities 424 in the system (e.g. as some species are sometimes caught jointly, one might have to 425 constraint ratios in fishing mortalities). Maximizing multispecies yield without con-426

straints would have given us the optimal combination of fishing mortalities, whereas 427 specifying how fishing mortalities are linked to each other gave us an estimate of 428 MMSY for a given multispecies fishing strategy. Some authors have already stressed 429 the inadequacy of unconstrained optimizing solutions in complex systems where dif-430 ferent objectives often have to be traded off against each other (Voss et al., 2014; Moffitt 431 et al., 2016; Tromeur and Doyen, 2018). As put forward by Fogarty (2014), ecosystem-432 based management might be a matter of agreeing on a satisfactory solution rather 433 than looking for the optimal one, and this requires to assess the performance of vari-434 ous management options regarding a specified set of objectives. 435

436

We only studied reference points associated with MMSY, but could reasonably ex-437 pect similar conclusions under other management objectives (e.g. conservation or eco-438 nomic objectives). The situation may even be clearer cut when one attempts to identify 439 thresholds at the point of ecosystem collapse, such as is being test-run under the IUCN 440 red listing process for ecosystems (Keith et al., 2013; Bland et al., 2018), and limit refer-441 ence points for different ecological indicators that signal the thresholds beyond which 442 an ecosystem is considered to be in a degraded state, such as was done in the IndiSeas 443 project (Shin et al., 2010a). 444

445

Although one motivation of this work was that unreliable estimations of catches 446 might undermine the assessment of the ecosystem relative to the objective of maxi-447 mizing sustainable catches, we did not exclude catch-based indicators from our study 448 altogether. Our catch-based indicators did not rely on absolute values of catches, but 449 rather reflected the species contribution to total catches or catches relative to biomass. 450 Whether relative values of catches are less biased than absolute values should be 451 explored if reference points on catch-based indicators are to be used as proxies for 452 MMSY. 453

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⁴⁵⁵ Reference points at MMSY or at fishing levels under specific management objec-

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tives could supplement the work that has already been carried out on indicator trends 456 (Blanchard et al., 2010; Coll et al., 2010, 2016). We would suggest that both approaches 457 (reference points and indicators trends) be given due attention as the responses of indi-458 cators is not as straightforward as initially thought. In particular, ecosystem indicators 459 do not always decrease with fishing pressure, as was found for some indicators under 460 specific fishing strategies. An increase in trophic -based indicators with fishing pres-461 sure is evident from research surveys (Shannon et al., 2014; Coll et al., 2016) and has 462 been found for both trophic- and size-based indicators under specific fishing strategies 463 in some modelling studies (Travers et al., 2006; Branch et al., 2010). 464

465

Apart from not decreasing with fishing pressure, some indicators might also show a non-monotonic response to fishing pressure. From our simulations, we noticed that the changes in slope in the response curves of indicators were often dependent on community shifts, some species taking advantage over others from a certain exploitation level. It is because such shifts in indicators' slope might occur on the trajectory towards MMSY that we strongly recommend considering indicator trends in addition to targeted values.

473

We also noticed that under many fishing strategies, total catches would not display 474 the typical bell-shaped curve often presented (Worm et al., 2009) but would instead 475 reach a plateau or only decrease very slowly once MMSY has been reached (Figure S2 476 Online Supplementary Material). The resilience of the ecosystem to high fishing 477 pressure in these particular scenarios could be explained by several factors: (i) only 478 fishing effort varied in our simulations, not size selectivity of a fishery, for example, 479 nor the fishing spatial distribution, which in reality may allow some age classes to be 480 inaccessible to the fishery; (ii) modelled fishing strategies did not include mesopelagic 481 fish as a caught species, hence preserving a potentially huge prey biomass fueling the 482 production of exploited species; (iii) the high intrinsic model growth rates of some 483 species such as anchovy, sardine and redeye; (iv) the modelled fishing seasonality or 484

age of recruitment to the fishery allowed part of the populations to reproduce before 485 being fished. All these factors in addition to the multispecies interactions and the high 486 primary production of the system could favor the persistence of modelled ecosystem 487 biomass under certain fishing scenarios, even at high fishing levels. This echos com-488 pensatory responses of harvested stocks that may arise when interactions with the rest 489 of the ecosystem are accounted for (Walters et al., 2005). Because this was not the core 490 issue of our paper we here provide plausible explanations until further work dedi-491 cated at properly identifying the mechanisms allowing such resilience is undertaken. 492 493

Importantly, depending on the fishing strategy, different indicators should be used 494 to evaluate how far the ecosystem is from MMSY (and hence from ecosystem overex-495 ploitation). Furthermore, indicators such as LFI, MTI or SSS responded differently 496 when calculated at different thresholds. This is an interesting feature to take into ac-497 count as it can improve the performance of these indicators in detecting when targets 498 or limits are reached. Therefore, we advise that preliminary model analyses specific to 499 the ecosystem and fishing strategy be carried out to capture the variable robustness of 500 indicator reference points. 501

502

Results from this study show that we can identify robust reference levels at MMSY 503 for specific indicators. Whether our conclusions hold when environmental variability 504 comes into play remains to be seen. Indeed, as the state of ecosystems is also strongly 505 driven by environmental factors (Cury and Shannon, 2004; Travers-Trolet et al., 2014b; 506 Fu et al., 2015; Large et al., 2015; Fu et al., 2018), higher uncertainty around indica-507 tor reference points is likely to arise if inter-annual climate variability or trend is taken 508 into account. Model simulations run to test performance of ecological indicators found 509 that in general, IndiSeas-proposed indicators were fairly good at responding to fishing 510 pressure even under environmental perturbations, although interpretation of indica-511 tor trends required careful consideration of ecosystem characteristics and fishing strat-512 egy (Shin et al., 2018). Nevertheless, it seems feasible to produce ecosystem-specific, 513

fishing-strategy-specific sub-sets of indicators with carefully determined reference levels to guide fisheries management decisions.

516

533

517 5 Conclusion

When the estimation of catches is undermined by illegal, unreported and unregulated 518 fishing, using other ecological indicators to monitor total catch (and ecosystem effects 519 of that catch) may be a useful and interesting alternative to assess how far we are from 520 maximizing sustainable catches. By exploring a wide range of fishing strategies, we 521 showed that we are very likely to find at least a robust proxy for MMSY using a set 522 of ecosystem indicators. We also highlighted that the set of ecosystem indicators po-523 tentially usable as warning signs that MMSY has been reached depends on the fishing 524 strategy, and may be fewer although perhaps less constrained in values than indica-525 tors that are useful for detecting ecosystem collapse (or severe degradation). Finally, 526 for provision of efficient management tools to implement EBFM, the robustness to en-527 vironmental variability of such ecosystem-based reference levels at MMSY remains to 528 be assessed. To identify and refine reference levels for the suite of ecological indicators 529 examined here, extensive model simulations are recommended of prospective fishing 530 strategies that are being/may be considered by managers in the Southern Benguela to 531 maximize sustainable catches under various climate scenarios. 532

534 6 Acknowledgments

This work is a contribution to the IndiSeas Working Group (www.indiseas.org). The authors would like to thank Laure Velez for helping with the MMSY algorithm. We would also like to thank the two anonymous reviewers for their useful comments on earlier versions of the manuscript.

539 7 Funding

540 F.B. was funded by the French-South African ICEMASA program and Institut pour la

541 Recherche et le Développement. L.J.S was funded by the Department of Science and

542 Technology/National Research Foundation South African Research Chair in Marine

543 Ecology and Fisheries, and Institut pour la Recherche et le Développement. Y.J.S and

⁵⁴⁴ P.V. were partly funded by the Fondation pour la Recherche sur la Biodiversité [APP-

545 SCEN-2010-II].

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Table S1: Osmose species' parameters. Highlighted in gray: parameters estimated by the calibration algorithm. More information on the parameters can be found on http://www.osmose-model.org

	Anchov	y Euphau	Shallow siintater hake	Deep water hake	Horse mack- erel	Meso- pelagics	Redeye	Sardine	Large pelag- ics	Snoek
Egg size (cm)	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Egg weight (kg)	5.39E- 04	5.39E- 04	5.39E- 04	5.39E- 04	5.39E- 04	5.39E- 04	5.39E- 04	5.39E- 04	5.39E- 04	5.39E- 04
Length to weight allometric power	3	3.16	3.0425	2.9759	3	3	3	3	3	3
Length to weight condition factor (<i>kg.cm</i> ⁻³)	0.007	0.00738	0.00654	0.00785	0.009	0.008	0.009	0.009	0.007	0.018
Lifespan (yr)	5	1	15	15	8	2	6	10	25	10
Maturity age (yr)	1	-	4	4	3	0.5	1	-	2	-
Maturity size (cm)	-	1.05	-	-	-	-	-	18	-	73
Relative fecundity (eggs/gram of mature female)	8000	42254	500	500	250	646	750	2400	150	130
Sex ratio	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
$\frac{1}{10}$ K (yr^{-1})	1.37	1.682	0.039	0.049	0.183	1.66	0.71	0.26	0.12	0.294
$\frac{1}{L_{\infty}}$ (cm)	14.8	1.84	270.6	219.4	54.5	7	30.1	26	116	115.3
$\overline{t_0 (\text{yr})}$	-0.03	-0.198	-0.73	-0.914	-0.65	0.06	0.28	-1.5	-1.47	-0.01
Linear age thresh- old (yr)	1	0.17	1	1	1	1	1	1	1	1
Natural mortality rate (yr^{-1})	0.403	0.1	0.228	0.174	0.314	0.226	0.208	0.365	0.228	0.132
Larval natural mortality rate (yr^{-1})	6.191	5.305	4.669	4.404	4.547	4.358	5.706	3.119	7.874	10.456
Predation efficiency	0.57	0.57	0.57	0.57	0.57	0.57	0.57	0.57	0.57	0.57

	Anchovy	Krill	Shallow water hake	Deep water hake	Horse mack- erel	Meso- pelagics	Redeye	Sardine	Large pelag- ics	Snoek
Max in- gestion rate $(g.g^{-1}.yr^{-1})$	3.5	3.5	3.22	3.15	3.5	3.5	3.5	3.5	2.7	3.15
Pred-prey size ratio max	10	15	3.5	3.5	10	2.5	10	100	3.5	3.5 -
(before/after threshold)	5	5	1.8	1.8	5	-	-	200	-	
Pred-prey size ratio min	100	300	50	50	100	100	100	200	70	70
(before/after threshold)	500	100	50	50	100	-	-	400	-	
Pred-prey size threshold (cm)	8	0.6	27	29	10	-	-	10	-	-
Mortality starvation rate (yr^{-1})	3	3	3	3	3	3	3	3	3	3
Current fishing mortality rate (yr^{-1})	0.142	0	0.334	0.357	0.050	0.001	0.050	0.190	0.138	0.229
Recruitment age to the fishery (yr)	0.62	1	2.5	1.9	2	1	1	1	1	3
Nb of schools	24	100	24	24	24	100	24	24	24	24

Table S1 Continued:

	Dinoflagellates	Diatoms	Ciliates	Copepods
Accessibility to fish	0.0269	0.0030	0.0142	0.1854
Conversion factor (mmol $N.m^{-2}$ to ton. km^{-2})	0.72	0.72	0.675	1
Maximal size (cm)	0.002	0.02	0.02	0.3
Minimal size (cm)	0.0002	0.002	0.002	0.02
TL	1	1	2	2.5

	Anchovy	Krill	Shallow water hake	Deep water hake	Horse mack- erel	Meso- pelagics	Redeye	Sardine	Large pelag- ics	Snoek
Predator	No	No	Yes	Yes	No	No	No	No	Yes	Yes
Surveyed	Yes	No	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes
Harvested	Yes	No	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes
Vulnerability	44	1	59	59	44	31	46	54	60	61

Table S2: Indicators' species parameters

⁷⁹² Surveyed species:

These are species sampled by researchers during routine surveys (as opposed to species sampled in catches by fishing vessels), and should include species of demersal and pelagic fish (bony and cartilaginous, small and large), as well as commercially important invertebrates (squids, crabs, shrimps...). Intertidal and subtidal crustaceans and molluscs such as abalones and mussels, mammalian and avian top predators, and turtles, should be excluded.

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⁸⁰⁰ Predatory fish species:

Predatory fish are considered to be all surveyed fish species that are not largely planktivorous (i.e. phytoplankton and zooplankton feeders should be excluded). A fish species is classified as predatory if it is piscivorous, or if it feeds on invertebrates that are larger than the macrozooplankton category (> 2cm). Detritivores should not be classified as predatory fish.

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⁸⁰⁷ Intrinsic Vulnerability:

The intrinsic vulnerability index of a species (IVIs) is based on life history traits and ecological characteristics, ranges from 0 to 100, with 100 being the most vulnerable. For more details, see (Cheung et al., 2007).

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Figure S1: Illustration of the different phases of the algorithm for reaching the multispecies maximum sustainable yield (MMSY). For each fishing strategy, the step of the fishing mortality multiplier λ is progressively refined from a coarse step ($\Delta\lambda_1$) to the finest step ($\Delta\lambda_3$)



Figure S2: Evolution of multispecies yield with fishing pressure across all simulated fishing strategies. In many cases, the multispecies yield curve does not display the typical bell-shaped curve often presented (Worm et 37, 2009) but rather decreases very slowly once MMSY has been reached or level off to a plateau.



Figure S2: Evolution of multispecies yield with fishing pressure across all simulated fishing strategies. In many cases, the multispecies yield curve does not display the typical bell-shaped curve often presented (Worm et **38**, 2009) but rather decreases very slowly once MMSY has been reached or level off to a plateau.



Figure S2: Evolution of multispecies yield with fishing pressure across all simulated fishing strategies. In many cases, the multispecies yield curve does not display the typical bell-shaped curve often presented (Worm et 3Ω, 2009) but rather decreases very slowly once MMSY has been reached or level off to a plateau.



Figure S2: Evolution of multispecies yield with fishing pressure across all simulated fishing strategies. In many cases, the multispecies yield curve does not display the typical bell-shaped curve often presented (Worm et 40, 2009) but rather decreases very slowly once MMSY has been reached or level off to a plateau.



Figure S2: Evolution of multispecies yield with fishing pressure across all simulated fishing strategies. In many cases, the multispecies yield curve does not display the typical bell-shaped curve often presented (Worm et 41, 2009) but rather decreases very slowly once MMSY has been reached or level off to a plateau.



Figure S2: Evolution of multispecies yield with fishing pressure across all simulated fishing strategies. In many cases, the multispecies yield curve does not display the typical bell-shaped curve often presented (Worm et 42, 2009) but rather decreases very slowly once MMSY has been reached or level off to a plateau.



Figure S2: Evolution of multispecies yield with fishing pressure across all simulated fishing strategies. In many cases, the multispecies yield curve does not display the typical bell-shaped curve often presented (Worm et 4B, 2009) but rather decreases very slowly once MMSY has been reached or level off to a plateau.



Figure S2: Evolution of multispecies yield with fishing pressure across all simulated fishing strategies. In many cases, the multispecies yield curve does not display the typical bell-shaped curve often presented (Worm et 41, 2009) but rather decreases very slowly once MMSY has been reached or level off to a plateau.



Figure S2: Evolution of multispecies yield with fishing pressure across all simulated fishing strategies. In many cases, the multispecies yield curve does not display the typical bell-shaped curve often presented (Worm et 45, 2009) but rather decreases very slowly once MMSY has been reached or level off to a plateau.



Figure S2: Evolution of multispecies yield with fishing pressure across all simulated fishing strategies. In many cases, the multispecies yield curve does not display the typical bell-shaped curve often presented (Worm et **4b**, 2009) but rather decreases very slowly once MMSY has been reached or level off to a plateau.