
Are maximum yields sustainable? Effect of intra-annual time-scales on MSY, stability and resilience

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Abstract :

The concept of Maximum Sustainable Yield (MSY) have been lying at the core of the theory of sustainable harvesting a fishery for decades and have become a key reference point for many fishing administrations, including the European Union. However, the existence of a MSY relies on the stability of a population equilibrium. This hypothesis, though always true in the original Schaeffer model, is still challenging in more realistic and recent population models. However, recent advances shows that fish population can exhibit complex dynamics that are ill described by the classical theory. In particular, processes occurring at intra-annual time scales can affect the stability of a population equilibrium even in a strictly single species case. Associated to stability, the resilience of the equilibrium (defined as an inverse return-time following a perturbation) also matters in a management purpose. Here, we introduce an analytical single population model in discrete time with a monthly time-step allowing temporal distinction between maturation and recruitment with density-dependent mortality and fishing exploitation. We show that, thanks to an appropriate population structure, we can easily derive inter-annual population equilibrium, and study their resilience and stability properties. Then, we show that under classical hypothesis concerning density-dependence, equilibrium stability is not guaranteed and that MSY can, in theory, be associated to unstable or low resilient states. However such destabilisation seems unlikely with realistic sets of parameters. Finally, a numerical illustration for sole (*Solea solea*) of the Bay of Biscay suggests that the value of MSY was sensitive to maturation period whereas viability, stability and resilience was more sensitive to timing of recruitment. The value of appeared robust to uncertainty concerning maturation and recruitment. We conclude by saying that even if the risk of destabilisation is low for real populations, the risk of decreased resilience near the border of extinction should be cared of.

Highlights

► With our new model we can easily link intra-annual to inter-annual dynamics. ► With our new model we can separate maturation from recruitment processes. ► For sole, maturation timing has an impact on MSY values but little impact on F_{MSY} . ► For sole, recruitment timing has an impact on stability and resilience of equilibrium.

Keywords : Difference equation, Intra-annual time-scales, Maximum yield, Resilience, Sensitivity

1. Introduction

Numerous examples of marine population collapses (Mullon et al., 2005; Pauly et al., 2005) led to the progressive recognition that world fisheries were exhaustible and that fishing could affect deeply the abundance of marine populations (Pauly et al., 2002). This concern, along with the will to maximize profits out of fisheries exploitation, fostered the development during the XX^{th} century of a theory of sustainable harvesting of a population. The idea that there is an optimal level of fishing effort emerged after pioneer works of Russell (1931), Hjort (1933) and Graham (1935), and led to the formalisation of the concept of Maximum Sustainable Yield (*MSY*) by Schaefer (1954).

Although early criticised (Larkin, 1977), this concept was highly successful amongst several fishing administrations worldwide (Mace, 2001; Mesnil, 2012), including the European Union which set the goal that all stocks reach levels of biomass compatible with the production of *MSY* by 2020 (European Union, 2013). For Finley (2009), however, this institutional success is more explained by its political implications than by the scientific strength of the concept in itself.

In practice, *MSY*-based management have evolved from a target point to be attained at all costs to a target range around the maximum taking into account uncertainties and allowing room to consider other management objectives or ecosystem aspects (Hilborn, 2010; Rindorf et al., 2017). In particular, the effect of uncertainty on several model inputs on the *MSY* have been largely studied (Zheng et al., 2019) and serves as a basis for fisheries advice (ICES, 2015). However, the sustainability of the *MSY* is still not clearly established and the effects of uncertainty of inputs on sustainability of this reference point have been little explored.

The concept of sustainability is ubiquitous in the policy realm but lack clear definition which does not always match with those employed by sci-

30 entists (Hilborn et al., 2015; Donohue et al., 2016). In the classical under-
31 standing of sustainability in fisheries as defined by Quinn and Collie (2005),
32 and which correspond to the early developments of harvesting theory, “sus-
33 tainable” is equivalent to “asymptotically stable” with the use of equilibrium
34 models. Indeed, in the original model of Schaefer (1954) the harvested pop-
35 ulation is described by a single differential equation, admitting a unique and
36 stable positive equilibrium. This is in line with the ancient conception that,
37 neglecting random fluctuations due to external factors, populations tend to
38 stabilise around an equilibrium value constrained by their environment. It
39 must be stressed out that in this framework, any population level can be con-
40 sidered as sustainable as long as it is positive and MSY is a natural target for
41 fishing management (Quinn and Collie, 2005). Even if the perception of sus-
42 tainability have evolved and now includes a large number of metrics (Quinn
43 and Collie, 2005; Hilborn et al., 2015; Donohue et al., 2016), the equilibrium-
44 based concept of MSY, as a target or as a threshold (Mace, 2001), remains
45 at the core of fishing management policies.

46 However, stability of exploited populations dynamics is not guaranteed.
47 Hsieh et al. (2006) showed empirically that increased fishing pressure had
48 a destabilising effect on populations in the sense that it tends to increase
49 abundance fluctuations. There is a growing debate concerning the processes
50 implicated in this destabilisation (Shelton and Mangel, 2011; Sugihara et al.,
51 2011; Rouyer et al., 2012) but Anderson et al. (2008) argued that increased
52 fluctuations were probably due to intrinsic dynamical effects associated to
53 changes in life-history parameters (*e.g.* intrinsic growth rate) in response to
54 fishing.

55 Beside the binary opposition between stable and unstable attractors in
56 population dynamics, the conceptually neighbouring notion of resilience, de-
57 fined as an inverse return-time to the equilibrium Pimm (1984), have impor-
58 tant management implications and is arousing a growing interest in ecological
59 literature (Grimm and Calabrese, 2011). Key questions related to this notion
60 are (i) whether or not ecological systems are likely to recover from a perturba-
61 tion fast enough so that the equilibrium-based approach remain meaningful,
62 and (ii) how exploitation and management are likely to affect this recovering
63 capacity. Several theoretical studies have thus recently explored the effect
64 of harvesting on resilience in relation with yields in single structured popu-
65 lation models (Lundström et al., 2019), in prey-predator systems (Tromeur
66 and Loeuille, 2017) or in tri-trophic food-chains Kar et al. (2019).

67 Many fish populations characterised by birth-pulse growth with well dis-

68 tinct cohorts (Laurec and Le Guen, 1981) are straightforwardly modelled
69 by the use of stock-recruitment relationships (Ricker, 1954). In this kind of
70 models, recruitment is a discrete event and is well represented by difference
71 equations. Such models are known to allow cyclic and chaotic dynamics even
72 for a single population (May, 1975) and lead to very complex dynamics (Tang
73 and Chen, 2002). This stresses out the importance of the mathematical formalism
74 employed and suggests that stability properties should not be taken
75 for granted when deriving reference points such as MSY.

76 A drawback of the use of stock recruitment relationships is the fact
77 that they synthesise in a single equation a large number of life-history processes
78 occurring at the youngest stages of individuals' life (Needle, 2002).
79 In Ricker (1954) pioneer work for example, maturation and recruitment are
80 confounded. However, life-history features such as maturation delay (Cole,
81 1954; Tuljapurkar, 1990; Koons et al., 2008) can have a large impact on the
82 population dynamics. Timing and duration of density-dependent processes,
83 including at time-scales shorter than one year, are also likely to have important
84 consequences (Ratikainen et al., 2007). For example, timing of seasonal
85 harvesting is known to affect the value of MSY (Kokko and Lindström, 1998;
86 Xu et al., 2005) and the stability of population equilibrium (Cid et al., 2014).
87 However, intra-annual processes are generally ignored in practice when deriving
88 reference points for harvested fish populations. This constitutes in itself
89 a specific form of uncertainty in models, which is likely to have important
90 management implications (Ratikainen et al., 2007).

91 In this study, we consider that stability *sensu stricto* and resilience are
92 key properties of sustainability. Here, we propose a theoretical model of
93 a single harvested population submitted to birth-pulse growth and inter-
94 stage density-dependence of juveniles. The latter proceeds by cannibalism
95 (or other induced mortality) of immature individual by mature ones, which
96 is well documented in a number of fish populations (Smith and Reay, 1991)
97 including some of importance for exploitation such as cod (Bogstad et al.,
98 1994; Uzars and Plikshs, 2000), and is known to be a major source of instability
99 in populations (Ricker, 1954). Our aim is to use this model to investigate
100 the consequences of the description at intra-annual time-scale of two
101 critical processes, namely (i) maturation and (ii) recruitment, on long-term
102 yields and their sustainability. A particular attention is given to the effect
103 of these processes on the MSY. The first process investigated, maturation,
104 is a purely biological process of critical importance that could not be controlled
105 by management. Maturation is tightly linked to density-dependence,

106 which is generally supposed to affect strongly immature individuals (Ricker,
107 1954; Rindorf et al., 2022), and to reproduction. It is subject to uncertainty,
108 given that knowledge for real species is generally available on a yearly basis
109 only (ICES, 2018). On the contrary, the second process, recruitment, de-
110 fined as the young fish arrival in the exploited portion of the population, can
111 be considered as a management control variable in the sense that it is par-
112 tially dependent on fishing equipment and behavior (Laurec and Le Guen,
113 1981). As being related to exploitation, it is likely to have consequences on
114 long-term yields and MSY.

115 This model and the whole set of hypotheses are presented in section
116 2. We then make the link between the monthly and yearly dynamics in
117 section 3, by showing that the dynamics can be represented by a first order
118 difference equation system. It is then possible to compute an inter-annual
119 equilibrium and to study his property within the classical dynamical system
120 theory framework. The modelling approach exposed in these sections is one
121 the main points of the present paper. In particular, we stress on the idea that
122 if we develop here an application constrained by a number of assumptions
123 that limit its generality, we opened the door to the development of alternative
124 models with varied assumptions but based on the same approach. In section
125 4, we give some details concerning the equilibrium properties of interest. We
126 then apply our model to a real population with data for the Bay of Biscay
127 sole (*Solea solea*). These applications are presented in section 5. Finally, our
128 findings are discussed in section 6.

129 2. Models & analysis

130 2.1. Construction of a properly-structured population model with a monthly 131 time-step

132 2.1.1. Population & time structure

133 Throughout this study, we model the monthly discrete dynamics of a
134 marine population exploited by fishing from a particular biological devel-
135 opment stage (recruited individuals). The population is described with a
136 structured abundance at each month t , represented by the vector $\underline{N}(t)$ with
137 $t = 1, \dots, +\infty$. Let us assume that in their life-time, individuals go through
138 three structuring events: (i) reproduction (*i.e.* production of immature indi-
139 viduals from mature ones), (ii) maturation (*i.e.* transformation of immature
140 individuals into mature ones) and (iii) recruitment. The latter is defined
141 (Laurec and Le Guen, 1981) as the entry of individuals into the exploited

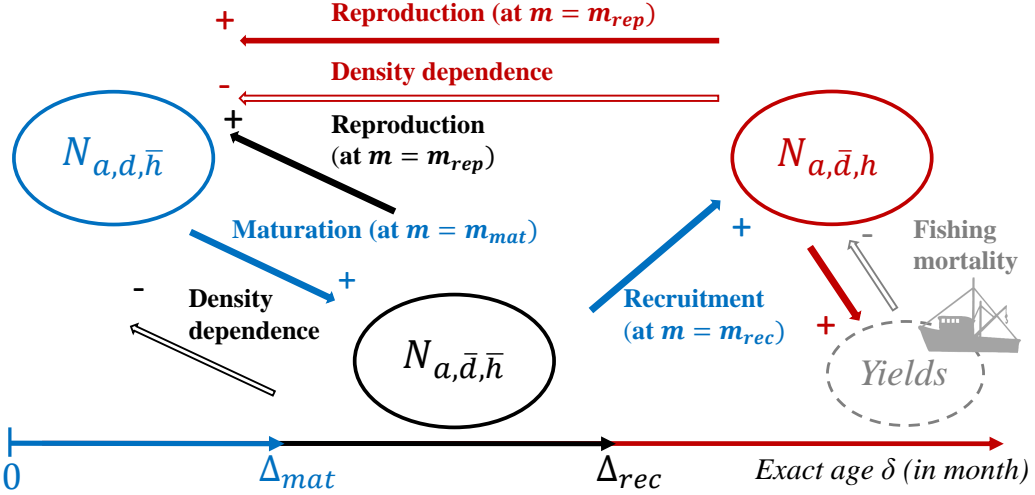


Figure 1: Conceptual view of the interactions between individuals and their influence on yields. Index $\{a = 0, \dots, > a_{rec}\}$ stands for round age in years, index $\{d, \bar{d}\}$ stands for density-dependence and index $\{h, \bar{h}\}$ stands for accessibility to fishing. Three groups must be considered depending of exact age δ (in months) of individuals : $\delta < \Delta_{mat}$ (in blue), $\Delta_{mat} \leq \delta < \Delta_{rec}$ (in black) and $\Delta_{rec} \leq \delta$ (in red). Depending on Δ_{mat} and Δ_{rec} , the relative duration of each fraction of the population will vary and have consequences on yields and their sustainability.

142 portion of the population. For sake of simplicity we assume that only mature
 143 individuals are exploited, *i.e.* maturation occurs before recruitment.

144 Contrarily to annual models where the life-cycle events undergone by
 145 individuals are assumed simultaneous, we assume here that new-born indi-
 146 viduals mature and recruit after a fixed number of months noted Δ_{mat} and
 147 Δ_{rec} respectively (as represented on time arrow in figure 1). Between two
 148 successive time-steps t and $t+1$, events happening in individuals lives depend
 149 on their exact age δ (in months) in comparison with Δ_{mat} and Δ_{rec} . Imma-
 150 ture individuals ($\delta \leq \Delta_{mat}$) are unable to reproduce, are not exploited and
 151 are assumed to undergo each month t a density-dependent mortality from
 152 mature individuals. Mature individuals ($\delta > \Delta_{mat}$) are able to reproduce
 153 and are assumed to undergo each month a constant natural mortality. Re-
 154 cruited individuals ($\delta > \Delta_{rec}$) undergo an additional fishing mortality and
 155 contribute to yields.

156 As represented in figure 1, the result of this distinction between immature,
 157 mature, unharvested and harvested individuals is that three homogeneous
 158 groups of individuals (represented in different colors on the figure) interact

159 with each other in different ways. Depending on the value of Δ_{mat} and Δ_{rec} ,
160 the relative importance of each process is expected to differ. First, density-
161 dependence is expected to have a larger effect on the overall dynamics if
162 Δ_{mat} is large. The relative position of Δ_{rec} to Δ_{mat} controls the amount of
163 time spent by mature individuals in the unspoiled situation characterized by
164 a higher survival rate than immature and recruited individuals. The longer
165 this duration time ($\Delta_{rec} - \Delta_{mat}$) is, the more numerous mature protected
166 individuals are, hence fostering reproduction. However it also affects the
167 number of immature individuals through the capacity of fishing to modulate
168 the effect of natural compensation within the population by removing can-
169 nibalistic adults. Indeed, individuals of age $\Delta_{mat} \leq \delta < \Delta_{rec}$ do not undergo
170 fishing mortality but exerts density-dependent mortality on immature ones.

In order to investigate the effect of the intra-annual timing of population structuring events ((i),(ii) and (iii) detailed above) on the long-term dynamics, we define the annual cycle as the repetition of a reproduction event. For simplicity reasons and without losing in genericity, we assumed that reproduction occurs at month $m_{rep} = 12$. Δ_{mat} and Δ_{rec} can be expressed as:

$$\begin{aligned}\Delta_{mat} &= 12 a_{mat} + m_{mat} \\ \Delta_{rec} &= 12 a_{rec} + m_{rec}\end{aligned}$$

171 where m_{mat} and m_{rec} are the respective months where maturation and re-
172 cruitment happen each year, and a_{mat} and a_{rec} are the respective number
173 of whole years before these events happen in individuals' life. We have
174 $1 \leq m_{mat} \leq m_{rep} = 12$ and $1 \leq m_{rec} \leq m_{rep} = 12$. Assuming $\Delta_{mat} \leq \Delta_{rec}$,
175 we also have $a_{mat} \leq a_{rec}$.

176 To switch from the time step t to a calendar time, We also define a
177 bijective function f which to each time-step t associates a value of month m
178 and year y :

$$\begin{aligned}f : \mathbb{N}^{+*} &\longrightarrow \{1, \dots, m_{rep} = 12\} \times \mathbb{N}^+, \\ f(t) &= (m, y), \\ m &= t - \lfloor \frac{t-1}{m_{rep}} \rfloor \times m_{rep} \\ y &= \lfloor \frac{t-1}{m_{rep}} \rfloor\end{aligned}\tag{1}$$

179 where $\lfloor \frac{t-1}{m_{rep}} \rfloor$ stands for the integer part of $\frac{t-1}{m_{rep}}$, and m_{rep} is the month at
180 the end of which reproduction happens.

181 We will then denote $\underline{N}(m, y)$ the vector of abundance at the end of month
182 m of the year y .

183 One of the main originalities of our model lies in the choice of the struc-
 184 ture of the population $\underline{N}(t)$ according to successive properly defined stages.
 185 Thanks to this particular structure, we will be able to perform easily the
 186 equilibrium and stability analysis in the next step. The stages are defined
 187 by the round age a in year (expressed as an integer number of whole years
 188 lived by individuals, as opposed to exact age δ in months), the maturity
 189 (characterised by constant instead of density-dependent natural mortality)
 190 and the accessibility to fishing. Individuals are arranged into $a_{rec} + 2$ modal-
 191 ities associated to round age a : $\{0, 1, \dots, a_{rec}, > a_{rec}\}$ (where $> a_{rec}$ stands
 192 for individuals of age strictly greater than a_{rec}), two modalities associated
 193 to maturity (density-dependant vs. independent): $\{d, \bar{d}\}$ and two modalities
 194 associated to fishing (harvested vs. unharvested) $\{h, \bar{h}\}$.

It follows from our set of assumptions that, for all t :

$$\begin{aligned} N_{a,d,\bullet}(t) &= 0, \quad \forall a > a_{mat}, \\ N_{a,\bar{d},\bullet}(t) &= 0, \quad \forall a < a_{mat}, \\ N_{a,\bullet,\bar{h}}(t) &= 0, \quad \forall a > a_{rec}, \\ N_{a,\bullet,h}(t) &= 0, \quad \forall a < a_{rec}, \end{aligned}$$

195 where $N_{a,d,\bullet}(t)$, $N_{a,\bar{d},\bullet}(t)$, $N_{a,\bullet,\bar{h}}(t)$, $N_{a,\bullet,h}(t)$ stands for the abundance of re-
 196 spectively immature, mature, harvested and unharvested individuals of round
 197 age a at time t .

Hence, we can write the vector of the structured population:

$$\underline{N}(t) = \underline{N}(m, y) = \begin{pmatrix} N_{0,d,\bar{h}}(m, y) \\ \vdots \\ N_{a_{mat},d,\bar{h}}(m, y) \\ N_{a_{mat},\bar{d},\bar{h}}(m, y) \\ \vdots \\ N_{a_{rec},\bar{d},\bar{h}}(m, y) \\ N_{a_{rec},\bar{d},h}(m, y) \\ N_{>a_{rec},d,h}(m, y) \end{pmatrix}$$

198 Figure 2 gives a schematic view of the complete population and time structure
 199 of our model.

200 2.1.2. Description of the monthly dynamics

201 As outlined above, the two modalities associated to maturity ($\{d, \bar{d}\}$) and
 202 to fishing accessibility ($\{h, \bar{h}\}$) have implications in terms of mortality.

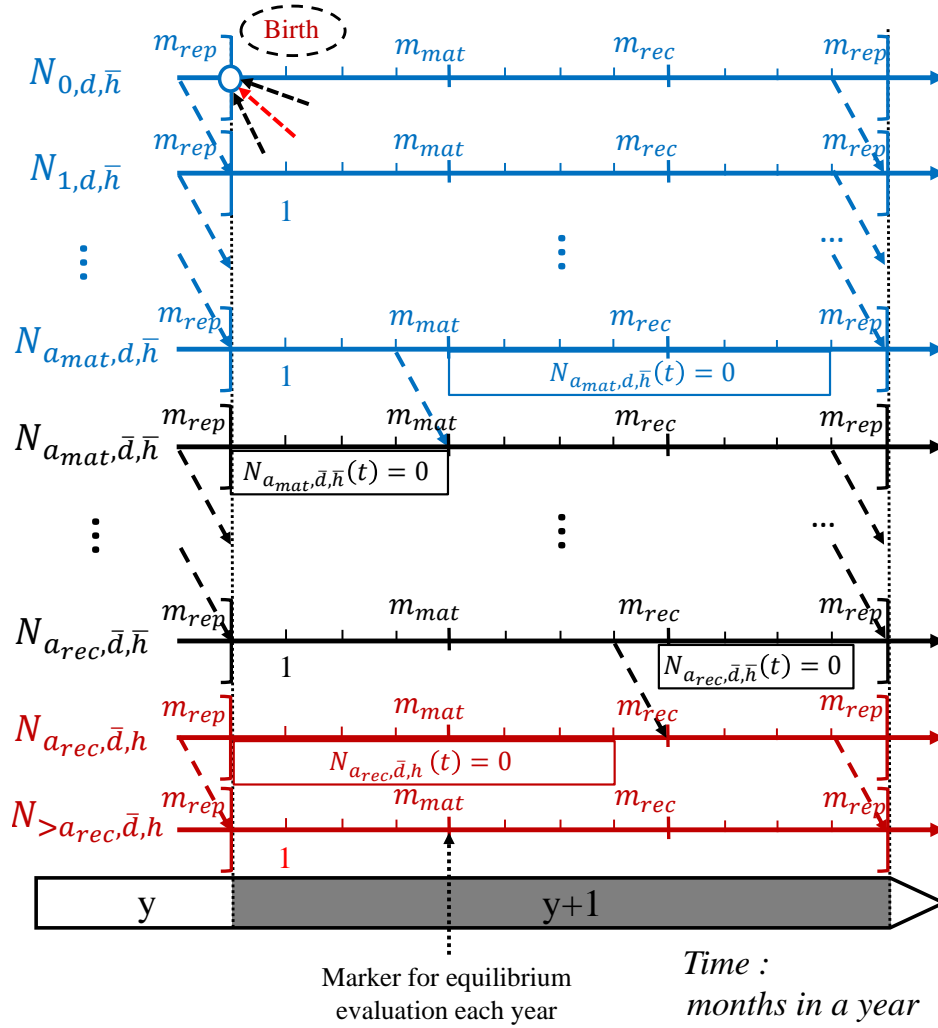


Figure 2: Conceptual view of the structured population and its dynamics represented in our model. Graduations are in months, and year succession is represented by the large arrow at the bottom, for all year y . The blue circle with dashed red and black arrows stands for the production of individuals of age 0 (“Birth”) at month $m = m_{rep}$. Dashed coloured arrows stand for class changes (*i.e.* aging, maturation or recruitment). Empty rectangles below axes mean that some classes are always empty during part of the year because of a class change happening during the year. Each month, individuals undergo a defined mortality as shown in figure 1. The position of month m_{mat} is indicated as being the month at which inter-annual equilibrium research is performed, for all year y .

203 We model explicitly a density-dependent mortality of immature individu-
 204 als at each time step, assuming after Ricker (1954) that mortality of immature
 205 individuals increases with the number of mature individuals. For the sake of
 206 simplicity, let the mortality of immature individuals between t and $t + 1$ be:

$$M_d(t + 1) = \mu N_{\bullet, \bar{d}, \bullet}(t) + \omega \quad (2)$$

207 where μ and ω are two positive constants and $N_{\bullet, \bar{d}, \bullet}(t)$ is the sum of mature
 208 individuals of all ages accessible to fishing at time t . The derived survival
 209 rate of immature individuals is expressed as: $S_d(t + 1) = e^{-M_d(t+1)}$.

210 Let the natural and fishing mortalities of mature individuals between
 211 time-steps t and $t + 1$ be two positive constants $M_{\bar{d}}$ and F . The derived
 212 survival rates for mature individuals, depending on if they are harvested or
 213 not, are expressed as $S_{\bar{d}, h} = e^{-(M_{\bar{d}}+F)}$ and $S_{\bar{d}, \bar{h}} = e^{-M_{\bar{d}}}$.

214 For each t , switching from t to (m, y) the abundance of the population
 215 can be analytically described from the abundance at time $t - 1$. For class
 216 $(0, d, \bar{h})$, we have for all y :

$$\begin{aligned} N_{0, d, \bar{h}}(1, y) &= N_{0, d, \bar{h}}(m_{rep}, y - 1) S_d(1, y) \\ N_{0, d, \bar{h}}(m, y) &= N_{0, d, \bar{h}}(m - 1, y) S_d(m, y), \quad \forall m \in \{2, \dots, m_{rep} - 1\} \\ N_{0, d, \bar{h}}(m_{rep}, y) &= r N_{\bullet, \bar{d}, \bullet}(m_{rep}, y) \end{aligned} \quad (3)$$

217 where r is mature individuals' fecundity and $N_{\bullet, \bar{d}, \bullet}(m_{rep}, y)$ is the sum of
 218 mature individuals at the end of month m_{rep} of year y .

219 For classes $(a1, d, \bar{h})$, $a1 \in \{1, \dots, a_{mat} - 1\}$, we have for all y :

$$\begin{aligned} N_{a1, d, \bar{h}}(1, y) &= N_{a1, d, \bar{h}}(m_{rep}, y - 1) S_d(1, y) \\ N_{a1, d, \bar{h}}(m, y) &= N_{a1, d, \bar{h}}(m - 1, y) S_d(m, y), \quad \forall m \in \{2, \dots, m_{rep} - 1\} \\ N_{a1, d, \bar{h}}(m_{rep}, y) &= N_{a1-1, d, \bar{h}}(m_{rep} - 1, y) S_d(m_{rep}, y) \end{aligned} \quad (4)$$

220 For classes (a_{mat}, d, \bar{h}) and $(a_{mat}, \bar{d}, \bar{h})$, we have for all y :

$$\begin{aligned} N_{a_{mat}, d, \bar{h}}(1, y) &= N_{a_{mat}, d, \bar{h}}(m_{rep}, y - 1) S_d(1, y) \\ N_{a_{mat}, d, \bar{h}}(m, y) &= N_{a_{mat}, d, \bar{h}}(m - 1, y) S_d(m, y), \quad \forall m \in \{2, \dots, m_{mat} - 1\} \\ N_{a_{mat}, d, \bar{h}}(m, y) &= 0, \quad \forall m \in \{m_{mat}, \dots, m_{rep} - 1\} \\ N_{a_{mat}, d, \bar{h}}(m_{rep}, y) &= N_{a_{mat}-1, d, \bar{h}}(m_{rep} - 1, y) S_d(m_{rep}, y) \end{aligned} \quad (5)$$

221 and

$$\begin{aligned}
N_{a_{mat}, \bar{d}, \bar{h}}(m, y) &= 0, \quad \forall m \in \{1, \dots, m_{mat} - 1\} \\
N_{a_{mat}, \bar{d}, \bar{h}}(m_{mat}, y) &= N_{a_{mat}, d, \bar{h}}(m_{mat} - 1, y) S_d(m_{mat}, y) \\
N_{a_{mat}, \bar{d}, \bar{h}}(m, y) &= N_{a_{mat}, \bar{d}, \bar{h}}(m - 1, y) S_{\bar{d}, \bar{h}}, \quad \forall m \in \{m_{mat} + 1, \dots, m_{rep} - 1\} \\
N_{a_{mat}, \bar{d}, \bar{h}}(m_{rep}, y) &= 0
\end{aligned} \tag{6}$$

222 Notice that, for all m , only one of these last two classes takes non-zero
223 values.

224 For classes (a_2, \bar{d}, \bar{h}) , $a_2 \in \{a_{mat} + 1, \dots, a_{rec} - 1\}$, we have for all y :

$$\begin{aligned}
N_{a_2, \bar{d}, \bar{h}}(1, y) &= N_{a_2, \bar{d}, \bar{h}}(m_{rep}, y - 1) S_{\bar{d}, \bar{h}} \\
N_{a_2, \bar{d}, \bar{h}}(m, y) &= N_{a_2, \bar{d}, \bar{h}}(m - 1, y) S_{\bar{d}, \bar{h}}, \quad \forall m \in \{2, \dots, m_{rep} - 1\} \\
N_{a_2, \bar{d}, \bar{h}}(m_{rep}, y) &= N_{a_2 - 1, \bar{d}, \bar{h}}(m_{rep} - 1, y) S_{\bar{d}, \bar{h}}
\end{aligned} \tag{7}$$

225 For classes $(a_{rec}, \bar{d}, \bar{h})$ and (a_{rec}, \bar{d}, h) , we have for all y :

$$\begin{aligned}
N_{a_{rec}, \bar{d}, \bar{h}}(1, y) &= N_{a_{rec}, \bar{d}, \bar{h}}(m_{rep}, y - 1) S_{\bar{d}, \bar{h}} \\
N_{a_{rec}, \bar{d}, \bar{h}}(m, y) &= N_{a_{rec}, \bar{d}, \bar{h}}(m - 1, y) S_{\bar{d}, \bar{h}}, \quad \forall m \in \{2, \dots, m_{rec} - 1\} \\
N_{a_{rec}, \bar{d}, \bar{h}}(m, y) &= 0, \quad \forall m \in \{m_{rec}, \dots, m_{rep} - 1\} \\
N_{a_{rec}, \bar{d}, \bar{h}}(m_{rep}, y) &= N_{a_{rec} - 1, \bar{d}, \bar{h}}(m_{rep} - 1, y) S_{\bar{d}, \bar{h}}
\end{aligned} \tag{8}$$

226 and

$$\begin{aligned}
N_{a_{rec}, \bar{d}, h}(m, y) &= 0, \quad \forall m \in \{1, \dots, m_{rec} - 1\} \\
N_{a_{rec}, \bar{d}, h}(m_{rec}, y) &= N_{a_{rec}, \bar{d}, h}(m_{rec} - 1, y) S_{\bar{d}, h} \\
N_{a_{rec}, \bar{d}, h}(m, y) &= N_{a_{rec}, \bar{d}, h}(m - 1, y) S_{\bar{d}, h}, \quad \forall m \in \{m_{rec} + 1, \dots, m_{rep} - 1\} \\
N_{a_{rec}, \bar{d}, h}(m_{rep}, y) &= 0
\end{aligned} \tag{9}$$

227 As well as for classes (a_{mat}, d, \bar{h}) and $(a_{mat}, \bar{d}, \bar{h})$, only one these last two
228 classes takes non-zero values, for all m .

229 Finally, for class $(> a_{rec}, \bar{d}, h)$, we have for all y :

$$\begin{aligned}
N_{>a_{rec}, \bar{d}, h}(1, y) &= N_{>a_{rec}, \bar{d}, h}(m_{rep}, y - 1) S_{\bar{d}, h} \\
N_{>a_{rec}, \bar{d}, h}(m, y) &= N_{>a_{rec}, \bar{d}, h}(m - 1, y) S_{\bar{d}, h}, \quad \forall m \in \{2, \dots, m_{rep} - 1\} \\
N_{>a_{rec}, \bar{d}, h}(m_{rep}, y) &= [N_{>a_{rec}, \bar{d}, h}(m_{rep} - 1, y) + N_{a_{rec}, \bar{d}, h}(m_{rep} - 1, y)] S_{\bar{d}, h}
\end{aligned} \tag{10}$$

230 Notice that above equations were detailed for the most complex version
231 of the model *i.e.* when $1 < a_{mat}$ and $1 < a_{rec} - a_{mat}$. However, they can be
232 easily reduced to any version of the model with $0 \leq a_{mat} \leq a_{rec}$ as long as
233 $\Delta_{mat} \leq \Delta_{rec}$.

234 This analytical model is implemented in R and reproduces correctly the
 235 discrete monthly dynamics of exploited marine population (see figure 3 for
 236 an illustration).

237 2.2. Connecting intra-annual and inter-annual time-scales

238 2.2.1. From a monthly dynamics to an annual dynamics

239 To investigate equilibrium properties of the model, we need to study the
 240 long-term evolution of the population abundance. Let $\underline{N}(m, y)$ be assessed at
 241 a particular arbitrary chosen month each year. Without the loss of generality,
 242 we set m at m_{mat} . We will see below that the choice of m_{mat} allows to reduce
 243 the dimension of the studied system. We therefore study the dynamics of
 244 $\underline{N}(m_{mat}, y)$ with respect to y .

First, it comes from equations (5), (6), (8) and (9) that at $m = m_{mat}$, two
 elements of $\underline{N}(m_{mat}, y)$ are always empty. Depending on the the ordering of
 m_{mat} and m_{rec} we have for all y :

$$\begin{cases} N_{a_{mat}, d, \bar{h}}(m_{mat}, y) = N_{a_{rec}, \bar{d}, h}(m_{mat}, y) = 0, & \text{if } m_{mat} \leq m_{rec} \\ N_{a_{mat}, d, \bar{h}}(m_{mat}, y) = N_{a_{rec}, \bar{d}, \bar{h}}(m_{mat}, y) = 0, & \text{else} \end{cases}$$

245 Therefore, we can always remove elements of $\underline{N}(m_{mat}, y)$ without losing in-
 246 formation while performing the analysis of the annual dynamics.

247 Then, we can derive from equations (3-10) the expression of $\underline{N}(m_{mat}, y+1)$
 248 for all y . If $m_{mat} \leq m_{rec}$, we get the system (17), expressed in table 3. Here,
 249 we focus on this particular case but the same reasoning is feasible for the
 250 alternative case when $m_{mat} > m_{rec}$ (see Appendix A for the associated
 251 developments).

252 Given some proper simplifications, $N_{\bullet, \bar{d}, \bullet}(m_{rep}, y)$, $\prod_{m=m_{mat}+1}^{m_{rep}} S_d(m, y)$
 253 and $\prod_{m=1}^{m_{mat}} S_d(m, y+1)$ can be formulated as functions of $\underline{N}(m_{mat}, y)$ (see
 254 Appendix B for proof) and system (17) can be expressed as a first-order
 255 difference system of dimension $a_{rec} + 2$. For all y , we get :

$$\left\{ \begin{array}{l} N_{0, d, \bar{h}}(m_{mat}, y + 1) = r \alpha_1 \Psi(\underline{N}_{\bar{d}}(m_{mat}, y)) e^{-\varphi_1(\underline{N}_{\bar{d}}(m_{mat}, y))} \\ N_{a_1, d, \bar{h}}(m_{mat}, y + 1) = \alpha_2 N_{a_1-1, d, \bar{h}}(m_{mat}, y) e^{-\varphi_2(\underline{N}_{\bar{d}}(m_{mat}, y))} \\ N_{a_2, \bar{d}, \bar{h}}(m_{mat}, y + 1) = \sigma N_{a_2-1, \bar{d}, \bar{h}}(m_{mat}, y) \\ N_{>a_{rec}, \bar{d}, h}(m_{mat}, y + 1) = \nu N_{>a_{rec}, \bar{d}, h}(m_{mat}, y) \\ \quad \quad \quad + \rho N_{a_{rec}, \bar{d}, \bar{h}}(m_{mat}, y) \end{array} \right. \quad (11)$$

256 with $a1 = 1, \dots, a_{mat}$ and $a2 = a_{mat} + 1, \dots, a_{rec}$. $\Psi(N_{\bar{d}}(t))$ is the number
 257 of spawner and $\varphi_n(N_{\bar{d}}(t))$ is a density-dependence function (see table 4 for
 258 detailed expressions). Moreover :

259 — $\Psi(N_{\bar{d}}(t))$ and $\varphi_n(N_{\bar{d}}(t))$ are linear combinations of $(N_{a,\bar{d},\bar{h}}(t))_{a=a_{mat}, \dots, a_{rec}}$
 260 and $(N_{a,\bar{d},h}(t))_{a=a_{rec}, >a_{rec}}$.

261 — $\alpha_n, \sigma, \nu, \rho$ are positive constants.

262 At this stage, given this first order difference equations system (11) we
 263 can perform easily the equilibrium and stability analysis of the population.

264 2.2.2. Expressions of equilibrium

In this study, we are interested in the equilibrium properties of $N(m_{mat}, y)$
 described by system (11). N^* is an inter-annual equilibrium if and only if it
 verifies:

$$N(m_{mat}, y + 1) = N(m_{mat}, y) = N^*(m_{mat})$$

265 System (11) always admits only one non-trivial equilibrium which is the
 266 solution of:

$$\begin{cases} N_{a_{mat},\bar{d},\bar{h}}^*(m_{mat}) = r \alpha_1 \alpha_2^{a_{mat}} \Psi(N_{\bar{d}}^*(m_{mat})) \\ \quad \times e^{-\varphi_1(N_{\bar{d}}^*(m_{mat})) - a_{mat} \varphi_2(N_{\bar{d}}^*(m_{mat}))} \\ N_{a2,\bar{d},\bar{h}}^*(m_{mat}) = \sigma N_{a2-1,\bar{d},\bar{h}}^*(m_{mat}) \\ N_{>a_{rec},\bar{d},h}^*(m_{mat}) = \nu N_{>a_{rec},\bar{d},h}^*(m_{mat}) + \rho N_{a_{rec},\bar{d},\bar{h}}^*(m_{mat}) \end{cases} \quad (12)$$

267 with $N_{\bar{d}}^*(m_{mat}) = {}^t (N_{a_{mat},\bar{d},\bar{h}}^*(m_{mat}), N_{a2,\bar{d},\bar{h}}^*(m_{mat}), N_{>a_{rec},\bar{d},h}^*(m_{mat}))$ and $a2 =$
 268 $a_{mat} + 1, \dots, a_{rec}$;

269

270 2.3. Equilibrium properties : equilibrium yields, stability & resilience

271 2.3.1. Maximum Sustainable Yield

272 The equilibrium yield can be straightforwardly derived from the equilib-
 273 rium abundance using the classical Baranov catch equation (Baranov, 1918),
 274 given that fishing and natural mortality of mature individuals are constant :

$$Y^*(m_{mat}) = N_{\bullet,\bar{d},h}^*(m_{mat}) (1 - e^{-(M_{\bar{d}}+F)}) \frac{F}{M_{\bar{d}} + F} \quad (13)$$

275 where $N_{\bullet, \bar{d}, h}^*(m_{mat}) = N_{a_{rec}, \bar{d}, h}^*(m_{mat}) + N_{>a_{rec}, \bar{d}, h}^*(m_{mat})$ is the total number
 276 of recruited individuals at month $m = m_{mat}$ at inter-annual equilibrium.

277 The value of inter-annual equilibrium at any month $m \neq m_{mat}$ can be
 278 easily computed by applying equations (3-10) to \underline{N}^* . Hence we can compute
 279 the total annual yield as:

$$Y_T^* = \sum_{m=0}^{m_{rep}} Y^*(m) \quad (14)$$

280 where $Y^*(m)$ is the inter-annual equilibrium yield at month m .

Let us consider at present that Y_T^* depends only on the control variable F . Unfortunately the expression of $Y_T^*(F)$ is too complex to analytically calculate the maximum of $Y_T^*(.)$ and derive the Maximum Sustainable Yield (MSY). Instead we performed a numerical optimization of $Y_T^*(.)$ using Brent's method (Brent, 1973) to get the value of MSY and F_{MSY} :

$$MSY = \max(Y_T^*(F))$$

$$F_{MSY} = \arg \max_F Y_T^*(F)$$

281 2.3.2. Equilibrium stability & resilience

282 Computation of yields at equilibrium and their optimisation does not
 283 inform us on the stability of this equilibrium and hence on sustainability
 284 of yields. As we succeeded to express the whole dynamics of the structured
 285 population as first order difference equation system, we can perform easily the
 286 stability analysis of the equilibrium by studying the property of the Jacobian
 287 matrix of system (11). The inter-annual equilibrium \underline{N}^* is locally stable if
 288 and only if:

$$|\lambda_i| < 1, \quad \forall i \in \{1, \dots, a_{rec} + 2\} \quad (15)$$

289 where $|\lambda_i|$ is the modulus of the i^{th} eigen value of the Jacobian matrix of
 290 the system at inter-annual equilibrium. See Appendix C for the general
 291 expression of the Jacobian matrix of system (11).

292 Expressions of eigenvalues are expected to be too complex to be ana-
 293 lytically tractable and interpretable especially when the system is of large
 294 dimension. We therefore calculated numerically the eigenvalues to detect
 295 stability changes using the basic "eigen" function of R software which relies
 296 on LAPACK routines (Anderson et al., 1999).

297 The stability properties of equilibrium depends on parameters. Hence,
 298 stability, instability, and extinction domains (*i.e* the set of parameters for
 299 which the equilibrium is stable, unstable and lesser than zero, respectively)
 300 represent volumes in a parameter space. In particular, we pay attention
 301 of the surfaces of stability, instability and extinction in the $r \times F$ plan.
 302 Variations along the r axis can represent differences of fecundity between
 303 stocks or differences in reproductive success for a same stock, whereas F is
 304 the main control variable when dealing with exploited systems. In such a
 305 plan, it is also possible to plot the value of F_{MSY} if it does exist, for each
 306 value of r .

307 When no destabilisation occurs, the stability properties of the equilibrium
 308 can be more finely defined by considering the resilience of this equilibrium.
 309 *Sensu* Pimm (1984), a system is all the more resilient that the characteristic
 310 return-time to equilibrium is short. This notion is related to stability and
 311 can be studied with the same mathematical tools. Hence, in discrete time
 312 this return-time is given by (Beddington et al., 1976):

$$\tau = \frac{1}{1 - |\lambda_{max}|} \quad (16)$$

313 where $|\lambda_{max}|$ is the modulus of the leading eigen value of the system. The
 314 return-time is one if the system returns instantaneously to his equilibrium
 315 and infinite when the equilibrium becomes unstable.

316 Considering that return-time is, just as yields, a function of F , we can define
 317 the same way as for F_{MSY} , a mortality F_{RMV} for ‘Resilience Maximising
 318 Yield’ for which resilience is maximum, *i.e.* associated return-time (denoted
 319 *MiRT*) is minimum. Mathematically:

$$F_{RMV} = \arg \min_F \tau(F)$$

$$MiRT = \tau(F_{RMV})$$

320 2.3.3. Sensitivity of MSY , stability domain and resilience to timing of mat- 321 uration and recruitment

322 Here, our aim is to assess the sensitivity of the equilibrium properties,
 323 namely MSY , F_{MSY} , $MiRT$ and F_{MiRT} values, extinction and instability
 324 domains (quantified by the areas under the curves A_{ext} and A_{stab} respectively)
 325 to intra-annual variations of maturation and recruitment, represented by pa-
 326 rameters Δ_{mat} and Δ_{rec} . The first one must be considered as a biological

327 parameter subject to epistemic uncertainty whereas the second can be con-
 328 sidered as a control variable insofar it is, at least theoretically, possible not to
 329 catch individuals under a defined age. Values for Δ_{mat} and Δ_{rec} are allowed
 330 to vary in a time-span shorter than one year. Such intra-annual dynamics are
 331 generally not taken into account when computing reference points for fish-
 332 eries management. Indeed, for most fish populations, information concerning
 333 maturation and recruitment are available on yearly basis only (ICES, 2018).
 334 We perform a variance-based sensitivity analysis based on 1) an experimen-
 335 tal design and 2) sensitivity indices associated to Δ_{mat} and Δ_{rec} (the inputs
 336 of the model) on each metric MSY , F_{MSY} , A_{ext} and A_{stab} (model outputs)
 337 derived from an ANOVA. Then we can compute the sensitivity index of each
 338 parameter, both for principal effect and interactions (see *e.g.* Faivre et al.
 339 (2013) for full details on the method). The experimental design is build com-
 340 bining all possibles values of Δ_{mat} and Δ_{rec} within defined ranges. These two
 341 parameters take values expanding on a time-span less or equal to one year,
 342 corresponding to realistic values for the Bay of Biscay sole (see table 5).

343 3. Application to the Bay of Biscay sole

344 3.1. Origin of data

345 Our model is general and flexible enough to be applied to any exploited
 346 population as long as maturation occurs before recruitment. However, for
 347 illustration purposes and also because the complexity of our model preclude
 348 the derivation of analytical results concerning stability or yield optimisation,
 349 we performed a numerical application.

350 In order to get numerical simulations somewhat realistic, we parameter-
 351 ized our model on the ground of (i) published life-history parameters, and (ii)
 352 stock assessment data, for the sole (*Solea solea*) in the Bay of Biscay. Sole is
 353 a highly valued demersal species targeted by a number of fishing fleets in the
 354 Bay of Biscay (Vigier et al., 2022) and is subject to a stock assessment by
 355 the International Council for the Exploration of the Sea (ICES) on a yearly
 356 basis (ICES, 2018).

357 All but two parameters where extracted directly from literature. Numerical
 358 values of all the parameters used in simulation, with their origin and
 359 meaning are presented in table 5.

360 The last two parameters μ and ω , which govern density-dependence, were
 361 estimated based on ICES stock assessment results (ICES, 2018; table 7.10
 362 p.277). The basic idea here is to fit a custom stock-recruitment relationship

363 on data (see Appendix D for more details). To distinguish the effect of
 364 intra-annual dynamics from the effect of density-dependence, μ and ω are
 365 reestimated at each change of Δ_{mat} and Δ_{rec} when assessing the sensitivity
 366 of the system to these parameters. μ and ω values obtained for each pair
 367 $(\Delta_{mat}, \Delta_{rec})$ considered are given in tables 6 and 7.

368 3.2. Monthly dynamics and inter-annual equilibrium of abundance

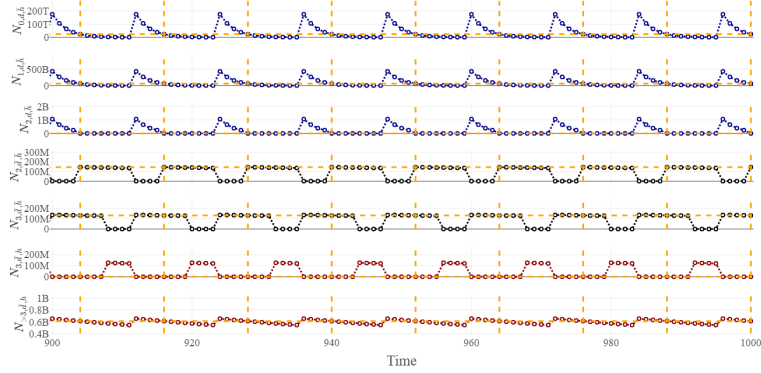
369 Once the model is fully parameterised, it is possible on the one hand
 370 to simulate the monthly dynamics with respect to equations (3-10), and on
 371 the other hand to compute the theoretical inter-annual equilibrium vector
 372 $\underline{N}^*(m_{mat})$. Both the abundance time series and the equilibrium abundance
 373 for each class are computed for the example of the sole of the Bay of Biscay
 374 (figure 3). In this example, the dynamics converges to a stable annual cycle
 375 represented by the inter-annual equilibrium $\underline{N}^*(m_{mat})$ (in dashed horizontal
 376 lines). The value of this equilibrium is expected to vary with model param-
 377 eters (see Appendix E for variations of $N_{amat, \bar{d}, \bar{h}}^*$ and of the sum of spawners
 378 for Bay of Biscay sole as a function of F , Δ_{mat} and Δ_{rec}).

379 3.3. Sensitivity of MSY to timing of maturation and recruitment

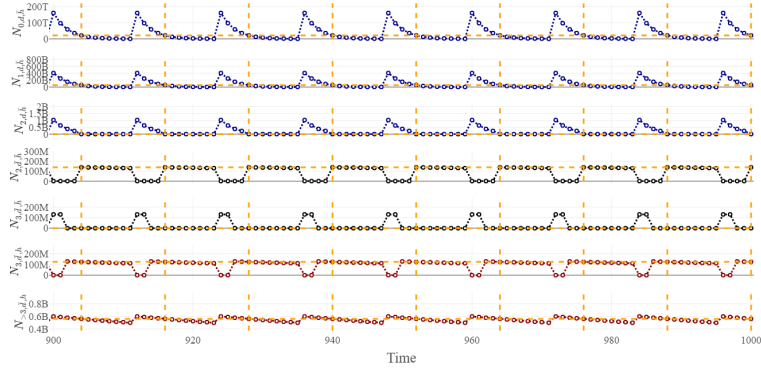
380 The equilibrium yield of the sole of the Bay of Biscay is computed for a
 381 range of monthly fishing mortality $F \in [0; 0.4]$ and is numerically optimised
 382 as a function of F to get the MSY. We assessed their sensitivity to Δ_{mat} and
 383 Δ_{rec} varying in a range shorter than 12 months, with $\Delta_{mat} = 25, 26, \dots, 33$
 384 (*i.e.* between the first and ninth month of the year) and $\Delta_{rec} = 37, 38, \dots, 46$.

385 First, it appears clearly that the value of MSY is much more sensitive to
 386 variations of Δ_{mat} ($SI = 0.98$) than to Δ_{rec} whereas the position of F_{MSY} is
 387 sensitive to both ($SI = 0.56$ for Δ_{mat}) as shown in figure 4a and 4b. In fact,
 388 it appears that whereas MSY undergoes large variations when Δ_{mat} or even
 389 Δ_{rec} are varied, F_{MSY} remains remarkably constant around $F = 0.01$.

390 When Δ_{mat} only varies, the duration of immature phase and mature
 391 unharvested vary (respectively in blue and black on figure 1). An increase
 392 in Δ_{mat} translates into a longer period where individuals are submitted to a
 393 large density-dependent mortality (empty arrows in figure 1) and a shorter
 394 period of protection from fishing for adults. In this case, as represented in
 395 figure 5a, MSY is maximum when Δ_{mat} equals 25, *i.e.* when the density-
 396 dependent phase is short. An increase of one or very few months in Δ_{mat}
 397 is sufficient to cause sharp reductions in yields and MSY. F_{MSY} , on the
 398 contrary, increases very slightly when Δ_{mat} increases.



(a) $m_{mat} \leq m_{rec}$



(b) $m_{rec} < m_{mat}$

Figure 3: Simulated asymptotic behavior of the structured model with a monthly time-step, in both configurations ($m_{mat} \leq m_{rec}$ and conversely). Only the asymptotic abundance is plotted with month time-steps from 900 to 1000 ($t \in [900; 1000]$). The theoretical inter-annual equilibrium at $m = m_{mat}$ for each elements of $\underline{N}(m, y)$ is represented with horizontal dotted lines on each subplot. Periodic repetition of month m_{mat} is represented by vertical dotted lines. Parameters are set for the Bay of Biscay sole (see Appendix D for parameterization details) and lags are set differently in each column: (a) $\Delta_{mat} = 28$ (i.e. $a_{mat} = 2$, $m_{mat} = 4$) and $\Delta_{rec} = 44$ (i.e. $a_{rec} = 3$, $m_{rec} = 8$); and (b) $\Delta_{mat} = 28$ (i.e. $a_{mat} = 2$, $m_{mat} = 4$) and $\Delta_{rec} = 38$ (i.e. $a_{rec} = 3$, $m_{rec} = 2$).

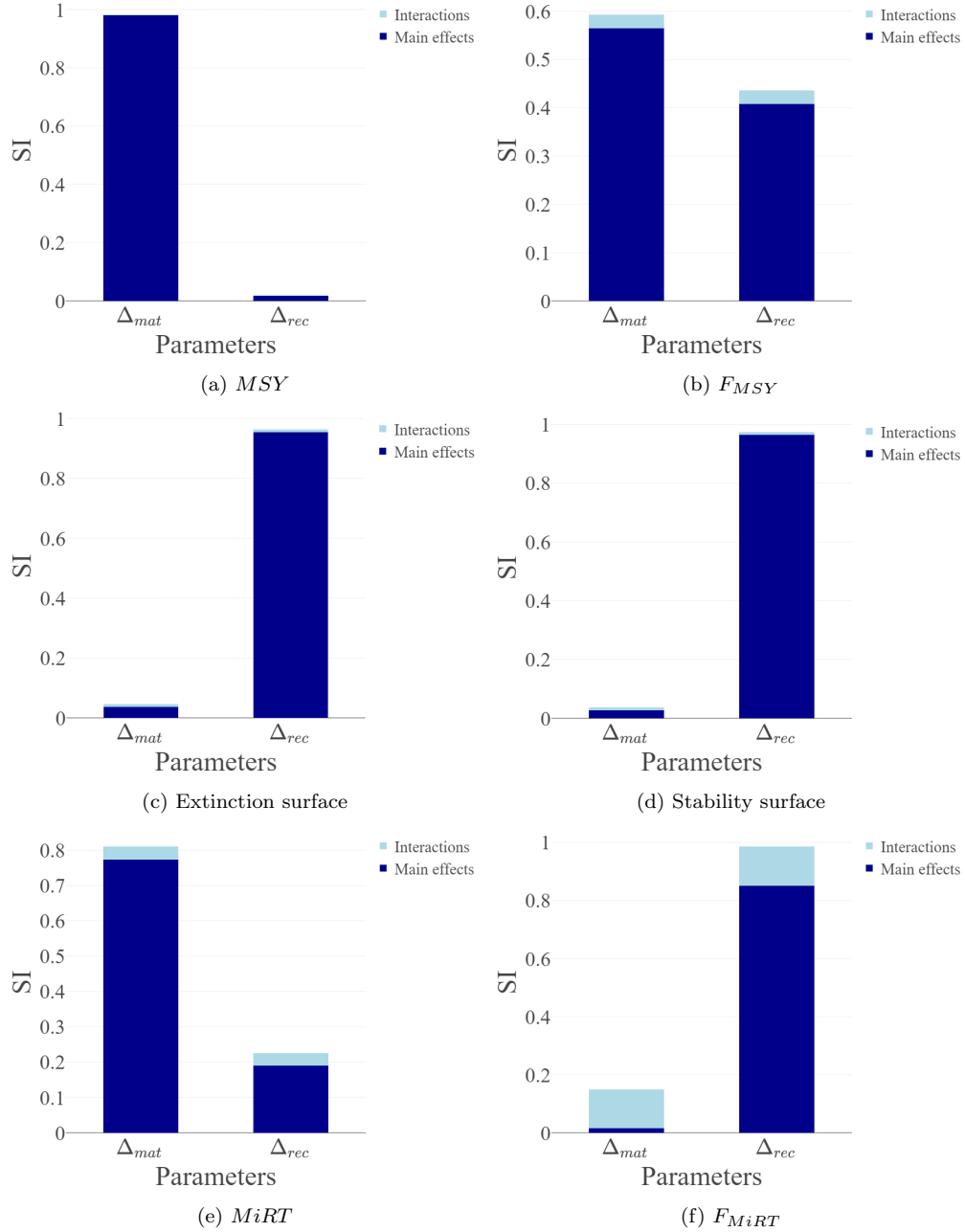


Figure 4: Sensitivity indices of parameters Δ_{mat} , Δ_{rec} for different model outputs: (a) MSY , (b) F_{MSY} , (c) surface in the $r \times F$ plan as represented in figure 6 where the population goes extinct, (d) surface in this plan where the inter-annual equilibrium is unstable, (e) $MiRT$, (f) F_{MiRT} .

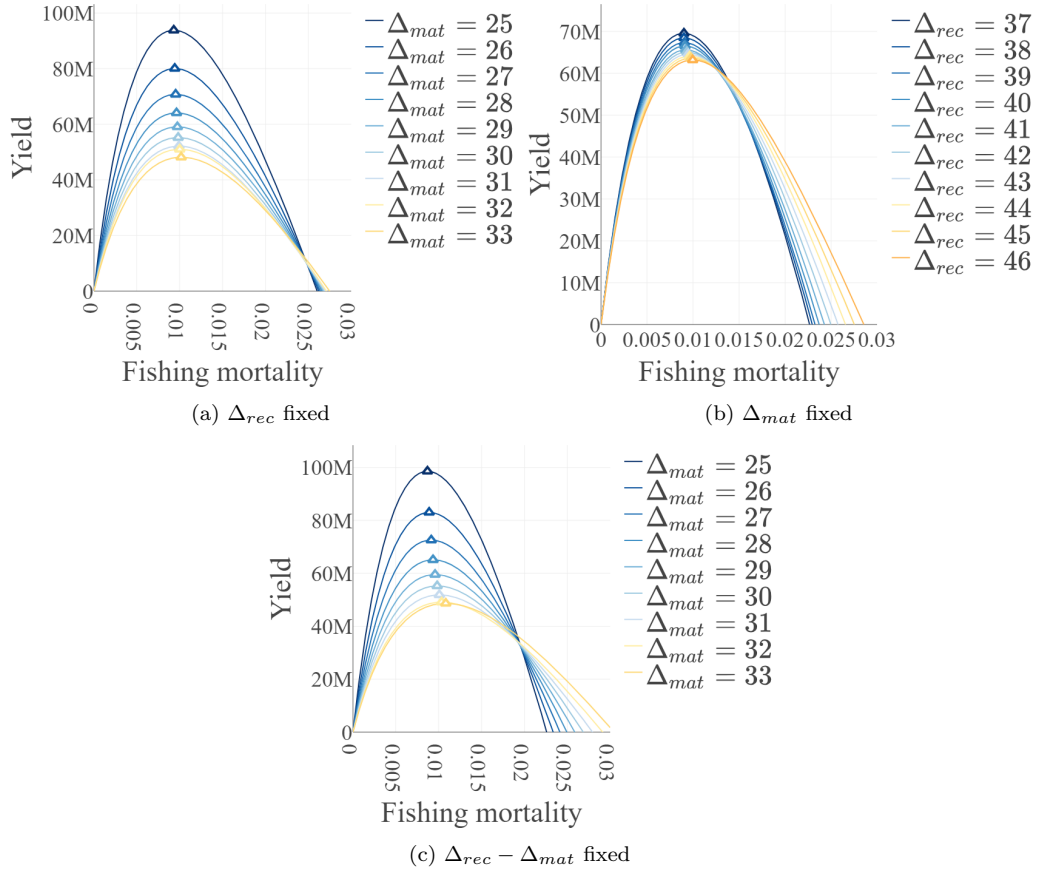


Figure 5: Total annual yields at inter-annual equilibrium as a function of fishing mortality (by month) and position of MSY when Δ_{mat} and/or Δ_{rec} vary and the system is parameterized for the sole of the Bay of Biscay. Coloured triangles correspond to MSY (numerically solved) and different colours indicate different values of Δ_{mat} and/or Δ_{rec} depending on the case: (a) Δ_{mat} vary and $\Delta_{rec} = 44$; (b) Δ_{rec} vary and $\Delta_{mat} = 28$; (c) both Δ_{mat} and Δ_{rec} vary and their difference is constant and equals 14 ($\Delta_{mat} = 25, 26, \dots, 33$; $\Delta_{rec} = 39, 40, \dots, 47$).

399 When Δ_{rec} only varies and the duration of the density-dependent phase
 400 (in blue on figure 1) is kept constant. The only modification is hence on
 401 the balance between unharvested adult phase and harvested adult phase
 402 (respectively in black and red on figure 1). This translates into a modification
 403 of the ability of fishing to modulate natural regulation of the population
 404 which can be represented by the relative importance of red and black arrows
 405 on figure 1.

406 As shown in figure 5b, an increase in Δ_{rec} is associated to a decrease in
 407 MSY but much smaller than when Δ_{mat} is varied, as well as a slight increase
 408 in F_{MSY} and extinction mortality (*i.e* the smallest value of $F > 0$ that brings
 409 null yields because of extinction of the population).

410 When Δ_{mat} and Δ_{rec} are varied jointly so that the mature unharvested
 411 phase (in black on figure 1) is constant in duration, the general shape of the
 412 curves obtained (figure 5c) presents properties of the first two ones. On the
 413 one hand, variations of MSY are large as when Δ_{mat} only is varied, but on
 414 the other hand we get an increase in extinction mortality that was observed
 415 when Δ_{rec} only was varied.

416 3.4. Sensitivity of stability domain to timing of recruitment and maturing

417 The domain of viability and of stability of the population in the $r \times F$
 418 plan is also affected when Δ_{mat} and/or Δ_{rec} vary, although the second one
 419 has a much larger effect (figure 4c and 4d). Indeed, sensitivity index of Δ_{rec}
 420 is of 0.95 for the surface of viability domain and of 0.96 for the surface of
 421 stability domain in the considered section of $r \times F$ plan, which means that
 422 most of the variance in those surfaces are explained by variations of Δ_{rec} .

423 In the three cases investigated (variations of Δ_{mat} only, Δ_{rec} only or
 424 joint variations), population can be brought to extinction by increasing F or
 425 reducing r . Equilibrium can be destabilised by increasing r or increasing F ,
 426 and F_{MSY} always increase with r .

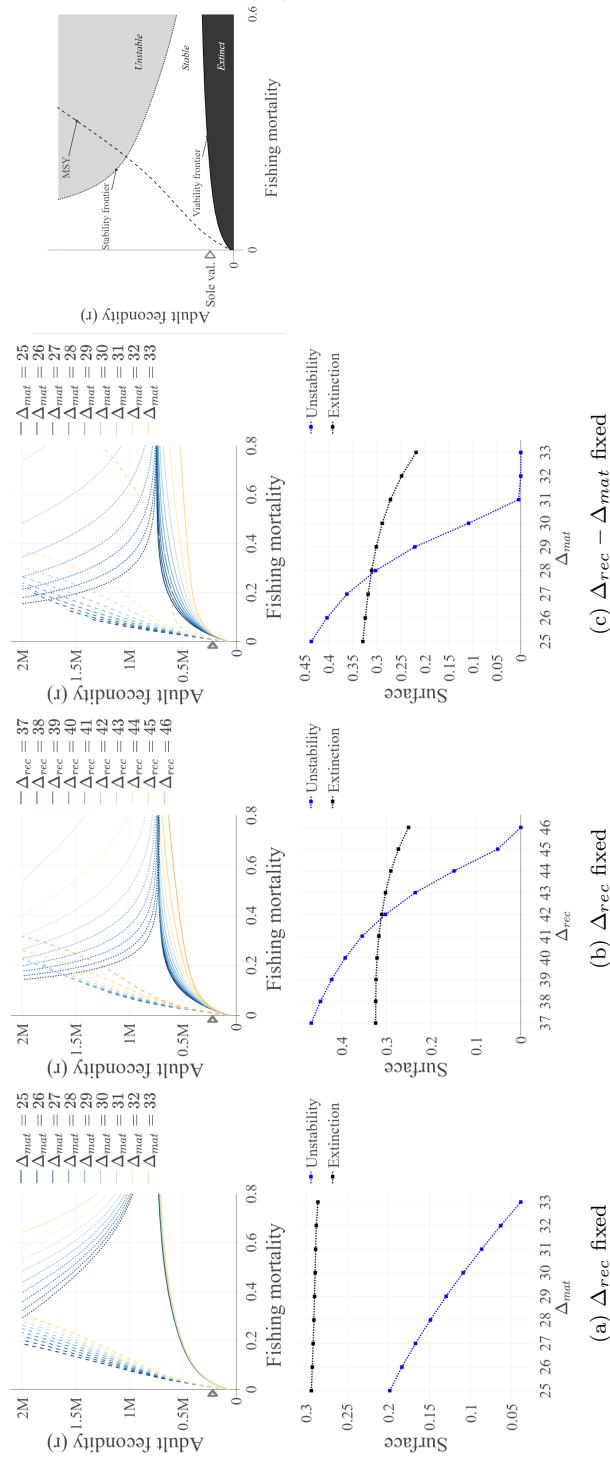


Figure 6: Stability of inter-annual equilibrium and viability domain, with associated surfaces (expressed as a proportion of the represented portion of the plan) in the $r \times F$ plane when Δ_{mat} and/or Δ_{rec} vary. All other parameters are set for the Bay of Biscay sole. For a given $(\Delta_{mat}, \Delta_{rec})$ pair corresponding to a colour shade, the solid line indicates the viability frontier, the dotted line indicates the stability frontier of the inter-annual equilibrium. The delimited zones are described schematically in table 5) is indicated by the grey triangle. Finally, the dash line indicates the position of the F_{MSY} for different values of r . The value of r for sole (cf. table 5) is indicated by the grey triangle. The three cases considered are: (a) Δ_{mat} vary and $\Delta_{rec} = 44$; (b) Δ_{rec} vary and $\Delta_{mat} = 28$; (c) both Δ_{mat} and Δ_{rec} vary and their difference is constant and equals 14 ($\Delta_{mat} = 25, \dots, 33$; $\Delta_{rec} = 39, \dots, 47$).

427 In the first case (variation of Δ_{mat} , see figure 6a), viability frontiers are al-
428 most superposed and stability surface increases slightly when Δ_{mat} increases.
429 This quite surprising result suggests that a long immature phase has a stabi-
430 lizing effect on the population, probably a consequence of spreading in time
431 density-dependent processes (as illustrated in figure 1).

432 When Δ_{rec} only varies (figure 6b), as was seen before, an increase in Δ_{rec}
433 value increases the viability surface of the population. Indeed for a same
434 value of parameter r , a higher F brings population to extinction when Δ_{rec}
435 is high. Moreover, as was stated above, a difference of one or very few months
436 can have large consequences in terms of viability. This is especially true for
437 species with large values of r .

438 Variations of Δ_{rec} also have important consequences concerning the posi-
439 tion of the stability frontier. As with Δ_{mat} variations, for a given r the value
440 of F necessary to destabilise inter-annual equilibrium is higher when Δ_{rec} is
441 high. This means that protection of mature individuals from fishing also has
442 a stabilizing effect on the population.

443 As was also stated before, the value of F_{MSY} is quite insensitive to vari-
444 ations of Δ_{mat} and Δ_{rec} , especially when r is low. By superimposing curves
445 for F_{MSY} with stability domain, we can see that MSY can in fact, at least
446 theoretically, be associated to an unstable *i.e.* non-sustainable state. How-
447 ever considering realistic values for r (of the same order of magnitude as the
448 sole of the Bay of Biscay, say 0.2M), it is clear that the population is much
449 more likely to become extinct than to get his equilibrium destabilised, given
450 the respective positions of the stability and viability frontiers (figure 6).

451 When Δ_{mat} and Δ_{rec} are varied jointly so that the mature unharvested
452 phase is constant in duration (figure 6c), differences with the pattern observed
453 for Δ_{rec} (figure 6b) concerning stability and viability frontier are small. How-
454 ever, differences exist on F_{MSY} curves. By contrast to the pattern observed
455 for Δ_{mat} variations only (figure 6a), they are interrupted when r is increased
456 beyond a certain threshold. This interruption is due to a modification of
457 the yield curve's shape, the optimum being replaced by a plateau (see figure
458 E.11 in appendices). In this configuration the MSY strictly speaking (*i.e.*
459 the optimum) was always stable in the ranges of r and F considered.

460 In difference equations models, it is well known (Ricker, 1954) that pop-
461 ulation stability can be visualised by plotting the stock-recruitment relation-
462 ship. In our model, the relation between the number of individuals partici-
463 pating to reproduction (*i.e.* the “stock”) and the associated number of
464 individuals entering the exploited portion of the population (*i.e.* the “recruit-

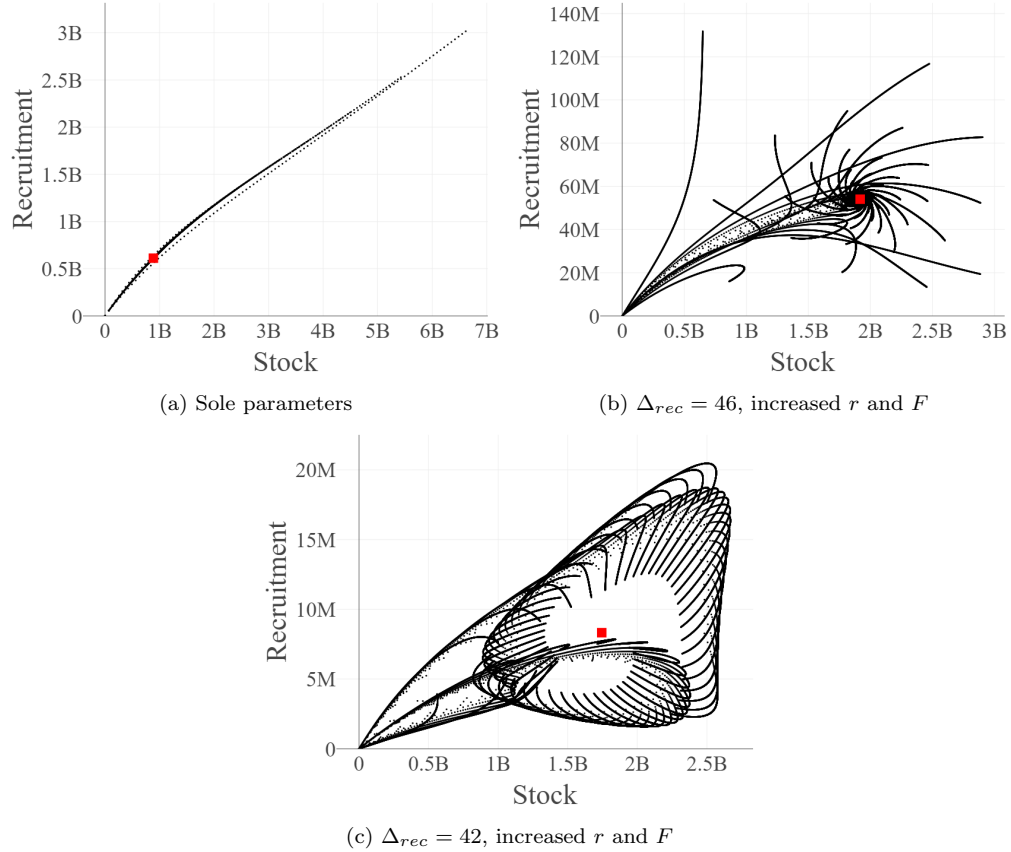


Figure 7: Stock-recruitment relationship extracted from simulated time-series of the model. Each black point represents an association of a given stock (number of mature individuals at m_{mat}) with the corresponding recruitment (recruited individuals as defined in our model) after a_{rec} years, at the same month m_{mat} . Values are simulated by running the model for 1000 time steps with 1000 initial conditions evenly distributed between a stock of 10 and 10^{10} individuals. Equilibrium stock and recruitment are represented by the red square. Different sets of parameters are tested: (a) model parameterised for sole with $\Delta_{mat} = 28$ and $\Delta_{rec} = 44$, (b) same parameters but with μ and ω re-estimated for $\Delta_{rec} = 46$, $r = 1.5 \times 10^6$, $F = 0.45$; (c) same parameters but with μ and ω re-estimated for $\Delta_{rec} = 42$, $r = 1.5 \times 10^6$, $F = 0.45$

465 ment”) emerges from density-dependent processes involving several classes of
466 individuals and occurring at different time-steps (see Appendix D for the
467 complete formulation of the relation between spawning stocks and associated
468 recruitment). However, it is possible to generate observations of recruitment
469 as a function of stock by running the model for a number of time steps with
470 different initial conditions.

471 When the model is run with realistic parameters for sole (figure 7a), which
472 corresponds to a region at the bottom-left of the parameter plan represented
473 in figure 6 (indicated in this figure by the grey triangles), the observed re-
474 lationship is monotonous and steadily increasing. It shows here no evidence
475 of decreased recruitment for high values of stock. Observations are roughly
476 arranged along a continuous curve which means that oscillations are quickly
477 damped.

478 When we move to a higher region of $r \times F$ plan presented in figure 6,
479 with $r = 1.5 \times 10^6$ and $F = 0.45$, we can observe more complex dynami-
480 cal behaviours, as well as the destabilisation of equilibrium with a decreased
481 Δ_{rec} . In the case where $\Delta_{rec} = 46$ (figure 7b) for example, which corre-
482 sponds to a stable region of the parameter space (see figure 6b) there is a
483 concentration of points around the equilibrium value which indicates stabil-
484 ity of the latter, even if large oscillations are observed before stabilisation.
485 When Δ_{rec} is decreased from 46 to 42, we move from a stable to an unsta-
486 ble region of the parameter space (see figure 6b). Then, we can observe no
487 stock-recruitment pairs in the neighbourhood of the equilibrium (figure 7c)
488 which is a clear sign of destabilisation of the equilibrium. Instead, we get
489 very complex trajectories which indicate apparition of chaotic oscillations.

490 Although we observed that, especially for the two cases with increased
491 r and F , a single value of stock could be associated to a set of possible
492 recruitment values, we can recognise in the scatter-plots the apparition of
493 the typical dome-shaped stock-recruitment relationship when moving from
494 a very stable to a less stable and unstable region of the parameter space
495 (figures 7a-7c).

496 3.5. Sensitivity of the resilience to timing of recruitment and maturing

497 Resilience also is affected by intra-annual variations of Δ_{mat} and Δ_{rec} .
498 Once again, the influence of Δ_{rec} is more pronounced than the influence
499 of Δ_{mat} . First of all it must be noticed that for most of the $(\Delta_{mat}, \Delta_{rec})$
500 pairs considered, we had F_{MiRT} very close to 0 which means that resilience
501 generally decreased with increasing F . Values of $MiRT$ were also largely

502 insensitive to variations of Δ_{mat} and Δ_{rec} . The very small variance of $MiRT$
503 was mainly explained by variations of Δ_{mat} ($SI = 0.77$) whereas the one of
504 F_{MiRT} was mainly explained by Δ_{rec} ($SI = 0.85$), as shown in figures 4e and
505 4f.

506 All resilience curves tended toward infinity when F increased. We found
507 not much difference between resilience curves when Δ_{mat} only was varied.
508 On the contrary, an increase of Δ_{rec} was associated to the vertical asymptote
509 moving to the right (figure 8b).

510 Combining the results to provide a biological interpretation for the Bay
511 of Biscay sole (with r supposed to be near 0.2M, see Appendix D for details
512 of parameters value), the loss of resilience observed when increasing r charac-
513 terises the approach of the viability frontier rather than the stability frontier.
514 The consequence of this observation is that it is possible to have population
515 weakly resilient even far from the stability frontier if the viability frontier is
516 near. Even when fishing at F_{MSY} this situation is likely to be problematic
517 when F_{MSY} is near from the frontier, *e.g* for species with low r or high Δ_{mat} .

518 4. Discussion and conclusion

519 Our aim in this study was to investigate the effect of processes occurring at
520 intra-annual time scales on the amount and sustainability of long-term yields
521 from a population, and on the widely used reference point known as MSY.
522 We considered an idealised population submitted to three structuring pro-
523 cesses namely reproduction, maturation and recruitment and described using
524 a deterministic, structured dynamic population model in monthly discrete-
525 time. The main originality of the modelling approach relies on the particular
526 way we structured the population in order to (i) make the analysis tractable,
527 (ii) link intra-annual and inter-annual time-scales and (iii) to avoid resorting
528 to stock-recruitment relationship to represent the dynamics. Most modelling
529 approaches use structuring by age (Marchal et al., 2009; Tahvonen, 2009;
530 Doyen et al., 2012; Nielsen and Berg, 2014), by size (Bartolino, 2011; Lind-
531 strøm et al., 2009) or by stage (Zipkin et al., 2008; Wikström et al., 2012; Liz
532 and Pilarczyk, 2012). In our modelling framework instead, the classes of the
533 population are defined by combining age (in year), maturity and accessibility
534 to fishing characteristics. Thanks to this original structure we were able on
535 the one hand, to simulate month by month the evolution of the population,
536 and on the other hand, to resume the inter-annual dynamics to a first order
537 difference equation system. This interesting result enabled us to compute

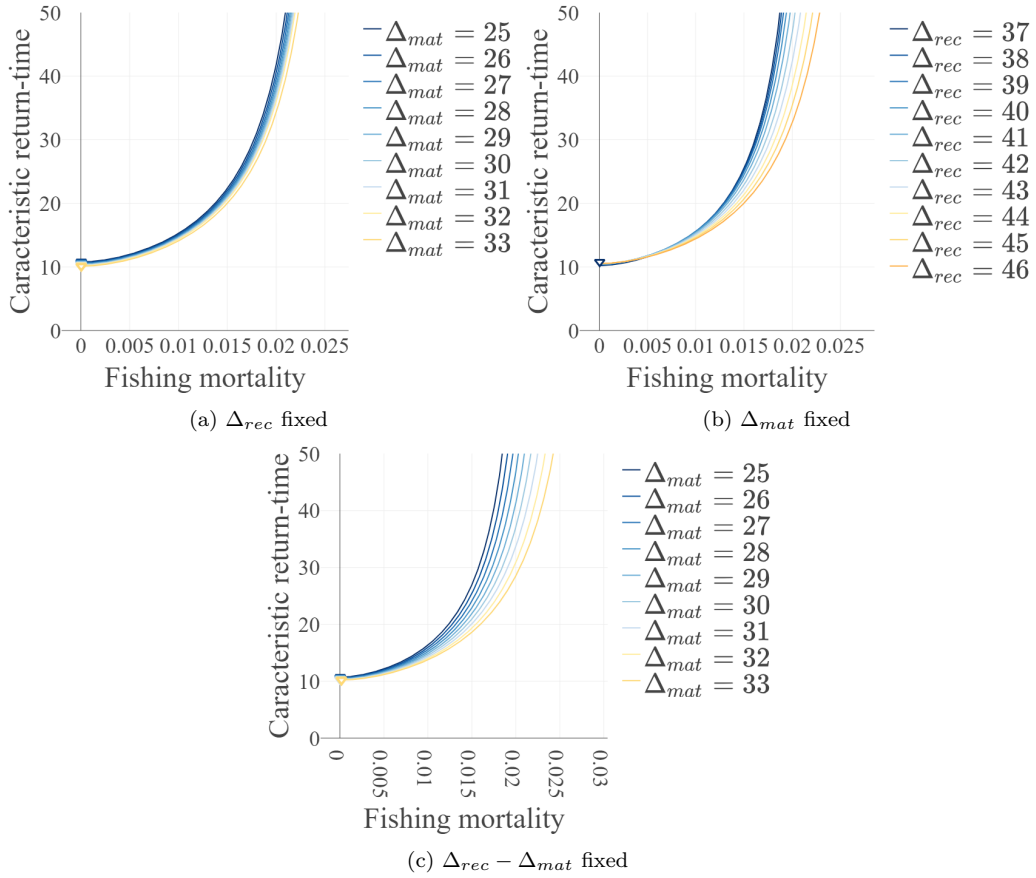


Figure 8: Characteristic return-time to inter-annual equilibrium as a function of fishing mortality (by month) when Δ_{mat} and Δ_{rec} vary and the system is parameterized for the Bay of Biscay sole. Different colours indicate different values of Δ_{mat} and/or Δ_{rec} depending on the case: (a) Δ_{mat} vary and $\Delta_{rec} = 44$; (b) Δ_{rec} vary and $\Delta_{mat} = 28$; (c) both Δ_{mat} and Δ_{rec} vary and their difference is constant and equals 14 ($\Delta_{mat} = 25, 26, \dots, 33$; $\Delta_{rec} = 39, 40, \dots, 47$).

538 analytically the inter-annual equilibrium and to assess numerically its stabil-
539 ity and resilience as a function of the model parameters. This is in our sense
540 one of the main innovation of our approach.

541 Application of the model was illustrated with parameters and data pub-
542 lished for the Bay of Biscay sole, although we stress that our model is gen-
543 eral and flexible enough to be applicable to any species whatever the ages
544 of maturation and recruitment. In our model, we hypothesized that recruit-
545 ment occurs after maturation but the reverse situation would constitute a
546 straightforward generalisation.

547 First, we found that yields curves shape was influenced by variations of
548 maturation lag Δ_{mat} and recruitment lag Δ_{rec} in different ways. The value of
549 MSY was more sensitive to Δ_{mat} whereas viability, stability and resilience
550 were more sensitive to Δ_{rec} . In classical stock-recruitment modelling (Hilborn
551 and Walters, 1992), all processes occurring before the age of first capture are
552 synthesised into a single stock-recruitment relationship (Bjorkstedt, 2000).
553 The advantage of our model is to separate explicitly maturation and recruit-
554 ment as processes of different nature. As a matter of fact, maturation is a
555 strictly biological process on which no control is possible whereas recruit-
556 ment is in part dependent of fishing behavior and gear (Laurec and Le Guen,
557 1981) so that it could be considered as a control variable. Simulations of
558 the emergent stock-recruitment relationship in our model show that under
559 certain conditions, this relationship can be complex and a single value of
560 stock associated to a large number of potential recruitment values. These
561 oscillations must be a consequence of the separation of the stock into differ-
562 ent stages. Soudijn and de Roos (2017) found that adding juvenile stages
563 in a population model enhanced population cycles and made dynamics more
564 realistic in the sense that they approximated better a physiologically struc-
565 tured model. Exhaustive description of attractors associated to observed
566 oscillations, although interesting, is beyond the scope of this study. It re-
567 mains that this result outlines the interest of modelling explicitly life-history
568 processes occurring in the youngest stages of the population. However, it is
569 true that the most complex dynamical behaviours were obtained with values
570 of fecundity probably unrealistically high. With realistic values of param-
571 eters, these quantities would have been quite well described by a classical
572 stock-recruitment function.

573 In practice, for most exploited species, these information on maturation
574 and recruitment are known, if at all, on a yearly basis only ICES (2018)
575 and the specific uncertainty related to timing and duration of processes on

576 intra-annual time-scales is generally ignored. The application of our model
577 to the Bay of Biscay sole is in line with other studies (Kokko and Lindström,
578 1998; Tang and Chen, 2004; Xu et al., 2005; Cid et al., 2014) concerning
579 the fact that intra-annual time-scales matter and that neglecting them can
580 lead to important errors. Here, we argue that timing of biological processes
581 and harvesting have different effects. With this example we show, on the
582 one hand, that ignoring intra-annual timing of maturation can have a large
583 impact on the computation of classical reference points such as MSY. On
584 the other hand, we found that the viability frontiers of the population was
585 sensitive to small variations in recruitment time. It is expected that these
586 aspects could be even more critical if the seasonality of fishing was considered
587 and F varied within the year as it is usually the case. Fortunately, the value
588 of F_{MSY} was insensitive to variations in Δ_{mat} and Δ_{rec} so that the advice
589 for the population management at F_{MSY} would not be much affected by
590 uncertainty concerning processes occurring at intra-annual time-scales.

591 The second aspect of our study was to quantify local stability of inter-
592 annual equilibrium as a measure of sustainability of yields drawn from the
593 population. There is a growing debate on whether the fish populations are
594 stable or not, and on the role of fishing on their destabilisation (Anderson
595 et al., 2008; Shelton and Mangel, 2011; Sugihara et al., 2011; Rouyer et al.,
596 2012). Our results support after other studies (Hsieh et al., 2006; Anderson
597 et al., 2008; Cid et al., 2014; Liz, 2017) the fact that single population's
598 equilibrium can be destabilised by increasing fishing mortality, but only for
599 species with very high fecundity. When parameterised for the Bay of Biscay
600 sole, the value of parameter r required to effectively destabilise the inter-
601 annual equilibrium is too high to be realistic and the population is more likely
602 to become extinct than to have his inter-annual equilibrium destabilised.

603 Shelton and Mangel (2011) assessed the stability of a Ricker model pa-
604 rameterised for 45 exploited stocks and concluded that the presence of deter-
605 ministic cyclic or chaotic behavior in real stocks was very unlikely. Our re-
606 sults are consistent with this prediction even if differences with their findings
607 must be noticed. In particular, an important difference concerns the modi-
608 fication of the stability region when the time between birth and maturation
609 increase. In our model, the stability region increases when Δ_{mat} increase, in
610 the sense that a higher F is necessary to destabilise the inter-annual equi-
611 librium. In their study, on the contrary, the stability region decreases with
612 each year added between birth and maturation. The explanation of this dif-
613 ference must rely on the different hypothesis concerning density dependence.

614 Indeed, in our model immature individuals' mortality is made dependent of
615 adult abundance at each month and not only on the abundance at birth-time
616 as it is the case in Ricker model. Unfortunately, our model is too complex
617 to get an analytical demonstration of this difference.

618 Our results demonstrate that the MSY can theoretically imply an unsta-
619 ble inter-annual equilibrium. This is in line with results obtained by Kokko
620 and Lindström (1998). This eventuality was also known in predator-prey
621 models (Beddington and Cooke, 1982) and in single species with Allee effect
622 (Ghosh et al., 2014). Then we agree with Beddington and Cooke (1982) that
623 sustainability of MSY reference points should not be taken for granted but
624 we temper this view by saying that the risk to get an unstable MSY in the
625 mono-specific case is very low. However, even in case of a stable equilib-
626 rium, resilience measured by the return time to this equilibrium should still
627 be considered. Indeed, as stated Beddington et al. (1976), in some cases,
628 *“perturbations may take so long to die away that effectively the populations*
629 *may never return to equilibrium within a biologically meaningful times-pan”*.
630 Such a situation would result in the impossibility of managing properly an
631 exploited system.

632 Assessment of resilience in exploited populations is a topic of growing
633 interest among empirical (Britten et al., 2014; Mumby et al., 2016) and the-
634 oretical ecologists. Tromeur and Loeuille (2017) and Kar et al. (2019) inves-
635 tigated relationship between the objectives of resilience and yields in food
636 chains and found a RMY distinct from the MSY , leaving room for a trade-off
637 between these objectives. Lundström et al. (2019) also explored trade-offs
638 between yields and a number of conservation objectives including resilience
639 on two structured single population models. One of their key result is that
640 resilience is highly correlated with biomass loss, suggesting to use this met-
641 rics as a proxy for resilience in practice. This is in line with our observation
642 that return-time to inter-annual equilibrium increase dramatically near the
643 viability frontier. Here, we predict that in most real exploited populations,
644 resilience will be harmed by approaching this frontier due to a lowered equi-
645 librium biomass, rather than by getting in an unstable region of parameter
646 space. In the theoretical studies above cited, values of parameters were set
647 arbitrarily in an exploratory purpose and their authors found an optimum of
648 resilience corresponding to a non-zero value of fishing mortality. Here, with a
649 set of realistic parameters, we located this optimum at very low, although non
650 zero, values of F . This would practically exclude some “win-win” situation
651 in which it would be possible to increase both yield and resilience.

652 Previous works proposed to manage the trade-off between yields and re-
653 siliance by acting on the distribution of effort on trophic level (Tromeur and
654 Loeuille, 2017; Kar et al., 2019) or on the stage development (juvenile *vs.*
655 adults) inside the population (Lundström et al., 2019). Our model is not de-
656 signed to answer these questions. Instead, we evaluated the effect of another
657 control parameter which is the timing of recruitment. In our application for
658 the Bay of Biscay sole, we found that variations in recruitment time had a
659 non-negligible effect on resilience curves although it did not affect much the
660 value and location of the optimum.

661 Our aim in this study was to propose a generalised and relatively simple
662 model to shade light on the effect of intra-annual time-scales in maturation
663 and recruitment processes which are of key importance in fisheries manage-
664 ment. Although we parameterised the model with published literature and
665 data concerning a real stock, this was on a qualitative and illustrative pur-
666 pose rather than to make quantitative predictions (*i.e.* to get possible rather
667 than exact values). We stress that our model is far too idealised to make
668 precise predictions and that available data are not designed for our model.

669 Our choice here was to formulate as simply as possible a model of density
670 dependence by cannibalism of adults on juveniles. Cannibalism is known to
671 be frequent in fish populations (Smith and Reay, 1991) including in highly
672 exploited stocks such as cod (Bogstad et al., 1994; Uzars and Plikshs, 2000).
673 Moreover cannibalism was at the core of development of Ricker historical
674 stock and recruitment theory (Ricker, 1954) and is a useful assumption in
675 the sense that it is the most straightforward process of over-compensatory
676 mortality. Other processes such as competition for food and space (Biro
677 et al., 2003) are known to potentially give rise to the same type of mortal-
678 ity. Rindorf et al. (2022) gave support to Ricker’s (1954) assumptions by
679 showing that most of exploited stocks undergo density-dependence before re-
680 cruitment and that overcompensation was more likely to occur in demersal
681 stocks such as the Bay of Biscay of sole. From a dynamical point of view,
682 over-compensatory reproduction curves with inter-stage density-dependence
683 are known to cause more complex behaviours. We were interested in stability
684 and resilience properties of the population equilibrium and for that reason
685 adopting a number of Ricker’s assumptions was a way of not restricting the
686 dynamical potential of our model.

687 This is to our knowledge the first resilience analysis on a single exploited
688 population subject to cannibalistic density-dependence, as well as the first
689 evaluating the effect of intra-annual timing of maturation and recruitment

690 on resilience. Although we restricted ourselves to a particular case study
691 and made a number of assumptions that limit the generality of the presented
692 results, we stress that in future studies, the model could be modified in order
693 to address new questions while adopting a similar approach for structuring
694 the population in order to be able to study its dynamics easily as a first order
695 system. For example, instead of dealing with the case in which maturation
696 is separated from recruitment (what we did here), one could write another
697 slightly different model in which start of reproduction is separated from end
698 of density-dependent mortality. Alternatively, the reverse case where recruit-
699 ment occurs before maturation would be worth exploring given that it would
700 be verified in some species (ICES, 2018). All these extensions are permitted
701 by the conceptual framework presented in this study.

702 Moreover, in an operational purpose, one could be interested in expand-
703 ing this theoretical model to increase realism, at the cost of simplicity and
704 analytical tractability. A natural extension to it would be to add a representa-
705 tion of fecundity depending on length or weight of individuals. This function
706 would probably be species-dependent. Therefore, to maintain a broad scope
707 of conclusions, it would be necessary to explore a large panel of functions.
708 Also, the processes such as reproduction, recruitment and maturation were
709 considered instantaneous while they are likely spread over several months in
710 real populations. Finally other formulation for density-dependence including
711 form of functional response in the cannibalistic case could be tested.

712 More generally, the absence of consideration of process error (i.e. error
713 arising from under-specified models) limits the scope of our results. Here, we
714 presented some non-linear dynamics obtained assuming perfect knowledge of
715 the underlying mechanisms, but it remains true that non-linearities can be
716 enhanced in models containing process error when this error propagates in a
717 specific way (Anderson et al., 2008).

718 Our results suggest that ignoring intra-annual dynamics would result in
719 little error on F_{MSY} advice. However, we saw that small variations of the
720 recruitment time would have non negligible consequences on the fishing mor-
721 tality a population can support before extinction as well as on her resilience.
722 We recommend that the latter be taken into account in harvest management,
723 so that the sustainability of yields be guaranteed. A first step could be to
724 modify the F_{MSY} -range framework (Hilborn, 2010; Rindorf et al., 2017) to
725 include resilience objectives to be attained aside from high enough yields.

Table 1: Time and population structure notations.

Notation	Interpretation
t	Model time-step (expressed in months)
(m, y)	Time-step expressed as a calendar time (month and year)
δ	Exact age of individuals (in months)
a	Round age of individuals (in years)
d, \bar{d}	Density dependent/independent individuals (equivalent here to immature/mature individuals)
h, \bar{h}	Harvested/unharvested individuals
Δ_{mat}	Lag between birth and maturation (in months)
Δ_{rec}	Lag between birth and recruitment (in months)
a_{mat}	Minimum round age of matured individuals (in years)
a_{rec}	Minimum round age of recruited individuals (in years)
m_{mat}	Month of the year at which maturation occurs
m_{rec}	Month of the year at which recruitment occurs
m_{rep}	Month of the year at which reproduction occurs (by construction, we always have $m_{rep} = 12$)
$\underline{N}(t)$	Vector of the structured population at time t
$N_c(t)$	Number of individuals of class c at time t . The class c is defined by the intersection of groups of individuals of age a , immature/mature individuals (d, \bar{d}) and harvested/unharvested individuals (h, \bar{h}) , <i>e.g.</i> $N_{a_{mat}, d, \bar{h}}(t)$ is the number of immature, unharvested individuals of round age a_{mat} .
\bullet	Union of groups, <i>e.g.</i> $(\bullet, \bar{d}, \bullet)$ stands for the class of mature individuals of all ages, whether or not they are harvested.

Table 2: Model parameters and their interpretation

Parameter	Interpretation
r	Fecundity of mature individuals (number of eggs released in a year)
μ	Density-dependence factor
ω	Density-independent part of immature individuals' mortality
$M_d(t)$	Immature individuals' mortality at time t
$M_{\bar{d}}$	Mature individuals' natural mortality (assumed to be constant)
$S_d(t+1)$	Survival rate of immature individuals between time-steps t and $t+1$
$S_{\bar{d},\bar{h}}$	Survival rate of mature, unharvested individuals between time-steps t and $t+1$ (assumed to be constant)
$S_{\bar{d},h}$	Survival rate of mature, harvested individuals between time-steps t and $t+1$ (assumed to be constant)
F	Fishing mortality by month (assumed to be constant)

Table 3: Expression of the inter-annual dynamics of $\underline{N}(m_{mat}, y)$ when $m_{mat} \leq m_{rec}$, for all y

$$\left\{ \begin{array}{l} N_{0, \bar{d}, \bar{h}}(m_{mat}, y + 1) = r N_{\bullet, \bar{d}, \bullet}(m_{rep}, y) \prod_{m=1}^{m_{mat}} S_d(m, y + 1) \\ N_{a_1, \bar{d}, \bar{h}}(m_{mat}, y + 1) = N_{a_1 - 1, \bar{d}, \bar{h}}(m_{mat}, y) \prod_{m=m_{mat}+1}^{m_{rep}} S_d(m, y) \prod_{m=1}^{m_{mat}} S_d(m, y + 1) \\ N_{a_2, \bar{d}, \bar{h}}(m_{mat}, y + 1) = N_{a_2 - 1, \bar{d}, \bar{h}}(m_{mat}, y) S_{\bar{d}, \bar{h}}^{m_{rep}} \\ N_{>a_{rec}, \bar{d}, \bar{h}}(m_{mat}, y + 1) = N_{>a_{rec}, \bar{d}, \bar{h}}(m_{mat}, y) S_{\bar{d}, \bar{h}}^{m_{rep}} \\ \quad + N_{a_{rec}, \bar{d}, \bar{h}}(m_{mat}, y) S_{\bar{d}, \bar{h}}^{m_{rec} - m_{mat}} S_{\bar{d}, \bar{h}}^{m_{rep} - (m_{rec} - m_{mat})} \end{array} \right. \quad (17)$$

with $a_1 = 1, \dots, a_{mat}$ and $a_2 = a_{mat} + 1, \dots, a_{rec}$

Table 4: Expressions of aggregated constants and auxiliary functions used in model development. $S_{\bar{d},\bar{h}}$ is the survival rate of mature, unharvested individuals. $S_{\bar{d},h}$ is the survival rate of mature, harvested individuals. μ and ω are the two constants in immature individuals' mortality function (2).

Number of spawners

$$\Psi(N_{\bar{d}}(t)) = \psi_1 \sum_{a=a_{mat}}^{a_{rec}-1} N_{a,\bar{d},\bar{h}}(t) + \psi_2 N_{a_{rec},\bar{d},\bar{h}}(t) + \psi_3 N_{>a_{rec},\bar{d},h}(t)$$

with

$$\psi_1 = S_{\bar{d},\bar{h}}^{m_{rep}-m_{mat}} \quad \psi_2 = S_{\bar{d},\bar{h}}^{m_{rec}-m_{mat}} S_{\bar{d},h}^{m_{rep}-m_{rec}} \quad \psi_3 = S_{\bar{d},h}^{m_{rep}-m_{mat}}$$

Expression of density-dependence, $\forall n \in \{1, 2\}$

$$\varphi_n(N_{\bar{d}}(t)) = \beta_n \sum_{a=a_{mat}}^{a_{rec}-1} N_{a,\bar{d},\bar{h}}(t) + \theta_n N_{a_{rec},\bar{d},\bar{h}}(t) + \kappa_n N_{>a_{rec},\bar{d},h}(t)$$

with

$$\begin{aligned} \beta_1 &= \mu \sum_{m=0}^{m_{mat}-1} S_{\bar{d},\bar{h}}^{m_{rep}-m_{mat}+m} & \kappa_1 &= \mu \sum_{m=0}^{m_{mat}-1} S_{\bar{d},h}^{m_{rep}-m_{mat}+m} \\ \beta_2 &= \beta_1 + \mu \sum_{m=0}^{m_{rep}-m_{mat}-1} S_{\bar{d},\bar{h}}^m & \kappa_2 &= \kappa_1 + \mu \sum_{m=0}^{m_{rep}-m_{mat}-1} S_{\bar{d},h}^m \end{aligned}$$

$$\begin{aligned} \theta_1 &= \mu S_{\bar{d},\bar{h}}^{m_{rec}-m_{mat}} \sum_{m=0}^{m_{mat}-1} S_{\bar{d},h}^{m_{rep}-m_{rec}+m} \\ \theta_2 &= \theta_1 + \mu \left[\sum_{m=0}^{m_{rec}-m_{mat}-1} S_{\bar{d},\bar{h}}^m + S_{\bar{d},\bar{h}}^{m_{rec}-m_{mat}} \sum_{m=0}^{m_{rep}-m_{rec}-1} S_{\bar{d},h}^m \right] \end{aligned}$$

Other aggregated constants

$$\begin{aligned} \alpha_1 &= e^{-\omega m_{mat}} & \sigma &= S_{\bar{d},\bar{h}}^{m_{rep}} & \rho &= S_{\bar{d},\bar{h}}^{m_{rec}-m_{mat}} S_{\bar{d},h}^{m_{rep}-(m_{rec}-m_{mat})} \\ \alpha_2 &= e^{-\omega m_{rep}} & \nu &= S_{\bar{d},h}^{m_{rep}} \end{aligned}$$

Table 5: Numerical values and origin of parameters used in simulation for the Bay of Biscay sole.

Parameter	Meaning	Value (fixed)	Ranges (sensitivity analysis)	Origin
r	adult fecundity	220646	$[1, 1.5 \times 10^6]$	Witthames et al. (1995)
$M_{\bar{d}}$	natural mortality (monthly)	0.1/12		classical assumption of ICES (2018)
F	fishing mortality (monthly)	0.1/12		assumed equal to natural mortality
Δ_{mat}	maturation delay (in months)		$\{25, \dots, 30\}$	arbitrary value verifying $a_{mat} = 2$ (ICES, 2018)
Δ_{rec}	recruitment delay (in months)		$\{37, \dots, 46\}$	arbitrary value verifying $a_{rec} = 3$ (ICES, 2018)
μ	density-dependence constant		see table 6	estimated
ω	density-dependence constant		see table 7	estimated

Table 6: Estimation of parameter μ for the different combinations of Δ_{mat} and Δ_{rec} .

	Δ_{rec}						
	37	38	39	40	41	42	43
Δ_{mat} 25	1.730×10^{-11}	1.644×10^{-11}	1.656×10^{-11}	1.666×10^{-11}	1.677×10^{-11}	1.686×10^{-11}	1.695×10^{-11}
26	1.909×10^{-11}	1.968×10^{-11}	1.920×10^{-11}	1.931×10^{-11}	1.94×10^{-11}	1.951×10^{-11}	1.961×10^{-11}
27	2.152×10^{-11}	2.145×10^{-11}	2.175×10^{-11}	2.160×10^{-11}	2.170×10^{-11}	2.181×10^{-11}	2.191×10^{-11}
28	2.367×10^{-11}	2.361×10^{-11}	2.359×10^{-11}	2.356×10^{-11}	2.368×10^{-11}	2.378×10^{-11}	2.388×10^{-11}
29	2.556×10^{-11}	2.547×10^{-11}	2.542×10^{-11}	2.539×10^{-11}	2.514×10^{-11}	2.549×10^{-11}	2.558×10^{-11}
30	2.722×10^{-11}	2.711×10^{-11}	2.702×10^{-11}	2.697×10^{-11}	2.694×10^{-11}	2.649×10^{-11}	2.703×10^{-11}
	Δ_{rec}						
	44	45	46				
Δ_{mat} 25	1.704×10^{-11}	1.712×10^{-11}	1.720×10^{-11}				
26	1.970×10^{-11}	1.980×10^{-11}	1.989×10^{-11}				
27	2.201×10^{-11}	2.210×10^{-11}	2.220×10^{-11}				
28	2.398×10^{-11}	2.408×10^{-11}	2.418×10^{-11}				
29	2.568×10^{-11}	2.577×10^{-11}	2.587×10^{-11}				
30	2.712×10^{-11}	2.721×10^{-11}	2.731×10^{-11}				

Table 7: Estimation of parameter ω for the different combinations of Δ_{mat} and Δ_{rec} .

	Δ_{rec}									
	37	38	39	40	41	42	43	44	45	46
Δ_{mat} 25	0.5369	0.5371	0.5372	0.5373	0.5374	0.5374	0.5375	0.5376	0.5377	0.5378
26	0.5163	0.5165	0.5167	0.5167	0.5169	0.5169	0.5170	0.5171	0.5172	0.5172
27	0.4971	0.4975	0.4977	0.4978	0.4979	0.4979	0.4980	0.4981	0.4982	0.4983
28	0.4793	0.4796	0.4799	0.4801	0.4803	0.4804	0.4804	0.4805	0.4806	0.4806
29	0.4628	0.4631	0.4634	0.4637	0.4639	0.4640	0.4641	0.4641	0.4642	0.4643
30	0.4473	0.4476	0.4479	0.4482	0.4485	0.4487	0.4488	0.4489	0.4489	0.4490

726 **Appendix A. Alternative case, when $m_{mat} > m_{rec}$**

727 The same way we deduced system (17) from equations (3-10) for the case
 728 when $m_{mat} \leq m_{rec}$, we can deduce from the same equations the system E.1,
 729 expressed in table E.8. As before, this system can be expressed as a first
 730 order difference equation (see Appendix B for proof):

$$\left\{ \begin{array}{l} N_{0,d,\bar{h}}(m_{mat}, y + 1) = r \alpha_1 \Phi(\underline{N}_{\bar{d}}(m_{mat}, y)) e^{-\xi_1(\underline{N}_{\bar{d}}(m_{mat}, y))} \\ N_{a1,d,\bar{h}}(m_{mat}, y + 1) = \alpha_2 N_{a1-1,d,\bar{h}}(m_{mat}, y) e^{-\xi_2(\underline{N}_{\bar{d}}(m_{mat}, y))} \\ N_{a2,\bar{d},\bar{h}}(m_{mat}, y + 1) = \sigma N_{a2-1,\bar{d},\bar{h}}(m_{mat}, y) \\ N_{a_{rec},\bar{d},h}(m_{mat}, y + 1) = \chi N_{a_{rec}-1,\bar{d},h}(m_{mat}, y) \\ N_{>a_{rec},\bar{d},h}(m_{mat}, y + 1) = \nu N_{>a_{rec},\bar{d},h}(m_{mat}, y) \\ \qquad \qquad \qquad \qquad \qquad + \nu N_{a_{rec},\bar{d},h}(m_{mat}, y) \end{array} \right. \quad (A.1)$$

731 with $a1 = 1, \dots, a_{mat}$ and $a2 = a_{mat} + 1, \dots, a_{rec} - 1$, $\Phi(\underline{N}_{\bar{d}}(t))$ the number
 732 of spawners, $\xi_n(\underline{N}_{\bar{d}}(t))$ a density-dependence function. Here, we have :

$$\Phi(\underline{N}_{\bar{d}}(t)) = \psi_1 \sum_{a=a_{mat}}^{a_{rec}-1} N_{a,\bar{d},\bar{h}}(t) + \psi_3 [N_{a_{rec},\bar{d},h}(t) + N_{>a_{rec},\bar{d},h}(t)]$$

733 and

$$\xi_n(\underline{N}_{\bar{d}}(t)) = \beta_n \sum_{a=a_{mat}}^{a_{rec}-2} N_{a,\bar{d},\bar{h}}(t) + \eta_n N_{a_{rec}-1,\bar{d},\bar{h}}(t) \\ + \kappa_n [N_{a_{rec},\bar{d},h}(t) + N_{>a_{rec},\bar{d},h}(t)]$$

734 where

$$735 \quad \eta_1 = \mu \left[S_{\bar{d},\bar{h}}^{m_{rep}+m_{rec}-m_{mat}} \sum_{m=0}^{m_{mat}-m_{rec}-1} S_{\bar{d},h}^m + \sum_{m=0}^{m_{rec}-1} S_{\bar{d},\bar{h}}^{m_{rep}-m_{mat}+m} \right]$$

$$736 \quad \eta_2 = \eta_1 + \mu \sum_{m=0}^{m_{rep}-m_{mat}-1} S_{\bar{d},\bar{h}}^m$$

737 $\chi = S_{\bar{d},\bar{h}}^{m_{rep}+m_{rec}-m_{mat}} S_{\bar{d},h}^{m_{mat}-m_{rec}}$ is a constant and all other parameters
 738 are the same as in model (11) (see table 4 for full detail).

739 The inter-annual equilibrium is solution of :

$$\left\{ \begin{array}{l}
N_{a_{mat}, \bar{d}, \bar{h}}^*(m_{mat}) = r \alpha_1 \alpha_2^{a_{mat}} \Phi(\underline{N}_{\bar{d}}^*(m_{mat})) \\
\quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \times e^{-\xi_1(\underline{N}_{\bar{d}}^*(m_{mat})) - a_{mat} \xi_2(\underline{N}_{\bar{d}}^*(m_{mat}))} \\
N_{a_2, \bar{d}, \bar{h}}^*(m_{mat}) = \sigma N_{a_2-1, \bar{d}, \bar{h}}^*(m_{mat}) \\
N_{a_{rec}, \bar{d}, h}^*(m_{mat}) = \chi N_{a_{rec}-1, \bar{d}, h}^*(m_{mat}) \\
N_{>a_{rec}, \bar{d}, h}^*(m_{mat}) = \nu \left[N_{>a_{rec}, \bar{d}, h}^*(m_{mat}) + N_{a_{rec}, \bar{d}, h}^*(m_{mat}) \right]
\end{array} \right. \quad (\text{A.2})$$

740 with

$$741 \quad \underline{N}_{\bar{d}}^*(m_{mat}) = {}^t \left(N_{a_{mat}, \bar{d}, \bar{h}}^*(m_{mat}), N_{a_2, \bar{d}, \bar{h}}^*(m_{mat}), N_{a_{rec}, \bar{d}, h}^*(m_{mat}), N_{>a_{rec}, \bar{d}, h}^*(m_{mat}) \right)$$

742 and $a_2 = a_{mat} + 1, \dots, a_{rec} - 1$.

743 Appendix B. Proof of result (11) and (A.1)

744 Expressions of systems (17) and (E.1) were deduced directly from the
745 month model represented by equations (3-10). To rewrite these two systems
746 as first-order difference equations systems we need to express:

- 747 1. $N_{\bullet, \bar{d}, \bullet}(m_{rep}, y)$
- 748 2. $\prod_{m=1}^{m_{mat}} S_d(m, y + 1)$
- 749 3. $\prod_{m=m_{mat}+1}^{m_{rep}} S_d(m, y)$

750 as functions of $\underline{N}(m_{mat}, y)$.

751 *Expression of $N_{\bullet, \bar{d}, \bullet}(m_{rep}, y)$*

752 For all y , we have: $N_{a_{mat}, \bar{d}, \bar{h}}(m_{rep}, y) = 0$ and $N_{a_{rec}, \bar{d}, h} = 0, \forall y$. Hence, if
753 $m_{mat} \leq m_{rec}$, we get after equations (3-10):

$$\begin{aligned}
N_{\bullet, d, \bullet}(m_{rep}, y) &= \sum_{a=a_{mat}+1}^{a_{rec}} N_{a, \bar{d}, \bar{h}}(m_{rep}, y) + N_{>a_{rec}, \bar{d}, h}(m_{rep}, y) \\
&= S_{\bar{d}, \bar{h}}^{m_{rep}-m_{mat}} \sum_{a=a_{mat}}^{a_{rec}-1} N_{a, \bar{d}, \bar{h}}(m_{mat}, y) \\
&\quad + N_{a_{rec}, \bar{d}, \bar{h}}(m_{mat}, y) \times S_{\bar{d}, \bar{h}}^{m_{rec}-m_{mat}} S_{\bar{d}, h}^{m_{rep}-m_{rec}} \\
&\quad + N_{>a_{rec}, \bar{d}, h}(m_{mat}, y) \times S_{\bar{d}, h}^{m_{rep}-m_{mat}} \\
&= \Psi(\underline{N}_{\bar{d}}(m_{mat}, y))
\end{aligned} \quad (\text{B.1})$$

754

Else, we get:

$$\begin{aligned}
N_{\bullet,d,\bullet}(m_{rep}, y) &= \sum_{a=a_{mat}+1}^{a_{rec}-1} N_{a,\bar{d},\bar{h}}(m_{rep}, y) + N_{>a_{rec},\bar{d},h}(m_{rep}, y) \\
&= S_{\bar{d},\bar{h}}^{m_{rep}-m_{mat}} \sum_{a=a_{mat}}^{a_{rec}} N_{a,\bar{d},\bar{h}}(m_{mat}, y) \\
&\quad + N_{a_{rec},\bar{d},h}(m_{mat}, y) \times S_{\bar{d},\bar{h}}^{m_{rep}-m_{mat}} \\
&\quad + N_{>a_{rec},\bar{d},h}(m_{mat}, y) \times S_{\bar{d},\bar{h}}^{m_{rep}-m_{mat}} \\
&= \Phi(N_{\bar{d}}(m_{mat}, y))
\end{aligned} \tag{B.2}$$

755 *Expression of $\prod_{m=1}^{m_{mat}} S_d(m, y+1)$*

756

We have, for all y :

$$\prod_{m=1}^{m_{mat}} S_d(m, y+1) = e^{-\omega m_{mat}} e^{-\mu [N_{\bullet,\bar{d},\bullet}(m_{rep}, y) + \sum_{m=1}^{m_{mat}-1} N_{\bullet,\bar{d},\bullet}(m, y+1)]} \tag{B.3}$$

with

$$\begin{aligned}
&N_{\bullet,\bar{d},\bullet}(m_{rep}, y) + \sum_{m=1}^{m_{mat}-1} N_{\bullet,\bar{d},\bullet}(m, y+1) \\
&= N_{a_{mat},\bar{d},\bar{h}}(m_{rep}, y) + \sum_{m=1}^{m_{mat}-1} N_{a_{mat},\bar{d},\bar{h}}(m, y+1) \\
&\quad + N_{a_{mat}+1,\bar{d},\bar{h}}(m_{rep}, y) + \sum_{m=1}^{m_{mat}-1} N_{a_{mat}+1,\bar{d},\bar{h}}(m, y+1) \\
&\quad + \dots \\
&\quad + N_{a_{rec},\bar{d},\bar{h}}(m_{rep}, y) + \sum_{m=1}^{m_{mat}-1} N_{a_{rec},\bar{d},\bar{h}}(m, y+1) \\
&\quad + N_{a_{rec},\bar{d},h}(m_{rep}, y) + \sum_{m=1}^{m_{mat}-1} N_{a_{rec},\bar{d},h}(m, y+1) \\
&\quad + N_{>a_{rec},\bar{d},h}(m_{rep}, y) + \sum_{m=1}^{m_{mat}-1} N_{>a_{rec},\bar{d},h}(m, y+1)
\end{aligned}$$

757

Moreover, after (3-10), we have for all y :

$$N_{a_{mat},\bar{d},\bar{h}}(m_{rep}, y) + \sum_{m=1}^{m_{mat}-1} N_{a_{mat},\bar{d},\bar{h}}(m, y+1) = 0 \tag{B.4}$$

758 and for all $a \in \{a_{mat} + 1, \dots, a_{rec} - 1\}$:

$$\begin{aligned}
& N_{a, \bar{d}, \bar{h}}(m_{rep}, y) + \sum_{m=1}^{m_{mat}-1} N_{a, \bar{d}, \bar{h}}(m, y + 1) \\
&= N_{a, \bar{d}, \bar{h}}(m_{rep}, y) \sum_{m=0}^{m_{mat}-1} S_{\bar{d}, \bar{h}}^m \\
&= N_{a-1, \bar{d}, \bar{h}}(m_{mat}, y) \sum_{m=0}^{m_{mat}-1} S_{\bar{d}, \bar{h}}^{m_{rep}-m_{mat}+m}
\end{aligned} \tag{B.5}$$

759 If $m_{mat} \leq m_{rec}$ we also have:

$$\begin{aligned}
& N_{a_{rec}, \bar{d}, \bar{h}}(m_{rep}, y) + \sum_{m=1}^{m_{mat}-1} N_{a_{rec}, \bar{d}, \bar{h}}(m, y + 1) \\
&= N_{a_{rec}-1, \bar{d}, \bar{h}}(m_{mat}, y) \sum_{m=0}^{m_{mat}-1} S_{\bar{d}, \bar{h}}^{m_{rep}-m_{mat}+m}
\end{aligned} \tag{B.6}$$

$$N_{a_{rec}, \bar{d}, h}(m_{rep}, y) + \sum_{m=1}^{m_{mat}-1} N_{a_{rec}, \bar{d}, h}(m, y + 1) = 0 \tag{B.7}$$

760 and

$$\begin{aligned}
& N_{>a_{rec}, \bar{d}, h}(m_{rep}, y) + \sum_{m=1}^{m_{mat}-1} N_{>a_{rec}, \bar{d}, h}(m, y + 1) \\
&= N_{>a_{rec}, \bar{d}, h}(m_{mat}, y) \sum_{m=0}^{m_{mat}-1} S_{\bar{d}, h}^{m_{rep}-m_{mat}+m} \\
&\quad + N_{a_{rec}, \bar{d}, \bar{h}}(m_{mat}, y) S_{\bar{d}, \bar{h}}^{m_{rec}-m_{mat}} \sum_{m=0}^{m_{mat}-1} S_{\bar{d}, h}^{m_{rep}-m_{rec}+m}
\end{aligned} \tag{B.8}$$

761 Else we have:

$$\begin{aligned}
& N_{a_{rec}, \bar{d}, \bar{h}}(m_{rep}, y) + \sum_{m=1}^{m_{mat}-1} N_{a_{rec}, \bar{d}, \bar{h}}(m, y + 1) \\
&= N_{a_{rec}, \bar{d}, \bar{h}}(m_{rep}, y) + \sum_{m=1}^{m_{rec}-1} N_{a_{rec}, \bar{d}, \bar{h}}(m, y + 1) + 0 \\
&= N_{a_{rec}-1, \bar{d}, \bar{h}}(m_{mat}, y) \sum_{m=0}^{m_{rec}-1} S_{\bar{d}, \bar{h}}^{m_{rep}-m_{mat}+m}
\end{aligned} \tag{B.9}$$

$$\begin{aligned}
& N_{a_{rec}, \bar{d}, h}(m_{rep}, y) + \sum_{m=1}^{m_{mat}-1} N_{a_{rec}, \bar{d}, h}(m, y + 1) \\
&= 0 + \sum_{m=m_{rec}}^{m_{mat}-1} N_{a_{rec}, \bar{d}, h}(m, y + 1) \\
&= N_{a_{rec}, \bar{d}, h}(m_{rec}, y + 1) \sum_{m=0}^{m_{mat}-m_{rec}-1} S_{\bar{d}, h}^m \\
&= N_{a_{rec}-1, \bar{d}, \bar{h}}(m_{mat}, y) S_{\bar{d}, \bar{h}}^{m_{rep}-m_{mat}+m_{rec}} \sum_{m=0}^{m_{mat}-m_{rec}-1} S_{\bar{d}, h}^m
\end{aligned} \tag{B.10}$$

762 and

$$\begin{aligned}
& N_{>a_{rec},\bar{d},h}(m_{rep}, y) + \sum_{m=1}^{m_{mat}-1} N_{>a_{rec},\bar{d},h}(m, y+1) \\
&= N_{>a_{rec},\bar{d},h}(m_{mat}, y) \sum_{m=0}^{m_{mat}-1} S_{\bar{d},h}^{m_{rep}-m_{mat}+m} \\
&\quad + N_{a_{rec},\bar{d},\bar{h}}(m_{mat}, y) \sum_{m=0}^{m_{mat}-1} S_{\bar{d},h}^{m_{rep}-m_{mat}+m}
\end{aligned} \tag{B.11}$$

763 By summing equations (B.4-B.5) and (B.6-B.8) if $m_{mat} \leq m_{rec}$, or (B.4-
764 B.5) and (B.9-B.11) otherwise, and injecting it into (B.3), we can rewrite the
765 product of interest as:

$$\prod_{m=1}^{m_{mat}} S_d(m, y+1) = \begin{cases} \alpha_1 \varphi_1(\underline{N}_{\bar{d}}(m_{mat}, y)) & \text{if } m_{mat} \leq m_{rec} \\ \alpha_1 \xi_1(\underline{N}_{\bar{d}}(m_{mat}, y)) & \text{else} \end{cases} \tag{B.12}$$

766 see table 4 for exact formulation of α_1 , φ_1 and ξ_1 .

767 *Expression of $\prod_{m=m_{mat}+1}^{m_{rep}} S_d(m, y)$*

768 Likewise, we can express $\prod_{m=m_{mat}+1}^{m_{rep}} S_d(m, y)$ for all y as:

$$\prod_{m=m_{mat}+1}^{m_{rep}} S_d(m, y) = e^{-\omega(m_{rep}-m_{mat})} e^{-\mu \sum_{m=m_{mat}}^{m_{rep}-1} N_{\bullet,\bar{d},\bullet}(m,y)} \tag{B.13}$$

with

$$\begin{aligned}
& \sum_{m=m_{mat}}^{m_{rep}-1} N_{\bullet,\bar{d},\bullet}(m, y) \\
&= \sum_{m=m_{mat}}^{m_{rep}-1} N_{a_{mat},\bar{d},\bar{h}}(m, y) + \sum_{m=m_{mat}}^{m_{rep}-1} N_{a_{mat}+1,\bar{d},\bar{h}}(m, y) \\
&\quad + \dots \\
&\quad + \sum_{m=m_{mat}}^{m_{rep}-1} N_{a_{rec},\bar{d},\bar{h}}(m, y) + \sum_{m=m_{mat}}^{m_{rep}-1} N_{a_{rec},\bar{d},h}(m, y) \\
&\quad + \sum_{m=m_{mat}}^{m_{rep}-1} N_{>a_{rec},\bar{d},h}(m, y)
\end{aligned}$$

769 For all $a \in \{a_{mat}, \dots, a_{rec} - 1\}$, for all y , we have:

$$\sum_{m=m_{mat}}^{m_{rep}-1} N_{a,\bar{d},\bar{h}}(m, y) = N_{a,\bar{d},\bar{h}}(m_{mat}, y) \sum_{m=0}^{m_{rep}-m_{mat}-1} S_{\bar{d},h}^m \tag{B.14}$$

770 and

$$\sum_{m=m_{mat}}^{m_{rep}-1} N_{>a_{rec},\bar{d},h}(m, y) = N_{>a_{rec},\bar{d},h}(m_{mat}, y) \sum_{m=0}^{m_{rep}-m_{mat}-1} S_{\bar{d},h}^m \quad (\text{B.15})$$

771 If $m_{mat} \leq m_{rec}$ we also have, for all y :

$$\sum_{m=m_{mat}}^{m_{rep}-1} N_{a_{rec},\bar{d},\bar{h}}(m, y) = N_{a_{rec},\bar{d},\bar{h}}(m_{mat}, y) \sum_{m=0}^{m_{rec}-m_{mat}-1} S_{\bar{d},\bar{h}}^m + 0 \quad (\text{B.16})$$

772 and

$$\sum_{m=m_{mat}}^{m_{rep}-1} N_{a_{rec},\bar{d},h}(m, y) = N_{a_{rec},\bar{d},\bar{h}}(m_{mat}, y) \times S_{\bar{d},\bar{h}}^{m_{rec}-m_{mat}} \sum_{m=0}^{m_{rep}-m_{rec}-1} S_{\bar{d},h}^m \quad (\text{B.17})$$

773 Else we have:

$$\sum_{m=m_{mat}}^{m_{rep}-1} N_{a_{rec},\bar{d},\bar{h}}(m, y) = 0 \quad (\text{B.18})$$

774 and

$$\sum_{m=m_{mat}}^{m_{rep}-1} N_{a_{rec},\bar{d},h}(m, y) = N_{a_{rec},\bar{d},h}(m_{mat}, y) \sum_{m=0}^{m_{rep}-m_{mat}-1} S_{\bar{d},h}^m \quad (\text{B.19})$$

Hence, with notations exposed in table 4, we can write the double product:

$$\prod_{m=m_{mat}+1}^{m_{rep}} S_d(m, y) \prod_{m=1}^{m_{mat}} S_d(m, y+1) = \begin{cases} \alpha_2 \varphi_2(\underline{N}_{\bar{d}}(m_{mat}, y)) & m_{mat} \leq m_{rec} \\ \alpha_2 \xi_2(\underline{N}_{\bar{d}}(m_{mat}, y)) & \text{else} \end{cases}$$

775 Finally we get systems (11) and (A.1).

776 Appendix C. Jacobian of systems (11) and (A.1)

777 Let $J^*(m_{mat})$ be the Jacobian matrix of system (11) at equilibrium.

778 $J^*(m_{mat})$ is written:

$$J^*(m_{mat}) = \begin{pmatrix} 0 & \dot{j}_{0,a2} & \dot{j}_{0,a_{rec}} & \dot{j}_{0,a_{rec}+1} \\ \dot{j}_{a1,0} & \dot{j}_{a1,a2} & \dot{j}_{a1,a_{rec}} & \dot{j}_{a1,a_{rec}+1} \\ 0 & \dot{j}_{a2+1,a2} & 0 & 0 \\ 0 & 0 & \dot{j}_{a_{rec}+1,a_{rec}} & \dot{j}_{a_{rec}+1,a_{rec}+1} \end{pmatrix} \quad (C.1)$$

779

with $a1 = 1, \dots, a_{mat}$; $a2 = a_{mat}, \dots, a_{rec} - 1$ and:

$$\begin{aligned} \dot{j}_{0,a2} &= -r \alpha_1 [\beta_1 \Psi(\underline{N}_{\bar{d}}^*(m_{mat})) - \psi_1] e^{-\varphi_1(\underline{N}_{\bar{d}}^*(m_{mat}))} \\ \dot{j}_{0,a_{rec}} &= -r \alpha_1 [\theta_1 \Psi(\underline{N}_{\bar{d}}^*(m_{mat})) - \psi_2] e^{-\varphi_1(\underline{N}_{\bar{d}}^*(m_{mat}))} \\ \dot{j}_{0,a_{rec}+1} &= -r \alpha_1 [\kappa_1 \Psi(\underline{N}_{\bar{d}}^*(m_{mat})) - \psi_3] e^{-\varphi_1(\underline{N}_{\bar{d}}^*(m_{mat}))} \end{aligned}$$

780

$$\begin{aligned} \dot{j}_{a1,a1-1} &= \alpha_2 e^{-\varphi_2(\underline{N}_{\bar{d}}^*(m_{mat}))} \\ \dot{j}_{a1,a2} &= -\alpha_2 \beta_2 N_{a1-1,d,\bar{h}}^*(m_{mat}) e^{-\varphi_2(\underline{N}_{\bar{d}}^*(m_{mat}))} \\ \dot{j}_{a1,a_{rec}} &= -\alpha_2 \theta_2 N_{a1-1,d,\bar{h}}^*(m_{mat}) e^{-\varphi_2(\underline{N}_{\bar{d}}^*(m_{mat}))} \\ \dot{j}_{a1,a_{rec}+1} &= -\alpha_2 \kappa_2 N_{a1-1,d,\bar{h}}^*(m_{mat}) e^{-\varphi_2(\underline{N}_{\bar{d}}^*(m_{mat}))} \end{aligned}$$

$$\dot{j}_{a2+1,a2} = \sigma$$

$$\begin{aligned} \dot{j}_{a_{rec}+1,a_{rec}} &= \rho \\ \dot{j}_{a_{rec}+1,a_{rec}+1} &= \nu \end{aligned}$$

781

For system (A.1), the Jacobian matrix at equilibrium is of the same general shape but elements are instead:

782

$$\begin{aligned}
j_{0,a_2} &= -r \alpha_1 [\beta_1 \Phi(\underline{N}_{\bar{d}}^*(m_{mat})) - \psi_1] e^{-\xi_1(\underline{N}_{\bar{d}}^*(m_{mat}))}, & a_2 \neq a_{rec} - 1 \\
j_{0,a_{rec}-1} &= -r \alpha_1 [\eta_1 \Phi(\underline{N}_{\bar{d}}^*(m_{mat})) - \psi_1] e^{-\xi_1(\underline{N}_{\bar{d}}^*(m_{mat}))} \\
j_{0,a_{rec}} &= -r \alpha_1 [\kappa_1 \Phi(\underline{N}_{\bar{d}}^*(m_{mat})) - \psi_3] e^{-\xi_1(\underline{N}_{\bar{d}}^*(m_{mat}))} \\
j_{0,a_{rec}+1} &= -r \alpha_1 [\kappa_1 \Phi(\underline{N}_{\bar{d}}^*(m_{mat})) - \psi_3] e^{-\xi_1(\underline{N}_{\bar{d}}^*(m_{mat}))}
\end{aligned}$$

$$\begin{aligned}
j_{a_1,a_1-1} &= \alpha_2 e^{-\xi_2(\underline{N}_{\bar{d}}^*(m_{mat}))} \\
j_{a_1,a_2} &= -\alpha_2 \beta_2 N_{a_1-1,d,\bar{h}}^*(m_{mat}) e^{-\xi_2(\underline{N}_{\bar{d}}^*(m_{mat}))}, & a_2 \neq a_{rec} - 1 \\
j_{a_1,a_{rec}-1} &= -\alpha_2 \eta_2 N_{a_1-1,d,\bar{h}}^*(m_{mat}) e^{-\xi_2(\underline{N}_{\bar{d}}^*(m_{mat}))} \\
j_{a_1,a_{rec}} &= -\alpha_2 \kappa_2 N_{a_1-1,d,\bar{h}}^*(m_{mat}) e^{-\xi_2(\underline{N}_{\bar{d}}^*(m_{mat}))} \\
j_{a_1,a_{rec}+1} &= -\alpha_2 \kappa_2 N_{a_1-1,d,\bar{h}}^*(m_{mat}) e^{-\xi_2(\underline{N}_{\bar{d}}^*(m_{mat}))}
\end{aligned}$$

$$\begin{aligned}
j_{a_2+1,a_2} &= \sigma, & a_2 \neq a_{rec} - 1 \\
j_{a_2+1,a_{rec}-1} &= \chi
\end{aligned}$$

$$\begin{aligned}
j_{a_{rec}+1,a_{rec}} &= \nu \\
j_{a_{rec}+1,a_{rec}+1} &= \nu
\end{aligned}$$

784 See table 4 for formulations of all the constants.

785 Appendix D. Estimation of parameters for the Bay of Biscay sole

786 Assume that all the model parameters are known except μ and ω . Here,
787 we aim at fitting a custom stock-recruitment relationship compatible with
788 our model formulation to estimate those parameters. In the case where Δ_{mat}
789 and Δ_{rec} verify $m_{mat} \leq m_{rec}$, the population is governed by system (11). It
790 comes immediately from the formulation of the system that:

$$\begin{aligned}
N_{a_{mat},\bar{d},\bar{h}}(m_{mat}, y + a_{mat} + 1) &= r \alpha_1 \alpha_2^{a_{mat}} \Psi(\underline{N}_{\bar{d}}(m_{mat}, y)) \\
&\times e^{-\varphi_1(\underline{N}_{\bar{d}}(m_{mat}, y))} \\
&\times e^{-\sum_{i=1}^{a_{mat}} \varphi_2(\underline{N}_{\bar{d}}(m_{mat}, y+i))}
\end{aligned} \tag{D.1}$$

791 which is the number of newly mature individuals as a function of the set of
792 mature individuals of the a_{mat} years before.

793 To get the number of newly recruited individuals, we just need to take
794 into account the years between maturation and recruitment. We get:

$$\begin{aligned}
N_{a_{rec},\bar{d},\bar{h}}(m_{mat}, y + a_{rec} + 1) &= N_{a_{mat},\bar{d},\bar{h}}(m_{mat}, y + a_{mat} + 1) \\
&\times S_{\bar{d},\bar{h}}^{m_{rep}(a_{rec}-a_{mat})}
\end{aligned} \tag{D.2}$$

795 Let us pose: $X_3 = \frac{X_1}{\mu}$ and $X_4 = X_3 + \frac{X_2 - X_1}{\mu}$, where $X_n = \beta_n, \theta_n, \kappa_n$ (see
796 table 4 for computations of these constants), and let us define:

$$\begin{aligned}
\varphi(y) = & \beta_3 \sum_{a=a_{mat}}^{a_{rec}-1} N_{a,\bar{d},\bar{h}}(m_{mat}, y) \\
& + \beta_4 \sum_{i=1}^{a_{mat}} \sum_{a=a_{mat}}^{a_{rec}-1} N_{a,\bar{d},\bar{h}}(m_{mat}, y + i) \\
& + \theta_3 N_{a_{rec},\bar{d},\bar{h}}(m_{mat}, y) \\
& + \theta_4 \sum_{i=1}^{a_{mat}} N_{a_{rec},\bar{d},\bar{h}}(m_{mat}, y + i) \\
& + \kappa_3 N_{>a_{rec},\bar{d},h}(m_{mat}, y) \\
& + \kappa_4 \sum_{i=1}^{a_{mat}} N_{>a_{rec},\bar{d},h}(m_{mat}, y + i)
\end{aligned} \tag{D.3}$$

797 then we can express:

$$\varphi_1(\underline{N}_{\bar{d}}(m_{mat}, y)) + \sum_{i=1}^{a_{mat}} \varphi_2(\underline{N}_{\bar{d}}(m_{mat}, y + i)) = \mu \varphi(y) \tag{D.4}$$

798 Finally, with $\alpha_1 \alpha_2^{a_{mat}} = e^{-\omega(m_{mat} + a_{mat} m_{rep})}$ we can write the custom
799 stock-recruitment relationship as:

$$N_{a_{rec},\bar{d},\bar{h}}(m_{mat}, y + a_{rec} + 1) = r \sigma^{(a_{rec} - a_{mat})} \Psi(\underline{N}_{\bar{d}}(m_{mat}, y)) \times e^{-\mu \varphi(y) - \omega(m_{mat} + a_{mat} m_{rep})} \tag{D.5}$$

800 Conversely, in the case where Δ_{mat} and Δ_{rec} verify $m_{mat} > m_{rec}$, the rela-
801 tionship to be fitted is:

$$N_{a_{rec},\bar{d},h}(m_{mat}, y + a_{rec} + 1) = r \chi \sigma^{(a_{rec} - a_{mat} - 1)} \Phi(\underline{N}_{\bar{d}}(m_{mat}, y)) \times e^{-\mu \xi(y) - \omega(m_{mat} + a_{mat} m_{rep})} \tag{D.6}$$

802 where

$$\mu \xi(y) = \xi_1(\underline{N}_{\bar{d}}(m_{mat}, y)) + \sum_{i=1}^{a_{mat}} \xi_2(\underline{N}_{\bar{d}}(m_{mat}, y + i)) \tag{D.7}$$

803 Hence, one can estimate parameters μ and ω by non-linear regression for
804 any value of Δ_{mat} or Δ_{rec} , as long as sufficient data is available, assuming that
805 assessment is effectively made at $m = m_{mat}$. The regression was performed

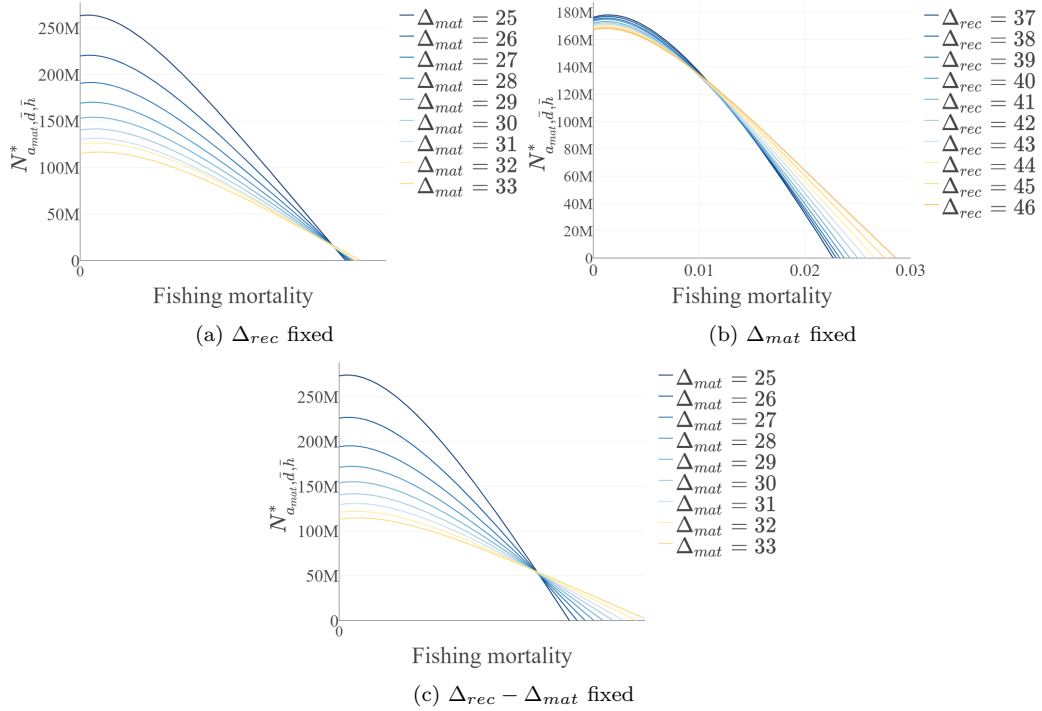


Figure E.9: Number of mature individuals of round age $a = a_{mat}$ at equilibrium ($m = m_{mat}$) as a function of fishing mortality (by month) when Δ_{mat} and Δ_{rec} vary and the system is parameterized for the Bay of Biscay sole. Different colours indicate different values of Δ_{mat} and/or Δ_{rec} depending on the case: (a) Δ_{mat} vary and $\Delta_{rec} = 44$; (b) Δ_{rec} vary and $\Delta_{mat} = 28$; (c) both Δ_{mat} and Δ_{rec} vary and their difference is constant and equals 14.

806 using the `nls` function of R software, and repeated each time Δ_{mat} or Δ_{rec}
 807 was modified.

808 Estimations of parameters μ and ω for each combinations of Δ_{mat} and
 809 Δ_{rec} considered are given in tables 6 and 7.

810 NB: often, data for age $a_{mat} \leq a < a_{rec}$ are not available. In this case,
 811 one can compute them by applying the right constant to the first known age
 812 class. That is what we did for the Bay of Biscay sole (with $a_{rec} - a_{mat} = 1$),
 813 considering that for all y : $N_{a_{mat}, \bar{d}, \bar{h}}(m_{mat}, y) = \frac{N_{a_{rec}, \bar{d}, \bar{h}}(m_{mat}, y+1)}{\sigma}$.

814 Appendix E. Supplementary outputs

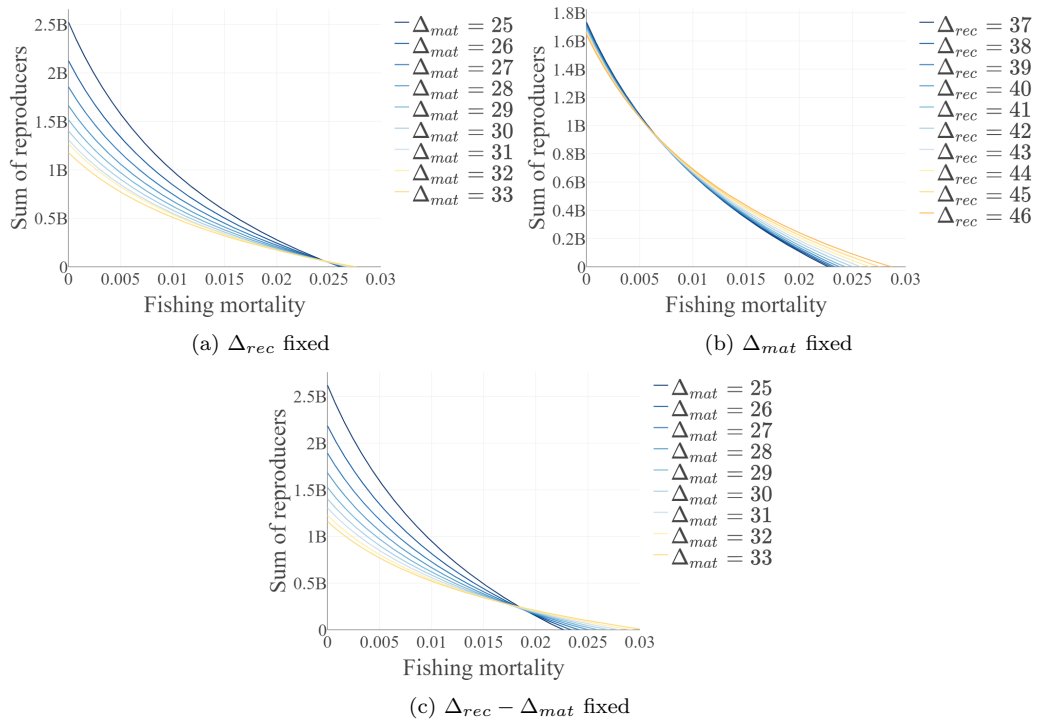


Figure E.10: Sum of reproducers at equilibrium at $m = m_{rep}$ as a function of fishing mortality (by month) when Δ_{mat} and Δ_{rec} vary and the system is parameterized for the Bay of Biscay sole. Different colours indicate different values of Δ_{mat} and/or Δ_{rec} depending on the case: (a) Δ_{mat} vary and $\Delta_{rec} = 44$; (b) Δ_{rec} vary and $\Delta_{mat} = 28$; (c) both Δ_{mat} and Δ_{rec} vary and their difference is constant and equals 14.

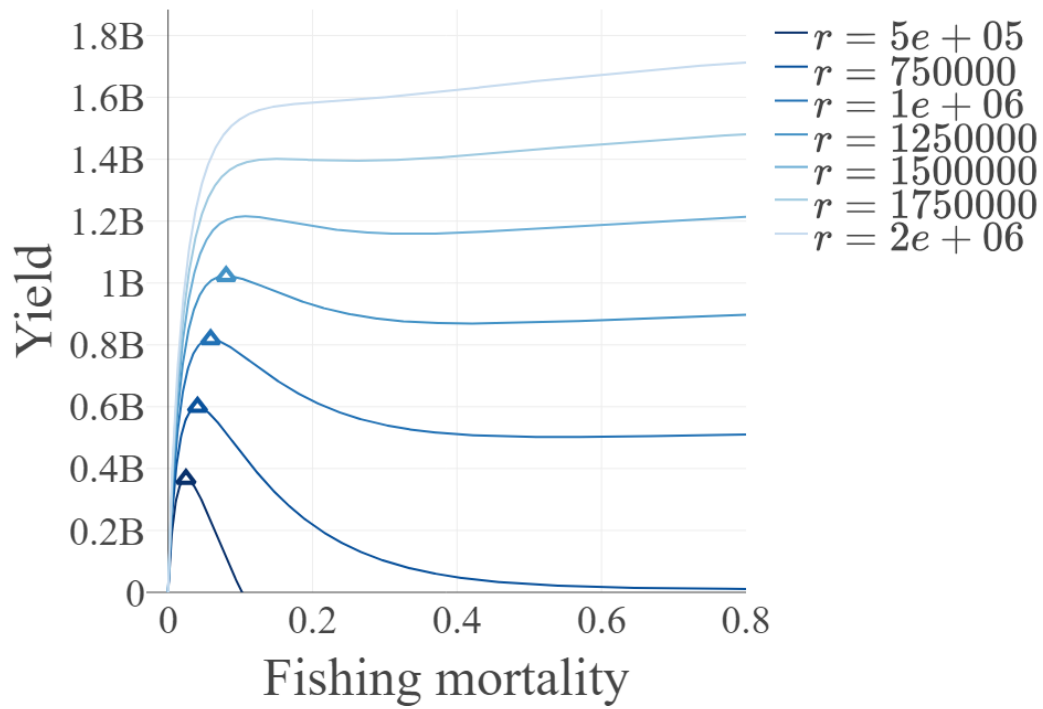


Figure E.11: Total annual yields at inter-annual equilibrium as a function of fishing mortality (by month) and position of MSY when r varies, $\Delta_{mat} = 25$ and $\Delta_{rec} = 39$ (all other parameters being the same as in table 5). Coloured triangles correspond to MSY (numerically solved) and different colours indicate different values of r .

Table E.8: Expressions of the inter-annual dynamics of $\underline{N}(m_{mat}, y)$ when $m_{mat} > m_{rec}$:

$$\left\{ \begin{aligned}
 N_{0, d, \bar{h}}(m_{mat}, y + 1) &= r N_{\bullet, \bar{d}, \bullet}(m_{rep}, y) \prod_{m=1}^{m_{mat}} S_d(m, y + 1) \\
 N_{a_1, d, \bar{h}}(m_{mat}, y + 1) &= N_{a_1 - 1, d, \bar{h}}(m_{mat}, y) \prod_{m=m_{mat} + 1}^{m_{rep}} S_d(m, y) \prod_{m=1}^{m_{mat}} S_d(m, y + 1) \\
 N_{a_2, \bar{d}, \bar{h}}(m_{mat}, y + 1) &= N_{a_2 - 1, \bar{d}, \bar{h}}(m_{mat}, y) S_{\bar{d}, \bar{h}}^{m_{rep}} \\
 N_{a_{rec}, \bar{d}, h}(m_{mat}, y + 1) &= N_{a_{rec} - 1, \bar{d}, \bar{h}}(m_{mat}, y) S_{\bar{d}, \bar{h}}^{m_{rep} - (m_{mat} - m_{rec})} S_{\bar{d}, h}^{m_{mat} - m_{rec}} \\
 N_{>a_{rec}, \bar{d}, h}(m_{mat}, y + 1) &= [N_{>a_{rec}, \bar{d}, h}(m_{mat}, y) + N_{a_{rec}, \bar{d}, h}(m_{mat}, y)] S_{\bar{d}, h}^{m_{rep}}
 \end{aligned} \right. \tag{E.1}$$

with $a_1 = 1, \dots, a_{mat}$ and $a_2 = a_{mat} + 1, \dots, a_{rec} - 1$

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