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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

## *Ecological indicators for an Ecosystem Approach to Fisheries*

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 the way to the concept of a more integrative Ecosystem Approach to Fisheries (EAF or EBFM- Ecosystem Based Fisheries Management) (Marasco et al., 2007; Ruckelshaus et al., 2008). Most importantly, EBFM embodies a desire to reconcile sometimes contradictory expectations from society regarding the ecosystem and the services it provides. EBFM also aims at moving beyond mono-specific approaches to fisheries. Some species cannot be evaluated or managed independently from others (by-catches, trophic interactions, competition for habitats), hence the necessity to establish management policies at the scale of an ecosystem rather than of a stock (Hall and Mainprize, 2004; Shannon et al., 2004; Mackinson et al., 2009). Finally, the transition towards an ecosystem approach to fisheries is particularly crucial as the mono-specific approach can be too lenient when applied to multiple species in parallel, potentially leading to the collapse of certain stocks (Ghosh and Kar, 2013; Voss et al., 2014).

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

30 time came to evaluate their usefulness and performance and select the ones best meet-  
31 ing the afore-mentioned requirements (Shin et al., 2012; Coll et al., 2016; Shin et al.,  
32 2018).

33

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

56

57 *Multispecies Maximum Sustainable Yield and fishing strategies*

58

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

65  
66 So far, the regulation of fishing effort has been the primary lever of action to en-  
67 sure the sustainability of a commercially exploited stock. Most often, when the state  
68 of a stock is evaluated, an estimate of the MSY is provided (and the associated fishing  
69 mortality  $F_{MSY}$ ) and translated into direct or indirect management decisions such as  
70 catch quotas until the next evaluation. Similar management procedures could be en-  
71 visaged at the ecosystem scale by estimating the ecosystem exploitation rate allowing  
72 maximisation of the total catches, also referred to as Multispecies Yield (MY) (Worm  
73 et al., 2009; Jennings and Collingridge, 2015).

74  
75 At the level of the ecosystem, the expected MMSY and the response of MY to fish-  
76 ing effort depend on how the latter is allocated between the different exploited stocks,  
77 hereafter referred to as the "fishing strategy". Recently, the fishing strategy has been  
78 shown to influence the performance of the fishing sector both in terms of production  
79 and conservation (Voss et al., 2014; Kolding et al., 2016). Because both the structure  
80 and productivity of an ecosystem largely depend on how it is exploited (Travers et al.,  
81 2006, 2010), it can be anticipated that, given the large range of potential harvesting  
82 strategies, a given management objective (e.g. MMSY) may be reached under differ-  
83 ent states of an ecosystem reflected by different values of ecosystem indicators. This  
84 potential variability of indicator reference points implies that they may not be consid-  
85 ered as intrinsic values of an ecosystem, disregarding how it is exploited. However,  
86 rather than an obstacle to the practical use of ecosystem reference points to guide man-  
87 agement decisions, their potential dependence on the fishing strategy could provide

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.

92

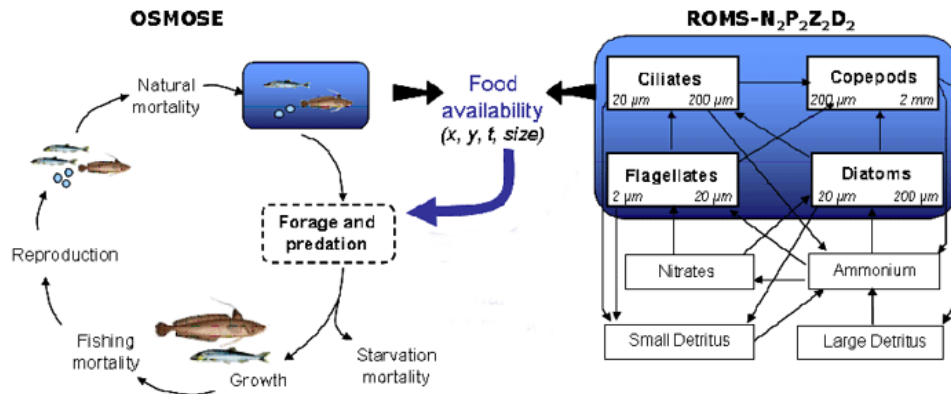
93 *The Southern Benguela case study*

94

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

## 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/>

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

127 applied ([www.osmose-model.org](http://www.osmose-model.org), Grüss et al. (2016)).

128

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

153

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

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

## 177 **2.2 Ecosystem Indicators**

178 Since landings data are known to be biased due to illegal, unreported and unregulated  
179 (IUU) fishing, which may represent up to one third of the global reported catches  
180 (Agnew et al., 2009), complementary indicator reference points other than those based  
181 solely on reported catches have the potential to improve the assessment of fishing  
182 impacts and to operationalize EBFM. The existence of reference points was tested for  
183 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	Type	Unit
Total Biomass	$TB$	$\sum_{sp} B_{sp}$	survey-based	$MT$
Inverse of fishing pressure	$B\_Y$	$TB / MY$	survey-based	$\emptyset$
Intrinsic Vulnerability Index of the landings	$IVI$	$\frac{\sum_{sp} IV I_{sp} \times Y_{sp}}{MY}$	catch-based	$\emptyset$
Large Fish Indicator	$LFI(size_{lim})$	$\frac{\sum_{size > size_{lim}} B_{size}}{TB}$	survey-based	$\emptyset$
Mean Size	$LG$	$\frac{\sum size}{N}$	survey-based	$cm$
Mean Life Span	$LS$	$\frac{\sum_{sp} max\ age_{sp} \times B_{sp}}{TB}$	survey-based	$year$
Mean Maximal Size	$MML$	$\frac{\sum_{sp} max\ size_{sp} \times B_{sp}}{TB}$	survey-based	$cm$
Marine Trophic Index	$MTI(TL_{lim})$	$\frac{\sum_{TL > TL_{lim}} TL \times Y_{TL}}{MY}$	catch-based	$\emptyset$
Proportion of predatory fish	$PF$	$\frac{B_{predators}}{TB}$	survey-based	$\emptyset$
Size spectrum slope	$SSS$	opposite slope of $\log(\text{abundance}) = f(\log(\text{size}))$	survey-based	$\emptyset$
Trophic level of landings	$TLL$	$\frac{\sum_{sp} TL_{sp} \times Y_{sp}}{MY}$	catch-based	$\emptyset$
Trophic level of surveyed community	$TLS$	$\frac{\sum_{sp} TL_{sp} \times B_{sp}}{TB}$	survey-based	$\emptyset$

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

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

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

202

## 203 **2.3 Testing the sensitivity of ecosystem-based reference points to** 204 **the fishing strategy**

### 205 **2.3.1 Reference points at MMSY**

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

211

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

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

226

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

- 235 1. A first estimate of  $\lambda_{MMSY}$  (the value of  $\lambda$  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  $\lambda_{MMSY}$  set the upper bound of a second screening of  $\lambda$  with  
 239 20  $\lambda$  values equally distributed between  $\lambda = 0$  and  $\lambda = \lambda_{MMSY} + 2 \times \Delta\lambda_1$ . So  
 240 the finer second step applied is  $\Delta\lambda_2 = \frac{\lambda_{MMSY} + 2 \times \Delta\lambda_1}{20}$ .
- 241 3. Finally,  $\lambda$  steps were further refined at the beginning of the MY curve (between

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

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

### 262 2.3.2 Testing the robustness of reference points across fishing strategies

263 For each indicator, the set of reference points at MMSY for the 200 simulated fishing  
264 strategies defined what we called its *reference distribution* (200 values per indicator),  
265 and the interdecile range  $[Q10; Q90]$  of this distribution defined its *reference interval*.  
266 The *total distribution* of an indicator referred to the whole set of values the latter could  
267 take, independently of the strategy or fishing intensity  $\lambda$ . It was reconstructed by ex-  
268 tracting 100 values of the indicator (equally distributed between  $\lambda = 0$  and  $\lambda_{MMSY}$  (20  
269 000 values per indicator)) for each strategy from the fitted indicator's curves for that

270 strategy .

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

276

277 For visualization purposes, and comparison between indicators, standardized in-  
278 dicators were calculated as:  $\frac{\text{value} - \text{mean of the total distribution}}{\text{standard deviation of the total distribution}}$ .

### 279 **2.3.3 Testing the robustness of reference points within fishing strategies**

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

## 292 **2.4 Focus on realistic fishing strategies in the Southern Benguela**

293 In addition to these exploratory analyses, we gave special attention to more realistic  
294 fishing strategies in the Southern Benguela. These strategies explicitly accounted for  
295 technical interactions among species simultaneously caught by a fishing fleet. Indeed,  
296 the various fishing fleets in the Southern Benguela are not species-specific (i.e. they

297 do not target a single species but catch many species in various proportions), and it is  
298 thus not realistic to apply uncorrelated fishing pressures on the various species. The  
299 same methodology as described in 2.3.3 was used to determine which indicators could  
300 be used as robust proxies for MMSY.

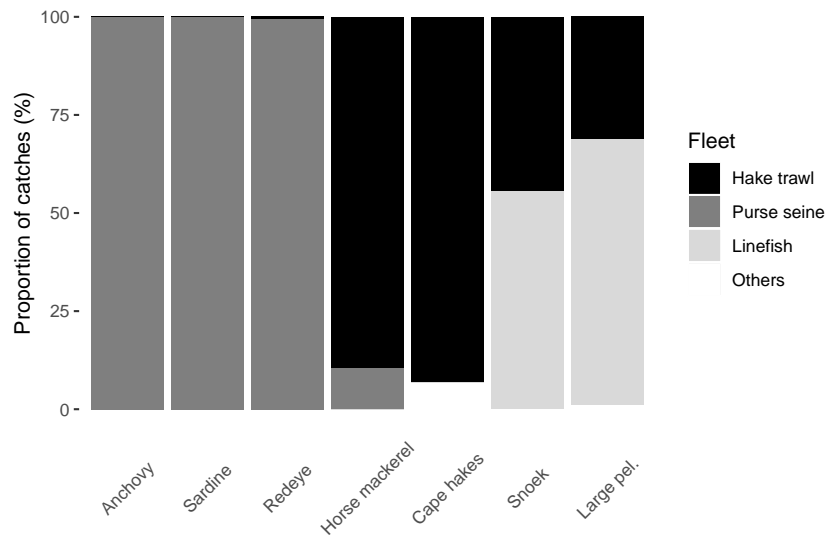
#### 301 **2.4.1 Reaching MMSY by increasing the fishing effort on all species**

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  $\lambda$  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**

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

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

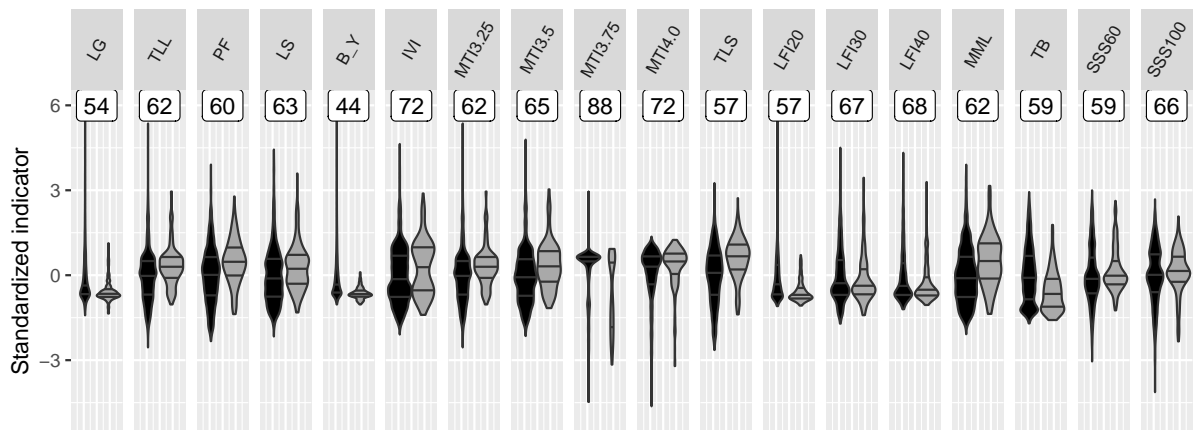


**Figure 2:** Mean contribution of each fishing sector to the landings of the modeled commercial species between 2003 and 2014

### 328 3 Results

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

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

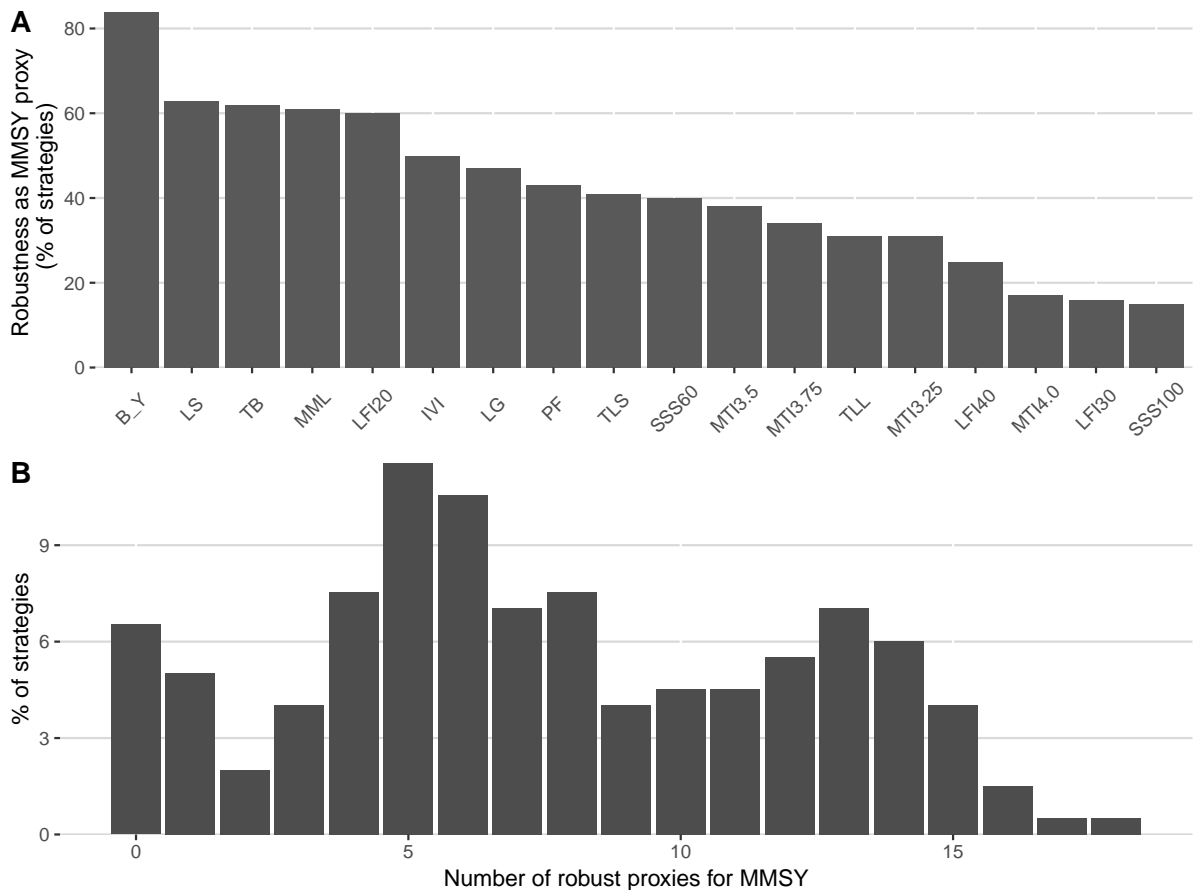


**Figure 3:** Distributions of the standardized indicators and their reference points (all randomly generated fishing strategies included). Refer to Table 1 for the indicators' definition. In black: the total distribution of all indicator values across all strategies ( $n=20000$ ), in gray: the reference 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.

### 3.2 Strategy-specific reference points at MMSY

As shown on Figure 4-A, all indicators were not equally useful in detecting when MMSY had been reached. The indicators *B\_Y*, *LS*, *TB*, *MML* and *LFI20* appeared as the most likely to provide robust proxies for MMSY, as their confidence interval at MMSY had less than 10% overlap with the total distribution of the indicator in more than 60% of the simulated strategies. It is worth noting that the thresholds used for calculating indicators such as the marine trophic index *MTI*, the large fish indicator *LFI* or the size spectrum slope *SSS* influenced their robustness. This is especially striking for the large fish indicator which could be used as a proxy in 60% of the strategies when calculated at a threshold of 20cm, but was only useful in 25% (respectively 16%) of the strategies when calculated at a threshold of 40cm (respectively 30cm). The size spectrum slope was in general more useful when calculated at a threshold of 60cm (40% of the strategies) than when calculated at a threshold of 100cm (15% of the strategies). The mean trophic index appeared slightly more likely to provide a robust proxy for MMSY when calculated at thresholds of 3.5 or 3.75 cm (respectively 38 and 34% of the strategies) than when using the commonly used threshold of 3.25 (31% of the strategies).



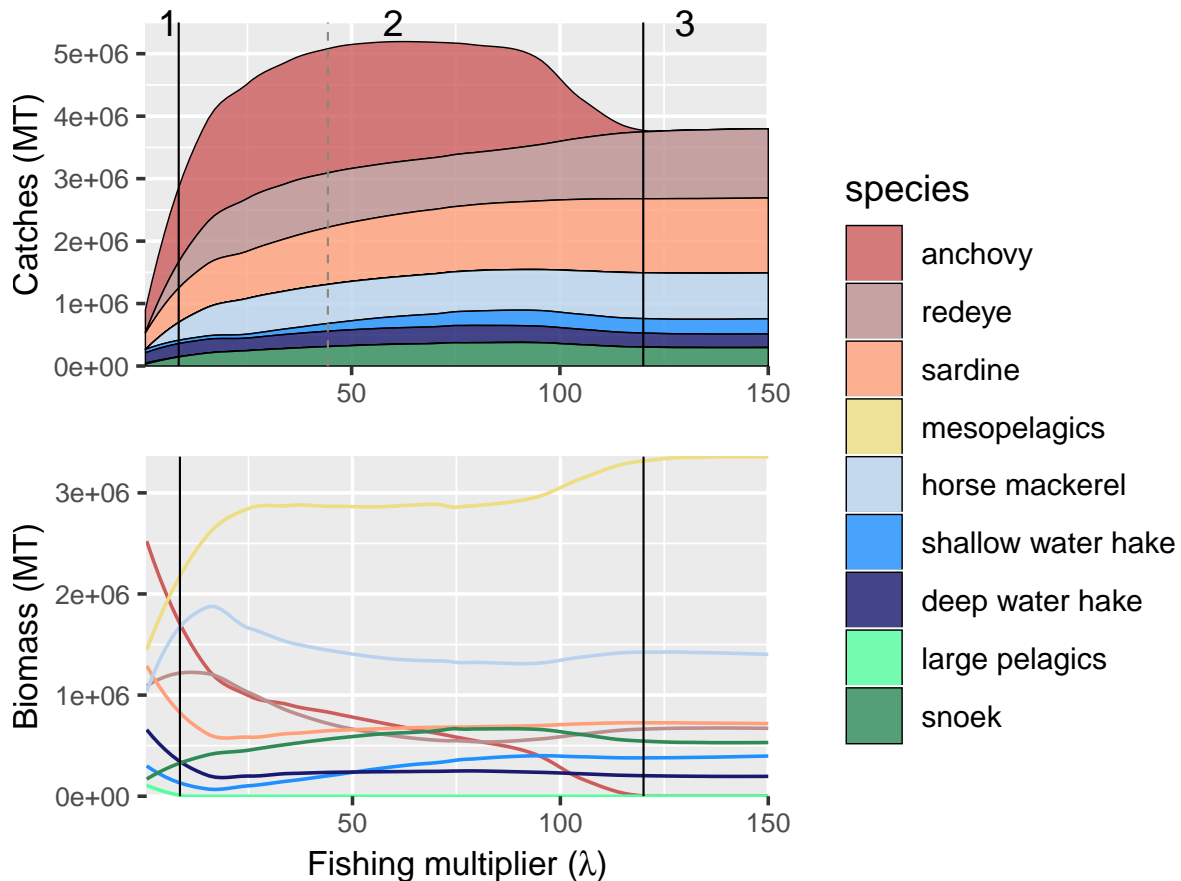


**Figure 4:** A- Percentage of strategies in which the indicator was a useful proxy for MMSY (i.e. less than 10% of the total distribution of the indicator fell within the 95% confidence interval of its reference point at MMSY)

B- Histogram of robust proxies for MMSY across the 200 simulated 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...

356

357 As shown on Figure 4-B, only 7% of strategies did not have a robust proxy indicator  
 358 for MMSY which means that at least one indicator among the proposed list provided  
 359 a robust proxy for MMSY in more than 93% of the strategies. MMSY could be detected  
 360 by more than one indicator in 88% of the strategies (bins 0 and 1 account for 12% of the  
 361 strategies). In those cases, monitoring the ecosystem with a suite of indicators rather  
 362 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

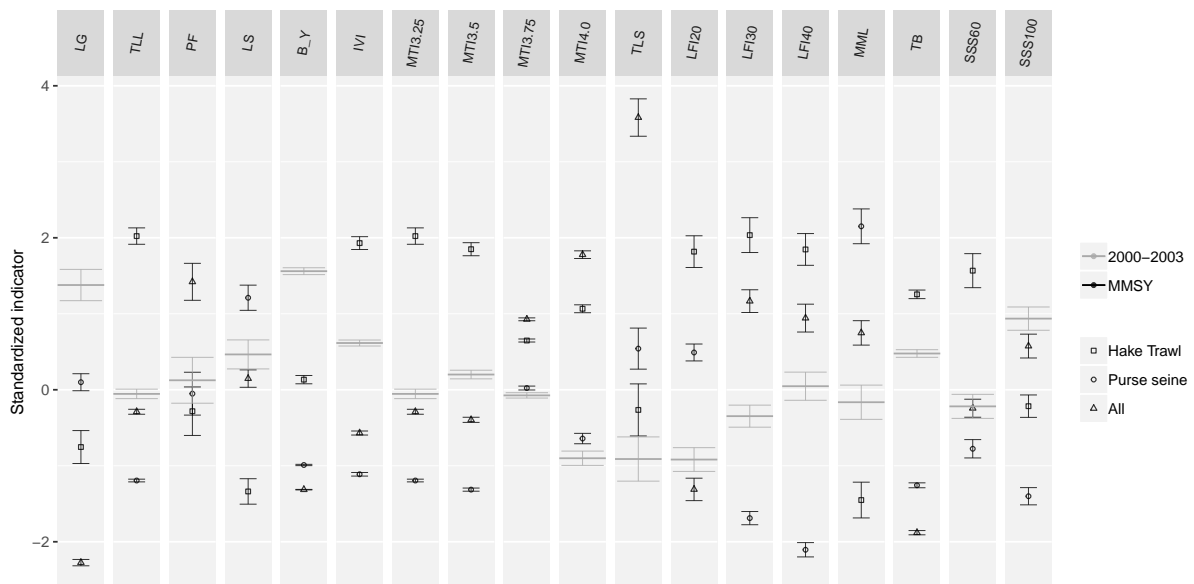
### 363 **3.3 Focus on more realistic fishing strategies**

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

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

373 this first phase. Biomass of both hake species also declined, and the large pelag-  
 374 ics collapsed quickly.

- 375 • Phase 2: Even though the biomass of anchovy kept decreasing, we observed a  
 376 shift in the ecosystem's dynamics. For sardine and hakes on one hand and redeye  
 377 and horse mackerel on the other hand, the dynamics in this second phase was  
 378 opposite to the one observed during the first phase. In this 2nd phase, the release  
 379 of competition for zooplankton was not sufficient to counter the still increasing  
 380 fishing pressure, and biomasses of both redeye and horse mackerel started de-  
 381 clining. In the meantime, the biomass of sardine and hakes increased as a re-  
 382 sult of predation and/or competition interactions. It is during this hypothetical  
 383 phase that multispecies yield reached its maximum value around 5,200,000 tons,  
 384 which is around 7 times the mean annual total catch between 2000 and 2003  
 385 ( $\lambda = 1$ ). At the end of the 2nd phase, anchovy collapsed.
- 386 • Phase 3: After the collapse of anchovy, the ecosystem reached an equilibrium  
 387 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

389 95% confidence interval are presented in Figure 6. As expected, the values of the refer-  
390 ence points depended on the fishing strategy under which MMSY was reached. More-  
391 over, for some indicators, we could not even provide a reference direction from the  
392 2000-2003 situation (i.e.  $\lambda = 1$ ) towards MMSY that would be common to all scenarios.  
393 For instance, the reference point at MMSY for the mean maximum length (*MML*) was  
394 lower than its 2000-2003 value when only the hake trawl fishery developed, whereas  
395 it was greater than the 2000-2003 value for the other scenarios. This highlights the fact  
396 that, even though those indicators were originally designed to decrease when fish-  
397 ing pressure increases, they do not always behave that way. The only indicators that  
398 showed a common reference direction in all three strategies were *LG*, *B\_Y*, *MTI3.75*,  
399 *MTI4.0*, *TLS*, and *SSS100*.

400

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

## 405 **4 Discussion**

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

**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			
TB			
TLL			
TLS			

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

417

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

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

436

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

445

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

454

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

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

465

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

473

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

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

493

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

502

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



514 fishing-strategy-specific sub-sets of indicators with carefully determined reference lev-  
515 els to guide fisheries management decisions.

516

## 517 **5 Conclusion**

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

533

## 534 **6 Acknowledgments**

535 This work is a contribution to the IndiSeas Working Group ([www.indiseas.org](http://www.indiseas.org)). The  
536 authors would like to thank Laure Velez for helping with the MMSY algorithm. We  
537 would also like to thank the two anonymous reviewers for their useful comments on  
538 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-  
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791 **Supplementary material**

**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>

	Anchovy	Euphausiid	Shallow water hake	Deep water hake	Horse mackerel	Mesopelagics	Redeye	Sardine	Large pelagics	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 ( $kg.cm^{-3}$ )	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
Von Bertalanffy parameters	K ( $yr^{-1}$ )	1.37	1.682	0.039	0.049	0.183	1.66	0.71	0.12	0.294
	$L_{\infty}$ (cm)	14.8	1.84	270.6	219.4	54.5	7	30.1	26	116
	$t_0$ (yr)	-0.03	-0.198	-0.73	-0.914	-0.65	0.06	0.28	-1.5	-1.47
	Linear age threshold (yr)	1	0.17	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

**Table S1 Continued:**

	Anchovy	Krill	Shallow water hake	Deep water hake	Horse mackerel	Mesopelagics	Redeye	Sardine	Large pelagics	Snoek
Max ingestion 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 (before/after threshold)	10	15	3.5	3.5	10	2.5	10	100	3.5	3.5
Pred-prey size ratio min (before/after threshold)	5	5	1.8	1.8	5	-	-	200	-	-
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

	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

**Table S2:** Indicators' species parameters

	Anchovy	Krill	Shallow water hake	Deep water hake	Horse mackerel	Meso-pelagics	Redeye	Sardine	Large pelagics	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

792 Surveyed species:

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

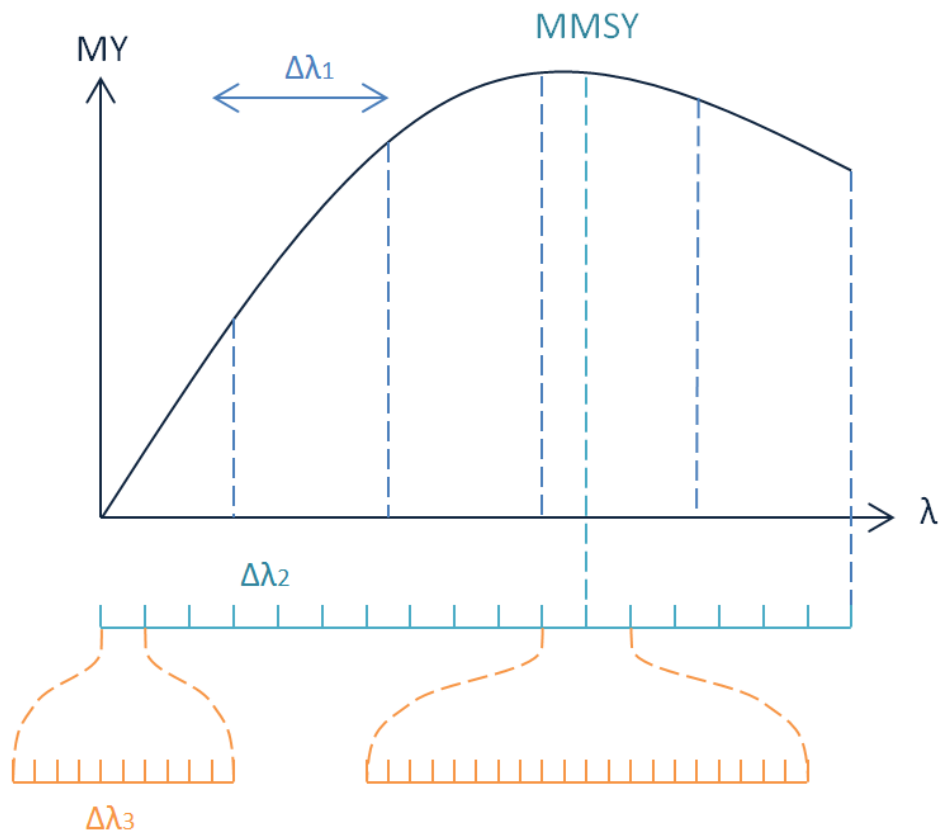
799 Predatory fish species:

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

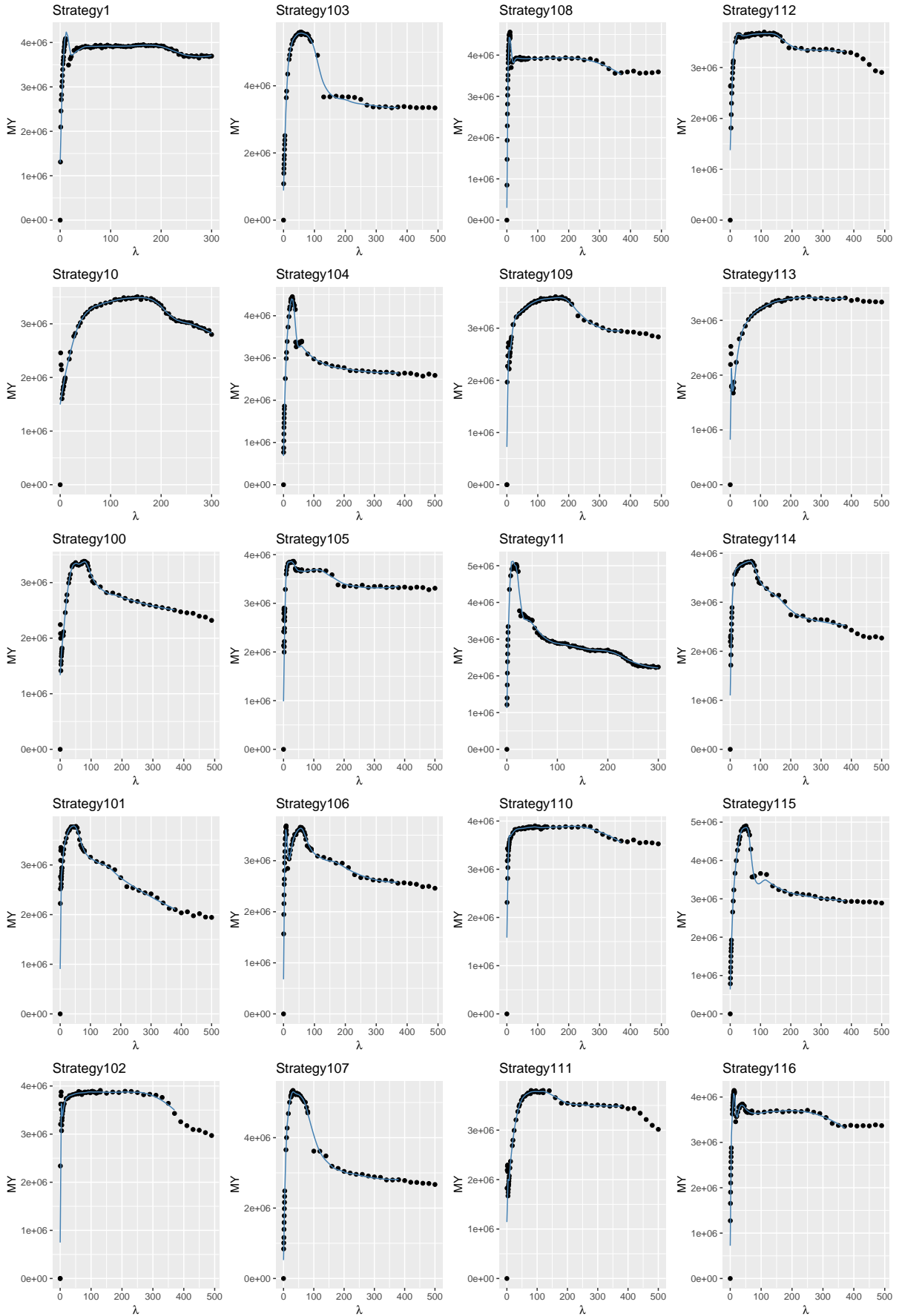
806 Intrinsic Vulnerability:

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

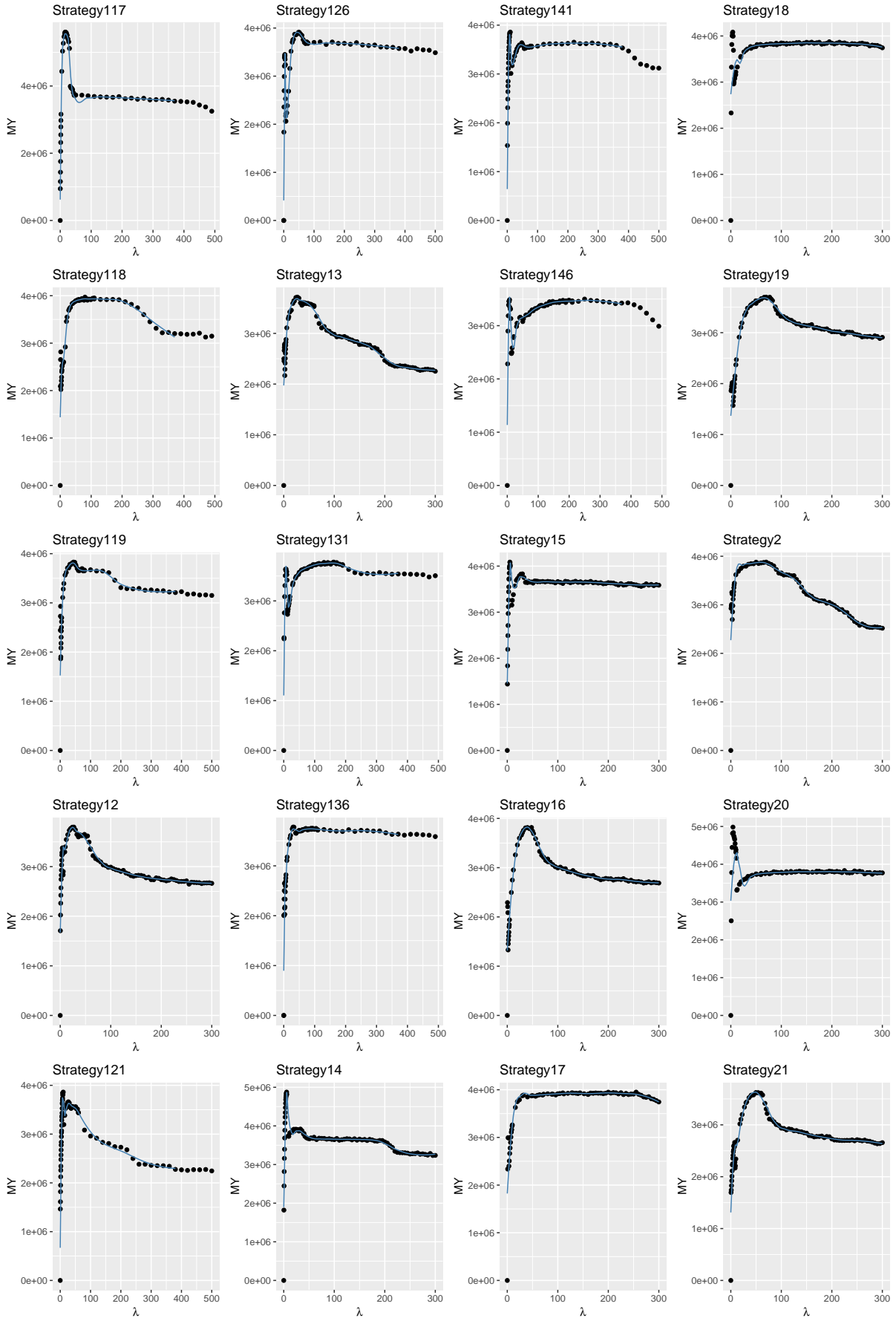
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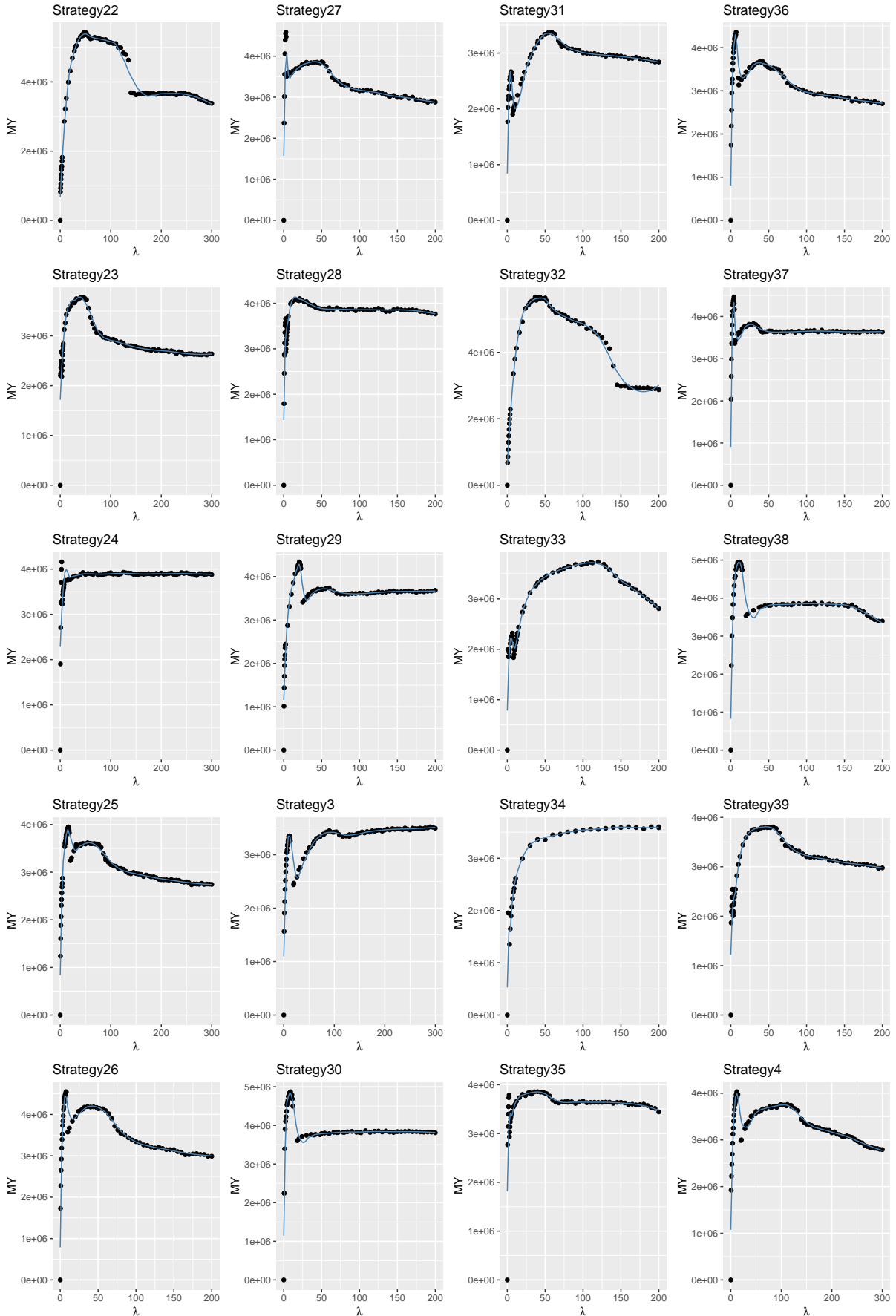
**Figure S1:** Illustration of the different phases of the algorithm for reaching the multispecies maximum sustainable yield (MMSY). For each fishing strategy, the step of the fishing mortality multiplier  $\lambda$  is progressively refined from a coarse step ( $\Delta\lambda_1$ ) to the finest step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



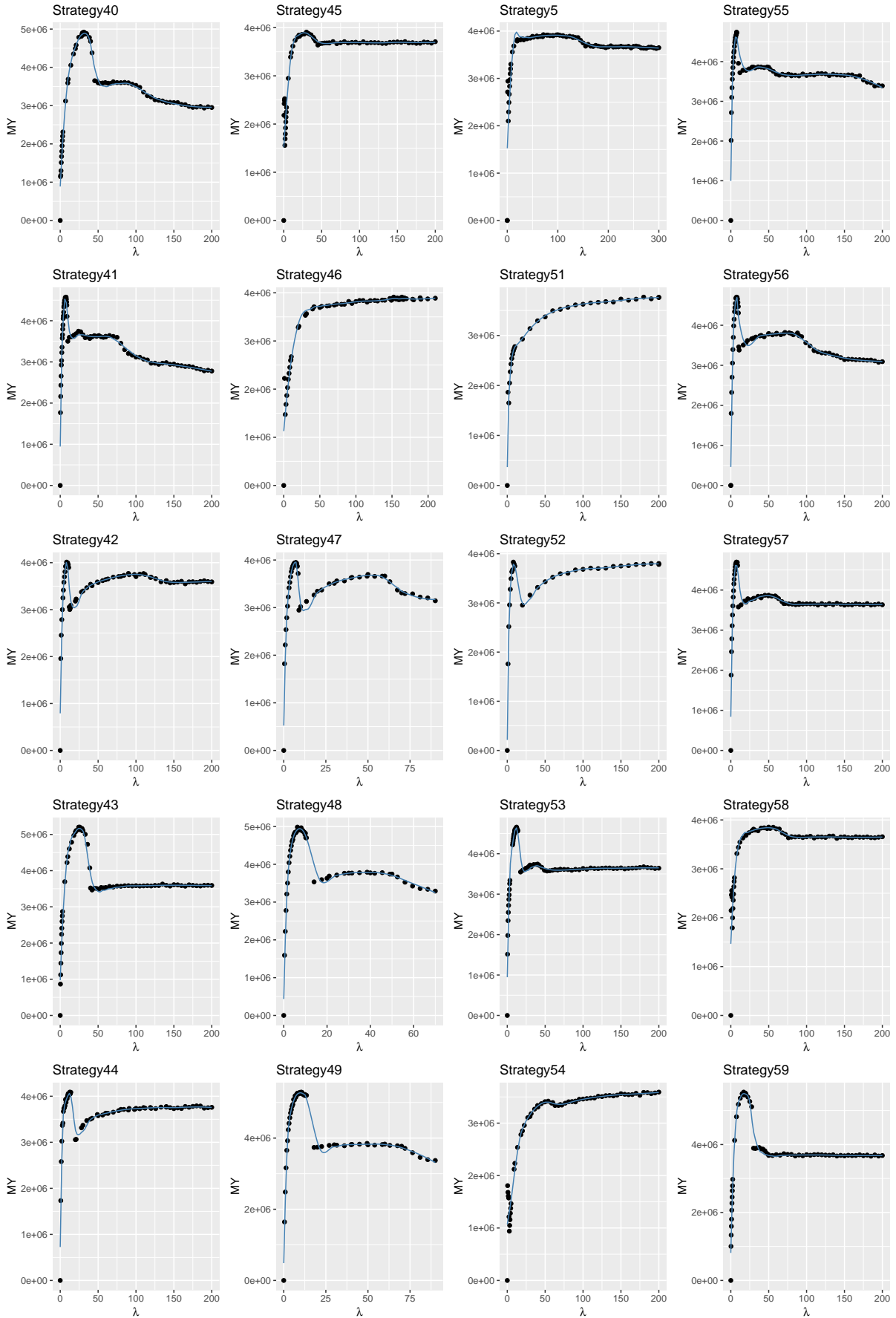
**Figure S2:** Evolution of multispecies yield with fishing pressure across all simulated fishing strategies. In many cases, the multispecies yield curve does not display the typical bell-shaped curve often presented (Worm et al., 2009) but rather decreases very slowly once MMSY has been reached or level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



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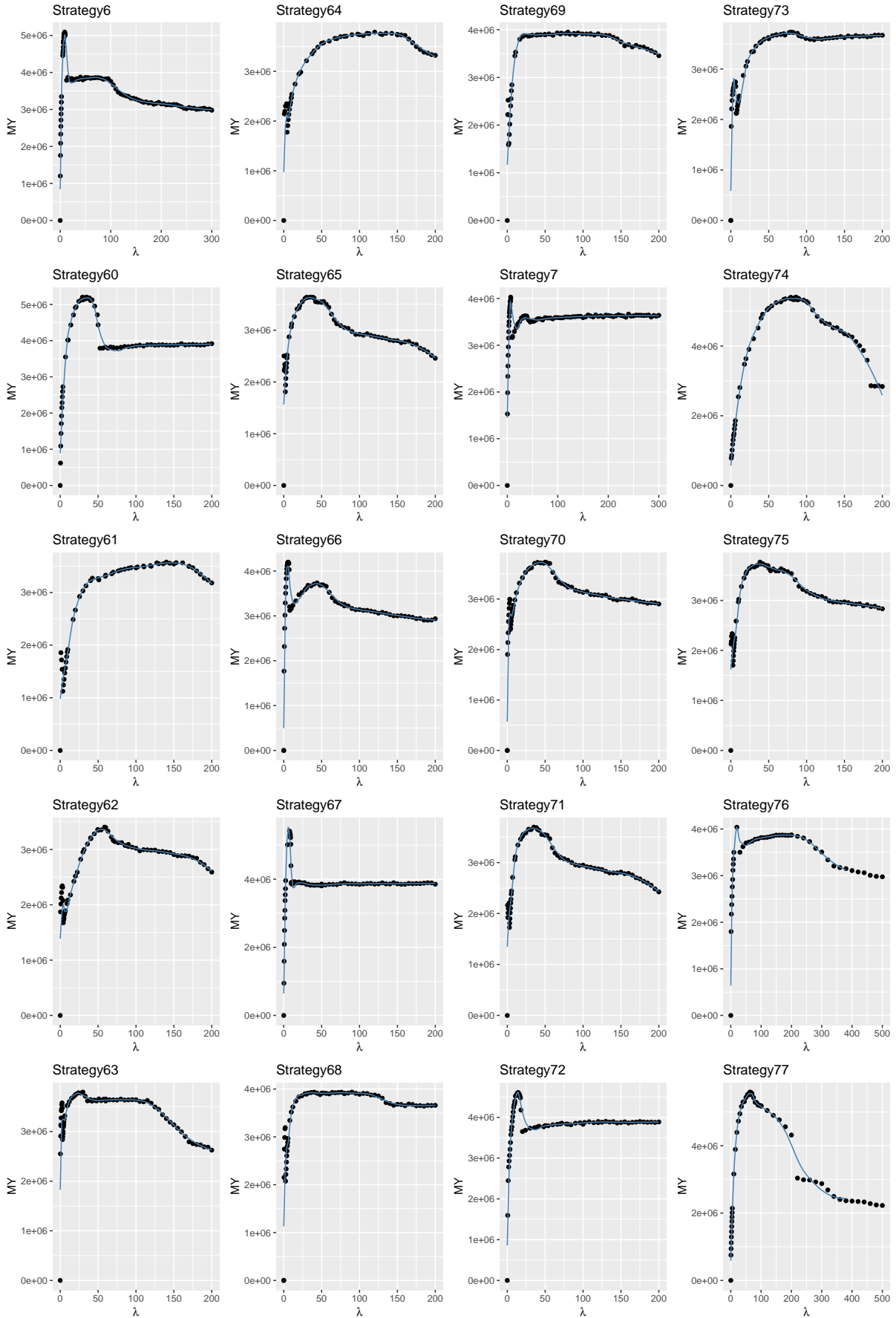


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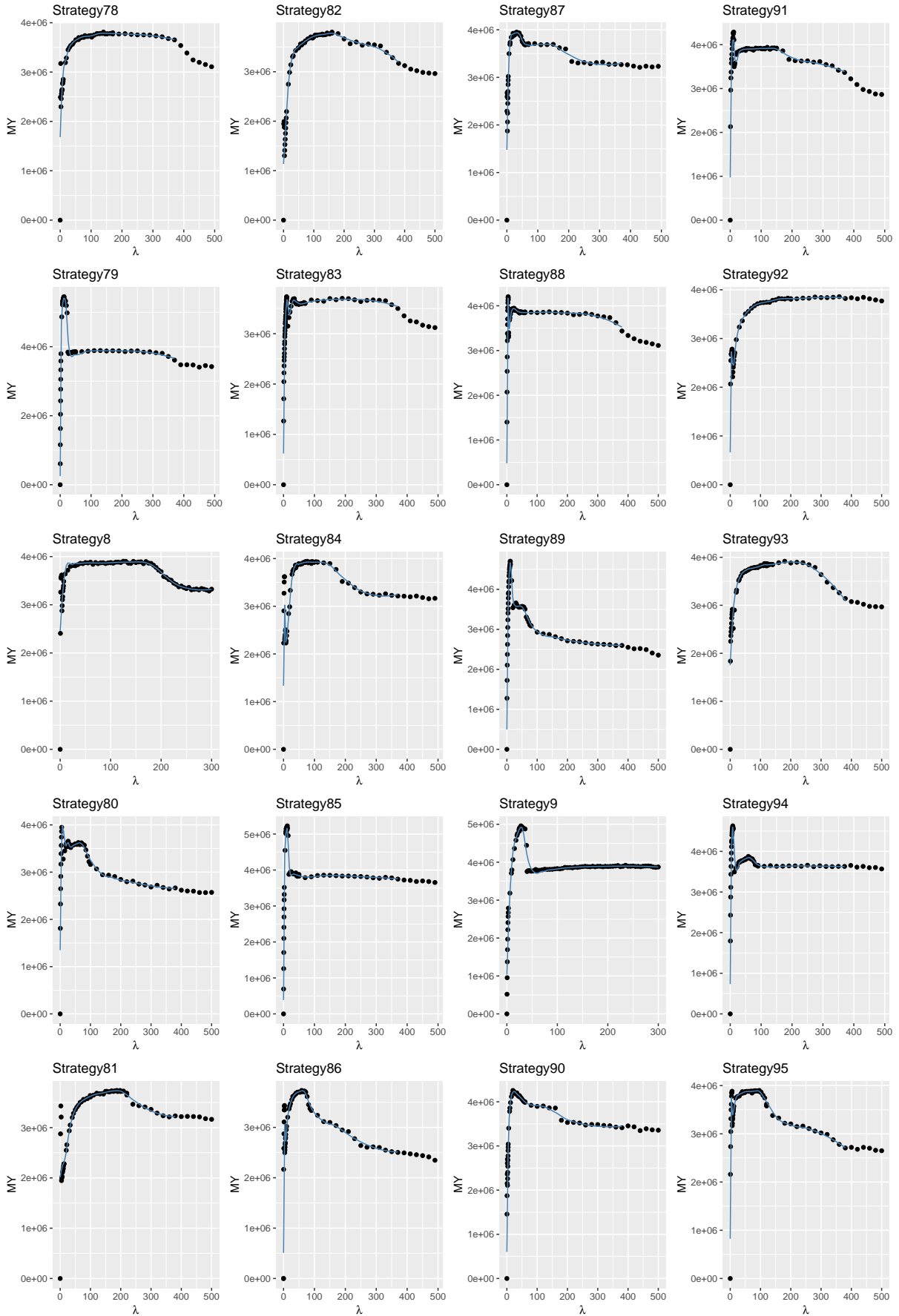


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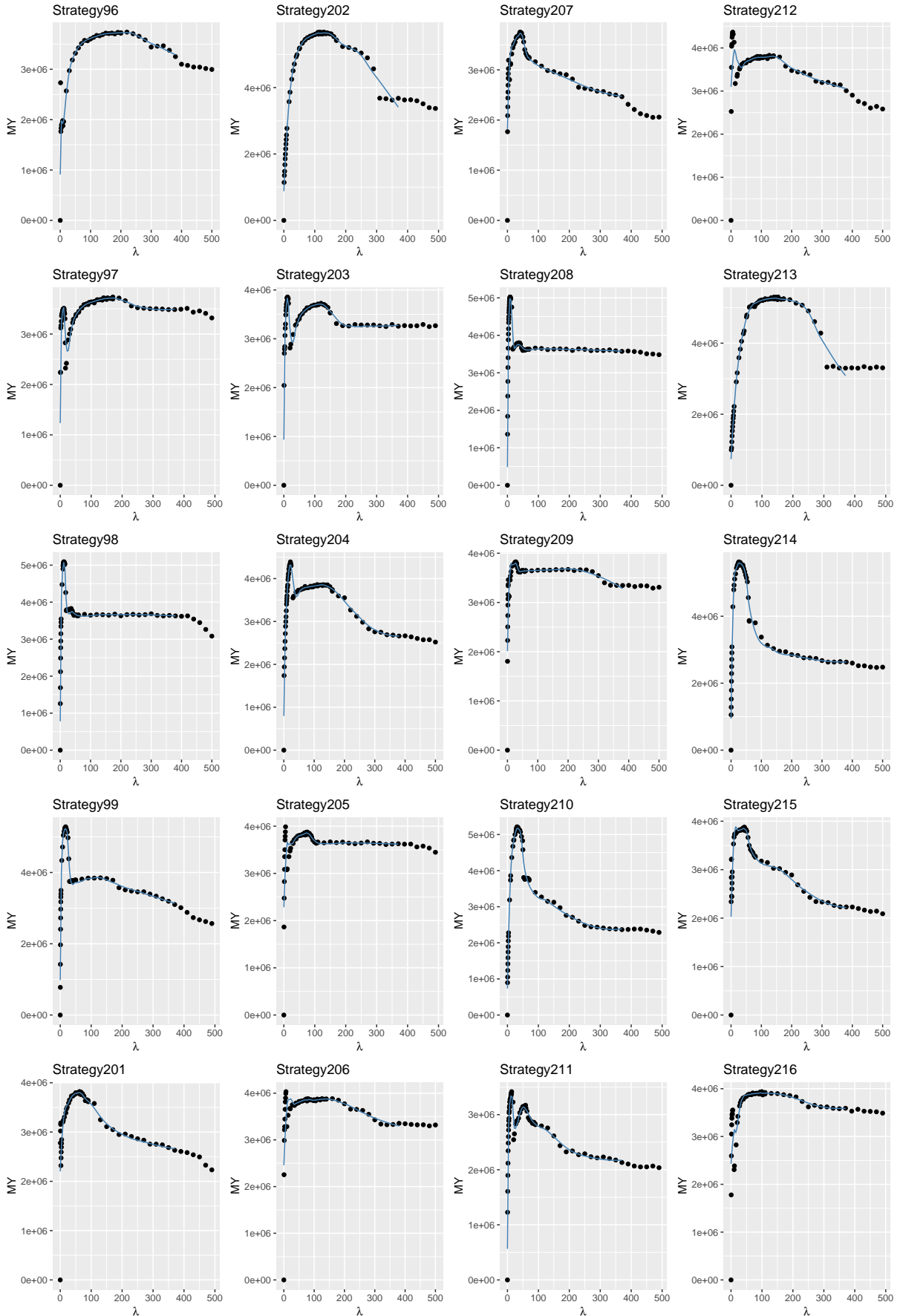




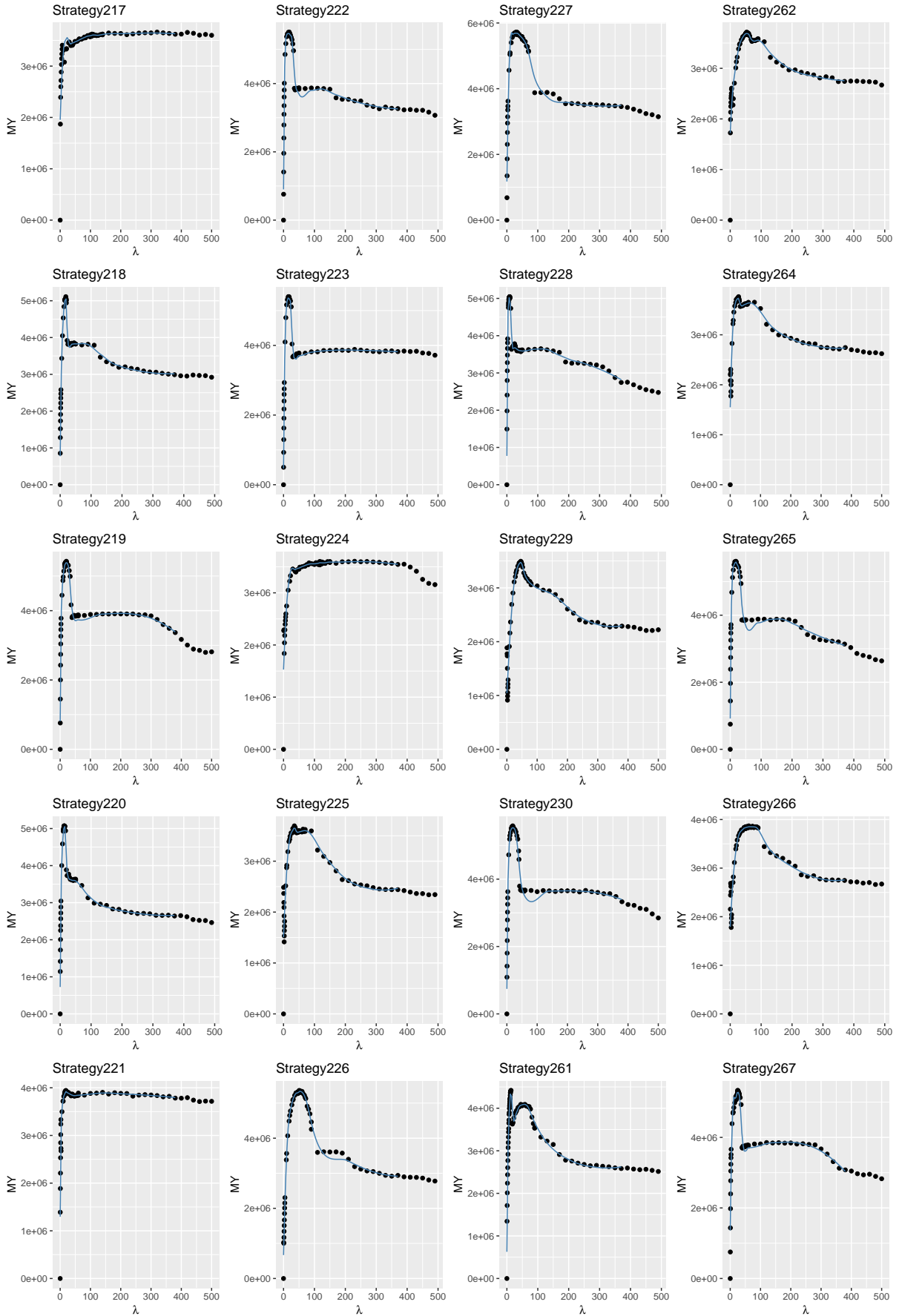
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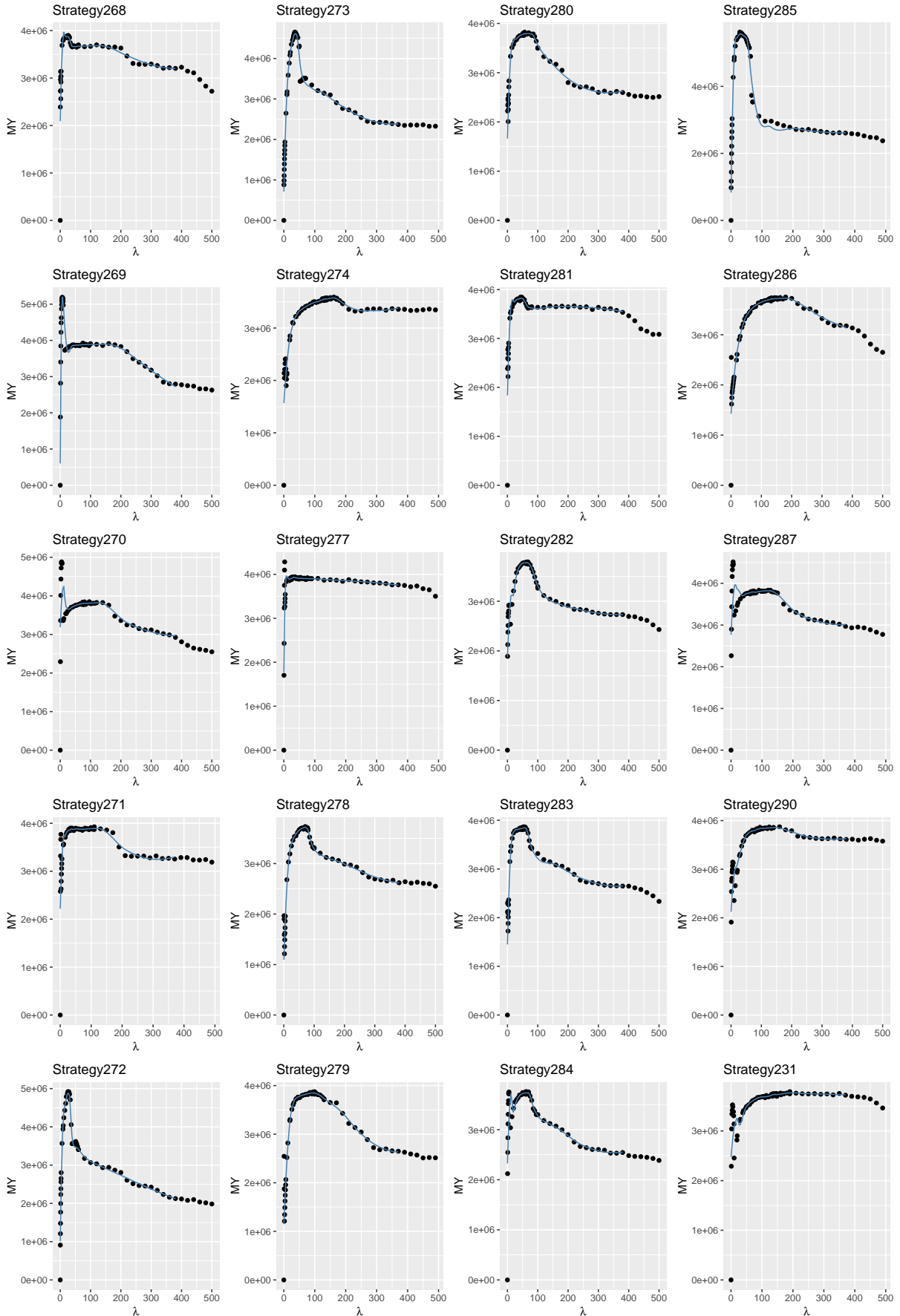
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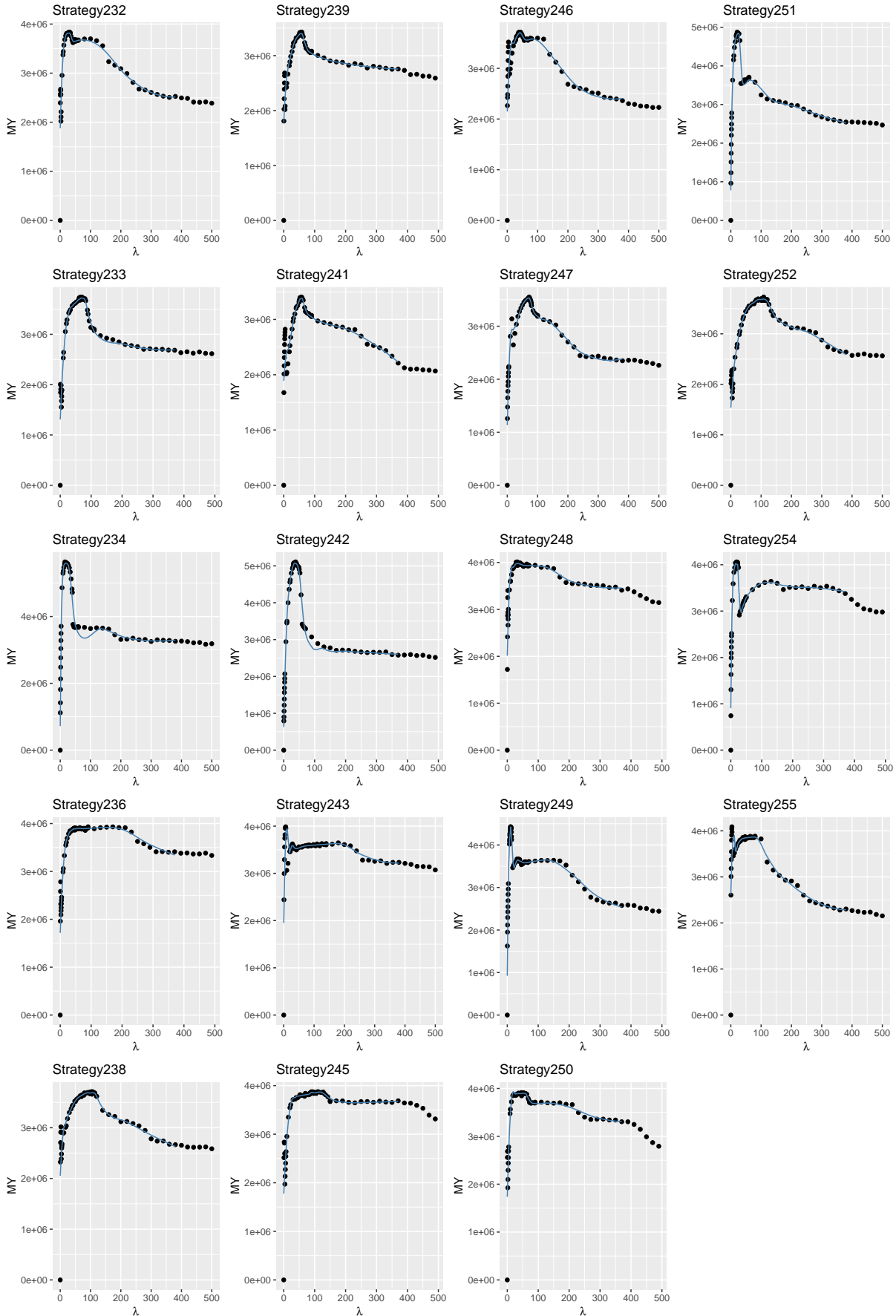
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