# 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, seasonal density-dependent processes 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 be associated to unstable or low resilient states. Finally, a numerical illustration for sole (*Solea solea*) of the Bay of Biscay suggests that small seasonal variations on maturation timing can have large effects on the value of MSY and its sustainability, whereas such variations on recruitment only had a limited effect. We therefore advocates a better integration of intra-

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annual time-scales in biological processes when deriving reference points.

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## 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 (Committee, 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 scientists (Hilborn et al., 2015; Donohue et al., 2016). In the classical understanding of sustainability in fisheries as defined by Quinn and Collie (2005), and which correspond to the early developments of harvesting theory, "sus-

tainable" is equivalent to "asymptotically stable" with the use of equilibrium models. Indeed, in the original model of Schaefer (1954) the harvested population is described by a single differential equation, admitting a unique and stable positive equilibrium. This is in line with the ancient conception that, neglecting random fluctuations due to external factors, populations tend to stabilise around an equilibrium value constrained by their environment. It must be stressed out that in this framework, any population level can be considered as sustainable as long as it is positive and MSY is a natural target for fishing management (Quinn and Collie, 2005). Even if the perception of sustainability have evolved and now includes a large number of metrics (Quinn and Collie, 2005; Hilborn et al., 2015; Donohue et al., 2016), the equilibrium-based concept of MSY, as a target or as a threshold (Mace, 2001), remains at the core of fishing management policies.

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

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

Many fish populations characterised by birth-pulse growth with well distinct cohorts (Laurec and Le Guen, 1981) are straightforwardly modelled by the use of stock-recruitment relationships (Ricker, 1954). In this kind of models, recruitment is a discrete event and is well represented by difference

equations. Such models are known to allow cyclic and chaotic dynamics even for a single population (May, 1975) and lead to very complex dynamics (Tang and Chen, 2002). This stresses out the importance of the mathematical formalism employed and suggests that stability properties should not be taken for granted when deriving reference points such as MSY.

More generally, order and duration of density-dependent processes occurring within a year and repeated periodically (what we call here after seasonal processes) play an important role in annual population dynamics (Ratikainen et al., 2007). For example, timing of seasonal harvesting is known to have consequences on the value of MSY (Kokko and Lindström, 1998; Xu et al., 2005) and on the stability of population equilibrium (Cid et al., 2014). However, seasonal processes are generally ignored in practice when deriving reference points for harvested fish populations. This constitutes in itself a specific form of uncertainty in models, which is likely to have important management implications (Ratikainen et al., 2007).

In this study, we consider that stability *sensu stricto* and resilience are key properties of sustainability. Here, we propose a theoretical model of a single harvested population submitted to birth-pulse growth and density-dependence of juveniles to investigate the consequences of the description at seasonal time-scale of two critical processes, namely (i) maturation and (ii) recruitment, on long-term yields and their sustainability. A particular attention is given to the effect of these processes on the MSY. The first process investigated, maturation, is a purely biological process of critical importance that could not be controled by management. Maturation is tightly linked to density-dependence, which is generally supposed to affect strongly immature individuals (Ricker, 1954; Rindorf et al., 2022), and to reproduction. It is subject to uncertainty, given that knowledge for real species is generally available on a yearly basis only (Committee, 2018). On the contrary, the second process, recruitment, defined as the young fish arrival in the exploited portion of the population, can be considered as a management control variable in the sense that is is partially dependent on fishing equipment and behavior (Laurec and Le Guen, 1981). As being related to exploitation, it is likely to have consequences on long-term yields and MSY.

This model and the whole set of hypotheses are presented in section 2. We then make the link between the monthly and yearly dynamics in section 3, by showing that the dynamics can be represented by a first order difference equation system. It is then possible to compute an inter-annual equilibrium and to study his property within the classical dynamical system

theory framework. In section 4, we give some details concerning the equilibrium properties of interest. Although the model is designed to be general and applicable to a large number of exploited populations, we illustrate the results with data for the Bay of Biscay sole (*Solea solea*). These applications are presented in section 5. Finally, our findings are discussed in section 6.

## 2. Models & analysis

### *2.1. Construction of a properly-structured population model with a monthly time-step*

#### *2.1.1. Population & time structure*

Throughout this study, we model the monthly discrete dynamics of a marine population exploited by fishing from a particular biological development stage (recruited individuals). The population is described with a structured abundance at each month $t$, represented by the vector $\underline{N}(t)$ with $t = 1, \ldots, +\infty$. Let us assume that in their life-time, individuals go through three structuring events: (i) reproduction (*i.e.* production of immature individuals from mature ones), (ii) maturation (*i.e.* transformation of immature individuals into mature ones) and (iii) recruitment. The latter is defined (Laurec and Le Guen, 1981) as the entry of individuals into the exploited portion of the population. For sake of simplicity we assume that only mature individuals are exploited, *i.e.* maturation occurs before recruitment.

Considering the seasonality of processes requires that assumptions are explicitly set regarding the intra-annual timing and sequence of the life-cycle events undergone by individuals when they are assumed simultaneous in annual models. Here, we assume that new-born individuals mature and recruit after a fixed number of months noted $\Delta_{mat}$ and $\Delta_{rec}$ respectively (as represented on time arrow in figure 1). Between two successive time-steps $t$ and $t+1$, events happening in individuals lives depend on their exact age $\delta$ (in months) in comparison with $\Delta_{mat}$ and $\Delta_{rec}$. Immature individuals ($\delta \leq \Delta_{mat}$) are unable to reproduce, are not exploited and are assumed to undergo each month $t$ a density-dependent mortality from mature individuals. Mature individuals ($\delta > \Delta_{mat}$) are able to reproduce and are assumed to undergo each month a constant natural mortality. Recruited individuals ($\delta > \Delta_{rec}$) undergo an additional fishing mortality and contribute to yields.

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

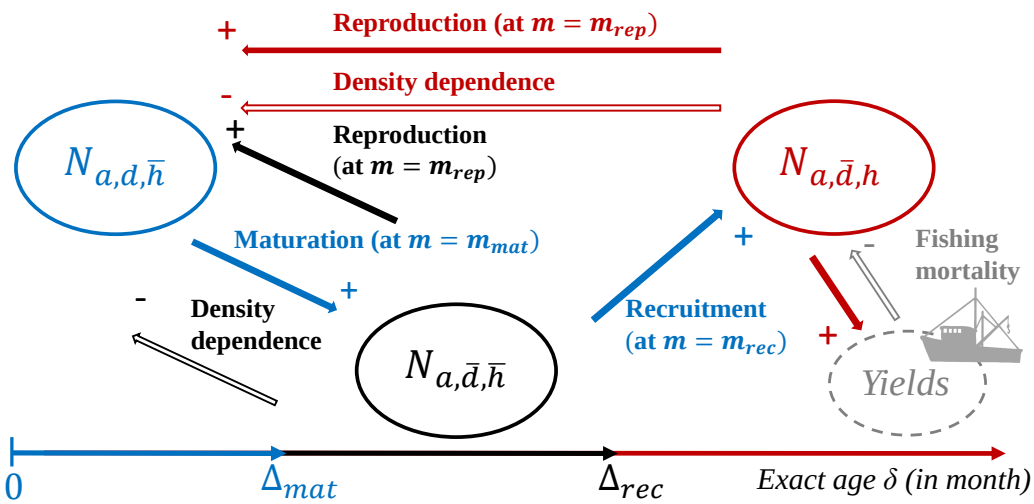



Figure 1: Conceptual view of the interactions between individuals and their influence on yields. Index $\{a = 0, \ldots, > a_{rec}\}$ stands for round age in years, index $\{d, \bar{d}\}$ stands for density-dependence and index $\{h, \bar{h}\}$ stands for accessibility to fishing. Three groups must be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

with each other in different ways. Depending on the value of $\Delta_{mat}$ and $\Delta_{rec}$, the relative importance of each process is expected to differ. First, density-dependence is expected to have a larger effect on the overall dynamics if $\Delta_{mat}$ is large. The relative position of $\Delta_{rec}$ to $\Delta_{mat}$ controls the amount of time spent by mature individuals in the unspoiled situation characterized by a higher survival rate than immature and recruited individuals. The longer this duration time $(\Delta_{rec} - \Delta_{mat})$ is, the more numerous mature protected individuals are, hence fostering reproduction. However it also affects the number of immature individuals through the capacity of fishing to modulate the effect of natural compensation within the population by removing cannibalistic adults. Indeed, individuals of age $\Delta_{mat} \leq \delta < \Delta_{rec}$ do not undergo 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 $m_{rep} = 12$. $\Delta_{mat}$ and $\Delta_{rec}$ can be expressed as:

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

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

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

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

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 the end of which reproduction happens.

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

One of the main originalities of our model lies in the choice of the structure of the population $\underline{N}(t)$ according to successive properly defined stages. Thanks to this particular structure, we will be able to perform easily the equilibrium and stability analysis in the next step. The stages are defined by the round age $a$ in year (expressed as an integer number of whole years lived by individuals, as opposed to exact age $\delta$ in months), the maturity (characterised by constant instead of density-dependent natural mortality) and the accessibility to fishing. Individuals are arranged into $a_{rec} + 2$ modalities associated to round age $a$: $\{0, 1, \ldots, a_{rec}, > a_{rec}\}$, two modalities associated to maturity (density-dependant vs. independent): $\{d, \bar{d}\}$ and two modalities associated to fishing (harvested vs. unharvested) $\{h, \bar{h}\}$.

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

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

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 respectively immature, mature, harvested and unharvested individuals of round age $a$ at time $t$.

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

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

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

*2.1.2. Description of the monthly dynamics*

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

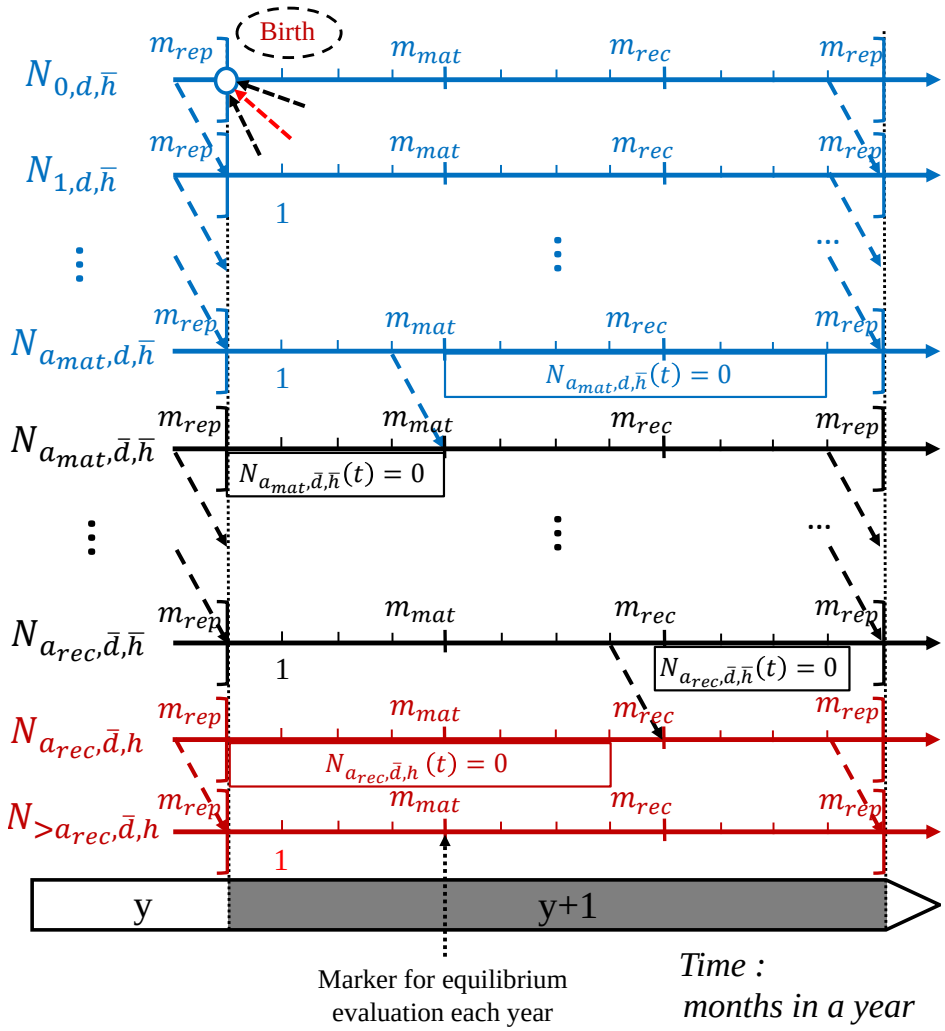



Figure 2: Conceptual view of the structured population and its dynamics represented in our model. Graduations are in months, and year succession is represented by the large arrow at the bottom, for all year $y$. The blue circle with dashed red and black arrows stands for the production of individuals 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 $y$.

We model explicitly a density-dependent mortality of immature individuals at each time step, assuming after Ricker (1954) that mortality of immature individuals increases with the number of mature individuals. Let the mortality of immature individuals between $t$ and $t+1$ be:

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

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

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

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

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

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

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

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

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

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

and

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

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

For classes $(a2,\bar{d},\bar{h}),\ a2 \in \{a_{mat}+1,\ \ldots,\ a_{rec}-1\}$, we have for all $y$:

$$
\begin{aligned}
&N_{a2,\bar{d},\bar{h}}(1,y) = N_{a2,\bar{d},\bar{h}}(m_{rep},y-1)\, S_{\bar{d},\bar{h}}\\
&N_{a2,\bar{d},\bar{h}}(m,y) = N_{a2,\bar{d},\bar{h}}(m-1,y)\, S_{\bar{d},\bar{h}},\ \forall\, m \in \{2,\ldots,m_{rep}-1\}\\
&N_{a2,\bar{d},\bar{h}}(m_{rep},y) = N_{a2-1,\bar{d},\bar{h}}(m_{rep}-1,y)\, S_{\bar{d},\bar{h}}
\end{aligned}
\tag{7}
$$

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

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

and

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

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

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

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

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

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

### *2.2. Connecting intra-annual and inter-annual time-scales*

#### *2.2.1. From a monthly dynamics to an annual dynamics*

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

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

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

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

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

$$\begin{cases} N_{0,d,\bar{h}}(m_{mat}, y+1) = r\,\alpha_1\,\Psi\left(\underline{N}_{\bar{d}}(m_{mat}, y)\right)\, e^{-\varphi_1(\underline{N}_{\bar{d}}(m_{mat},y))} \\ \\ N_{a1,d,\bar{h}}(m_{mat}, y+1) = \alpha_2\, N_{a1-1,d,\bar{h}}(m_{mat}, y)\, e^{-\varphi_2(\underline{N}_{\bar{d}}(m_{mat},y))} \\ \\ N_{a2,\bar{d},\bar{h}}(m_{mat}, y+1) = \sigma\, N_{a2-1,\bar{d},\bar{h}}(m_{mat}, y) \\ \\ N_{>a_{rec},\bar{d},h}(m_{mat}, y+1) = \nu\, N_{>a_{rec},\bar{d},h}(m_{mat}, y) \\ \qquad\qquad\qquad\qquad + \rho\, N_{a_{rec},\bar{d},\bar{h}}(m_{mat}, y) \end{cases} \tag{11}$$

with $a1 = 1, \ldots, a_{mat}$ and $a2 = a_{mat} + 1, \ldots, a_{rec}$. $\Psi\left(\underline{N}_{\bar{d}}(t)\right)$ is the number of spawner and $\varphi_n(\underline{N}_{\bar{d}}(t))$ is a density-dependence function (see table 4 for detailed expressions). Moreover :

- $\Psi\left(\underline{N}_{\bar{d}}(t)\right)$ and $\varphi_n(\underline{N}_{\bar{d}}(t))$ are linear combinations of $\left(N_{a,\bar{d},\bar{h}}(t)\right)_{a=a_{mat},\ldots,a_{rec}}$ and $\left(N_{a,\bar{d},h}(t)\right)_{a=a_{rec},>a_{rec}}$.
- $\alpha_n$, $\sigma$, $\nu$, $\rho$ are positive constants.

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

*2.2.2. Expressions of equilibrium*

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

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

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

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

with $\underline{N}^*_{\bar{d}}(m_{mat}) = {}^t\left(N^*_{a_{mat},\bar{d},\bar{h}}(m_{mat}), N^*_{a2,\bar{d},\bar{h}}(m_{mat}), N^*_{>a_{rec},\bar{d},h}(m_{mat})\right)$ and $a2 = a_{mat} + 1, \ldots, a_{rec}$;

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

*2.3.1. Maximum Sustainable Yield*

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

$$Y^*(m_{mat}) = N^*_{\bullet,\bar{d},h}(m_{mat})\,\left(1 - e^{-(M_{\bar{d}}+F)}\right)\,\frac{F}{M_{\bar{d}} + F} \tag{13}$$

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 of recruited individuals at month $m = m_{mat}$ at inter-annual equilibrium.

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

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

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 $Y^*_T(.)$ to get the value of MSY and $F_{MSY}$:

$$MSY = \max(Y^*_T(F))$$

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

*2.3.2. Equilibrium stability & resilience*

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

$$|\lambda_i| < 1, \qquad \forall i \in \{1, \ldots, a_{rec} + 2\} \tag{15}$$

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

Expressions of eigenvalues are expected to be too complex to be analytically tractable and interpretable especially when the system is of large dimension. We therefore calculated numerically the eigenvalues to detect stability changes.

The stability properties of equilibrium depends on parameters. Hence, stability, unstability, and extinction domains (*i.e* the set of parameters for

which the equilibrium is stable, unstable and lesser than zero, respectively) represent volumes in a parameter space. In particular, we pay attention of the surfaces of stability, unstability and extinction in the $r \times F$ plan. Variations along the $r$ axis can represent differences of fecundity between stocks or differences in reproductive success for a same stock, whereas $F$ is the main control variable when dealing with exploited systems. In such a plan, it is also possible to plot the value of $F_{MSY}$ if it does exist, for each value of $r$.

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

$$\tau = \frac{1}{1 - |\lambda_{max}|} \tag{16}$$

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

Considering that return-time is a function of $F$, we can define another reference point, the Resilience Maximising Yield ($RMY$) and its associated return-time ($MiRT$) as:

$$F_{RMY} = \arg\min_{F} \ \tau(F)$$

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

#### *2.3.3. Sensitivity of MSY, stability domain and resilience to seasonality of maturation and recruitment*

Here, our aim is to assess the sensitivity of the equilibrium properties, namely $MSY$, $F_{MSY}$, $MiRT$ and $F_{MiRT}$ values, extinction and unstability domains (quantified by the areas under the curves $A_{ext}$ and $A_{stab}$ respectively) to seasonal variations of maturation and recruitment, represented by parameters $\Delta_{mat}$ and $\Delta_{rec}$. The first one must be considered as a biological parameter subject to epistemic uncertainty whereas the second can be considered as a control variable insofar it is, at least theoretically, possible not to catch individuals under a defined age. Values for $\Delta_{mat}$ and $\Delta_{rec}$ are allowed

to vary in a time-span shorter than one year. Such seasonal variations are generally not taken into account when computing reference points for fisheries management. Indeed, for most fish populations, information concerning maturation and recruitment are available on yearly basis only (Committee, 2018). We perform a variance-based sensitivity analysis based on 1) an experimental design and 2) sensitivity indices associated to $\Delta_{mat}$, $\Delta_{rec}$ and $r$ (the inputs of the model) on each metric $MSY$, $F_{MSY}$, $A_{ext}$ and $A_{stab}$ (model outputs) derived from an ANOVA. Then we can compute the sensitivity index of each parameter, both for principal effect and interactions (see *e.g.* Faivre et al. (2013) for full details on the method). The experimental design is build combining all possibles values of $\Delta_{mat}$, $\Delta_{rec}$ and $r$ within defined ranges. $\Delta_{mat}$ and $\Delta_{rec}$ take values expanding on a time-span less or equal to one year and $r$ takes values within a range large enough to get contrasted results and including the realistic value extracted from literature for sole (see table 5).

## 3. Application to the Bay of Biscay sole

### *3.1. Origin of data*

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

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

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

The last two parameters $\mu$ and $\omega$, which govern density-dependence, were estimated based on ICES stock assessment results (ICES, 2018; table 7.10 p277). The basic idea here is to fit a custom stock-recruitment relationship on data (see Appendix D for more details).

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

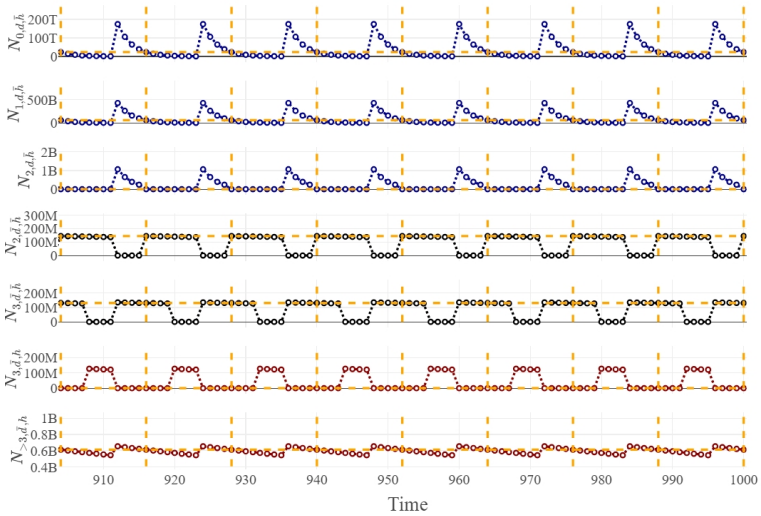
Once the model is fully parameterised, it is possible on the one hand to simulate the monthly dynamics with respect to equations (3-10), and on the other hand to compute the theoretical inter-annual equilibrium vector $\underline{N}^*(m_{mat})$. Both the abundance time series and the equilibrium abundance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

### 3.3. Sensitivity of MSY to the seasonality of maturation and recruitment

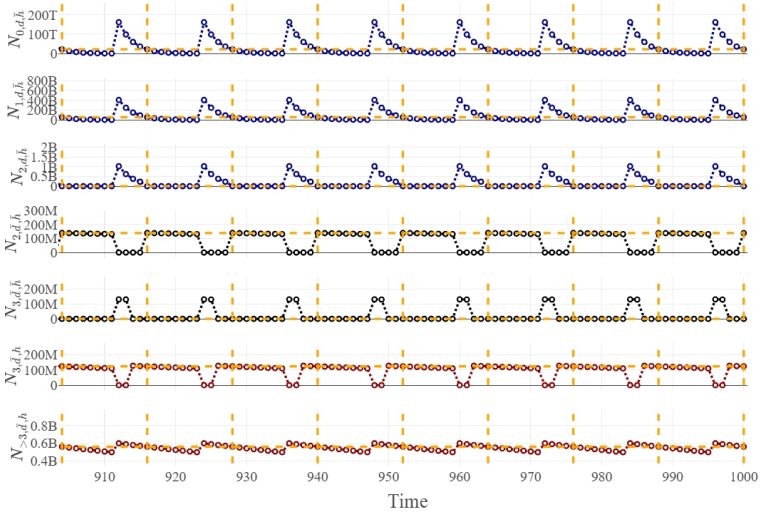
The equilibrium yield of the sole of the Bay of Biscay is computed for a range of monthly fishing mortality $F \in [0; 0.4]$ and is numerically optimised as a function of $F$ to get the MSY. We assessed their sensitivity to $\Delta_{mat}$ and $\Delta_{rec}$ varying in a range shorter than 12 months, with $\Delta_{mat} = 25, 26, \ldots, 30$ (*i.e.* between the first and ninth month of the year) and $\Delta_{rec} = 37, 38, \ldots, 46$. As observed in figure 5a, values of $\Delta_{mat} > 30$ lead to null catches for all $F$.

First, it appears clearly that both the value of $MSY$ and the position of $F_{MSY}$ are much more sensitive to variations of $\Delta_{mat}$ ($SI = 0.74$ for $MSY$ value and $SI = 0.0.73$ for $F_{MSY}$, total effects) than to $\Delta_{rec}$ ($SI = 5.9 \times 10^{-3}$ for $MSY$ value and $SI = 0.05$, for $F_{MSY}$ total effects), as shown in figure 4a and 4b. The parameter $r$ also plays an important role as could be expected ($SI = 0.34$ for $MSY$ values and $SI = 0.38$ for $F_{MSY}$, total effects) but not as important as $\Delta_{mat}$. Interestingly, for those two parameters, interactions effects are relatively important, in particular, for the parameter $r$ in predicting the value $F_{MSY}$, interaction effects are almost as important as main effects (0.17 and 0.21, respectively).

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

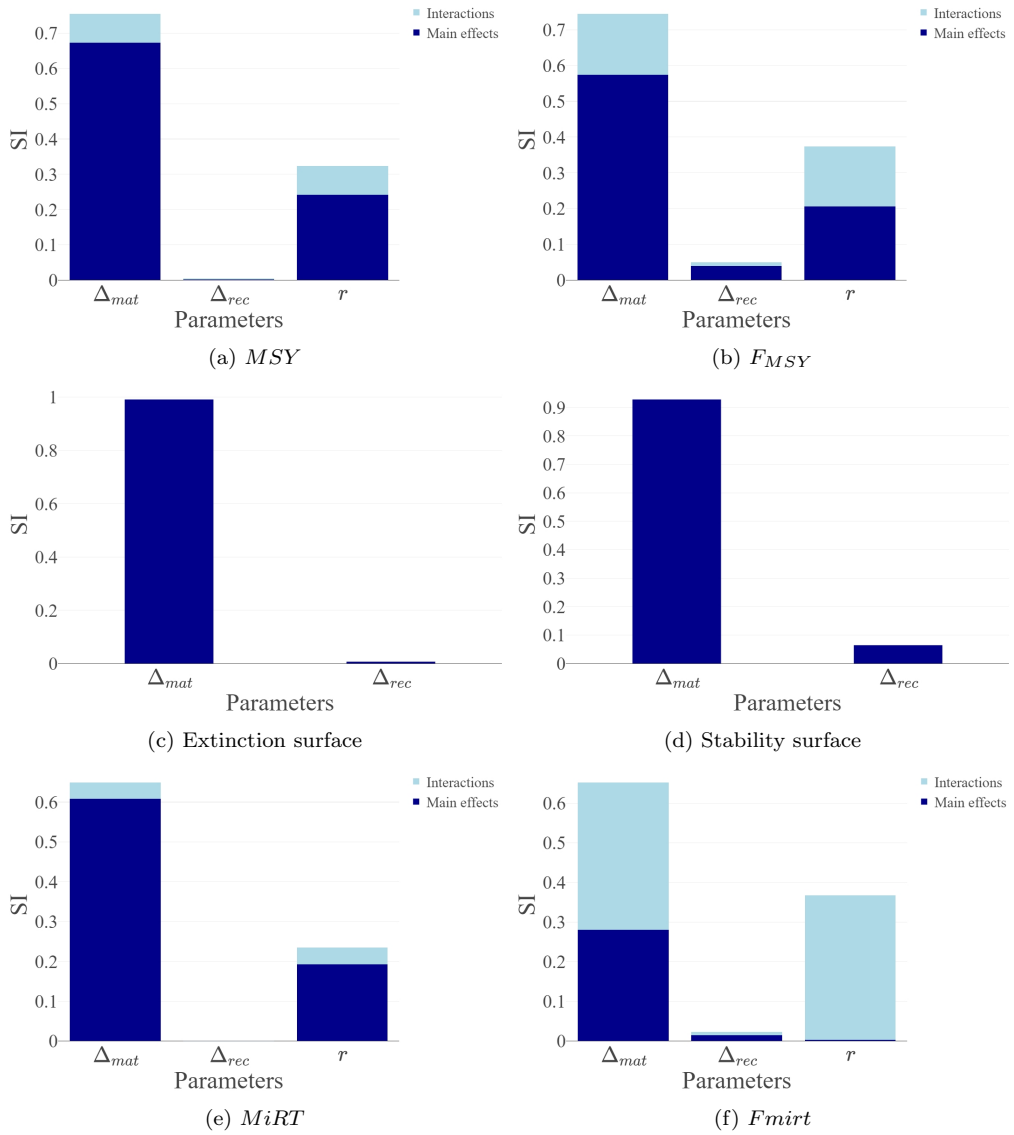



(a) $m_{mat} \leq m_{rec}$




(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.* $a_{rec} = 3$, $m_{rec} = 2$).




(a) $MSY$

(b) $F_{MSY}$

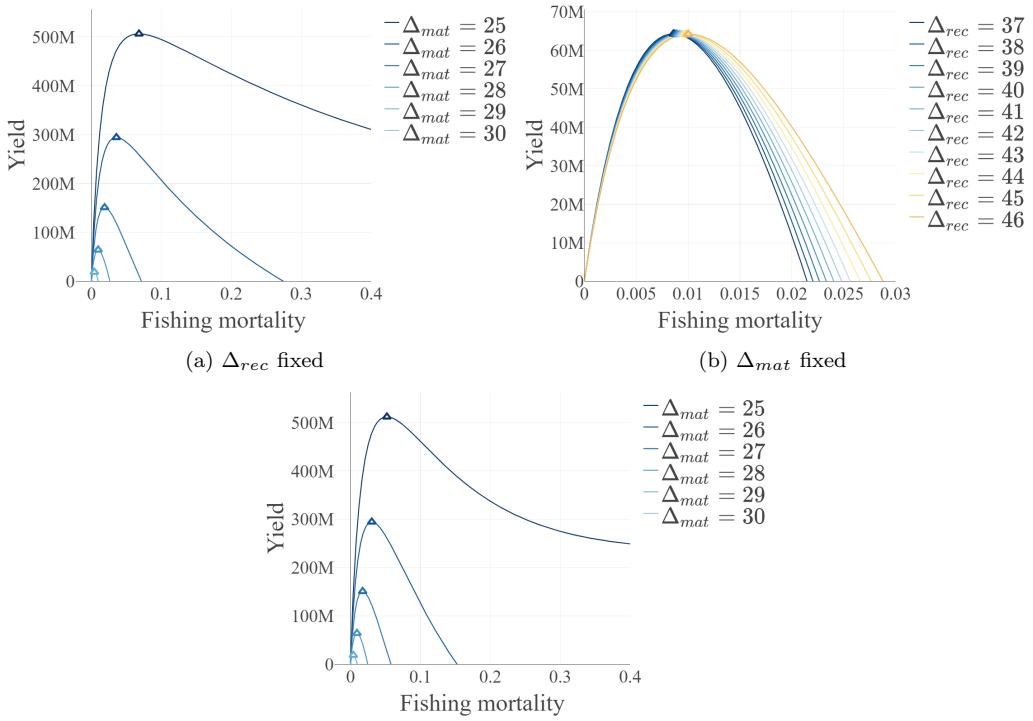
(c) Extinction surface

(d) Stability surface

(e) $MiRT$

(f) $Fmirt$

Figure 4: Sensitivity indices of parameters $\Delta_{mat}$, $\Delta_{rec}$ and $r$ (except for (c) and (d) where $r$ is a dimension of plan on which surfaces are measured) 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) $F_{MiRT}$.




(a) $\Delta_{rec}$ fixed

(b) $\Delta_{mat}$ fixed

(c) $\Delta_{rec} - \Delta_{mat}$ fixed

Figure 5: Total annual yields at inter-annual equilibrium as a function of fishing mortality (by month) and position of MSY when $\Delta_{mat}$ and/or $\Delta_{rec}$ 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 $\Delta_{mat}$ and/or $\Delta_{rec}$ depending on the case: (a) $\Delta_{mat}$ vary and $\Delta_{rec} = 44$ ; (b) $\Delta_{rec}$ vary and $\Delta_{mat} = 28$ ; (c) both $\Delta_{mat}$ and $\Delta_{rec}$ vary and their difference is constant and equals 14 ($\Delta_{mat} = 25, 26, \ldots, 30$ ; $\Delta_{rec} = 39, 40, \ldots, 44$).

$F_{MSY}$ also clearly decreases when $\Delta_{mat}$ increases. Both tend to zero values when $\Delta_{mat}$ is around 30. With maturation lags higher than this threshold, the population is no longer viable (*i.e.* the population collapses).

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

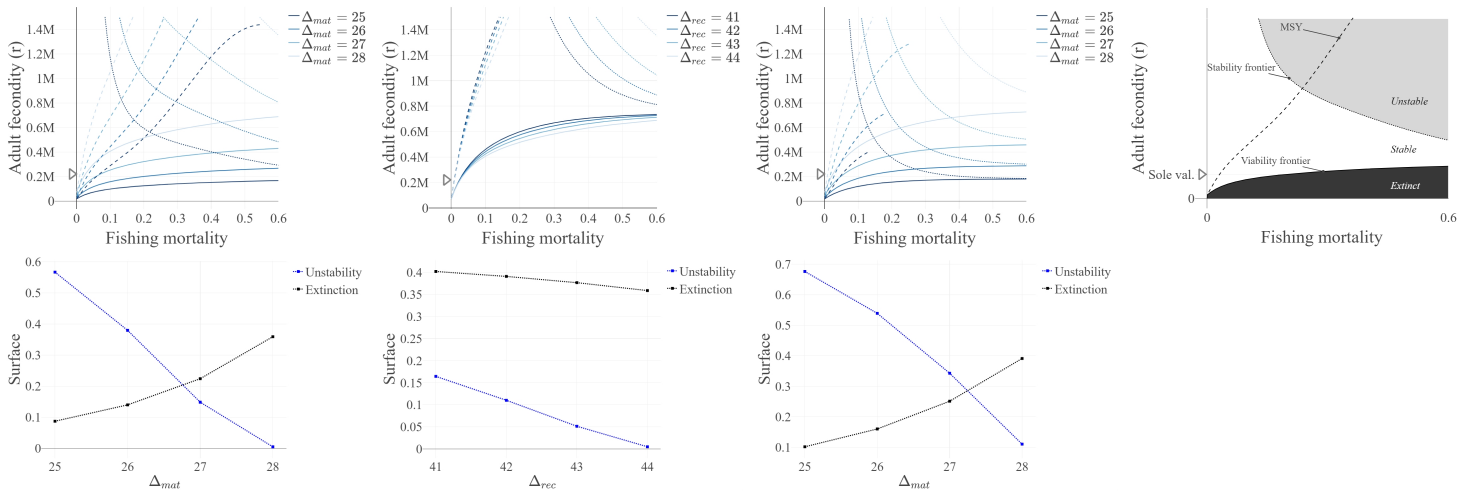
As shown in figure 5b), an increase in $\Delta_{rec}$ is associated to an increase in $F_{MSY}$, as well as extinction mortality (*i.e* the smallest value of $F > 0$ that brings null yields because of extinction of the population). However, the impact is small as compared as the impact of $\Delta_{mat}$ (figure 5a). Likewise, the value of MSY is relatively constant with the variations of recruitment lag considered here.

When $\Delta_{mat}$ and $\Delta_{rec}$ are varied jointly so that the mature unharvested phase (in black on figure 1) is constant in duration, the general shape of the curves obtained (figure 5c) are similar to those obtained when $\Delta_{mat}$ only is varied 5a. However, extinction mortalities for the same value of $\Delta_{mat}$ are lesser in figure 5c than in figure 5a. In this way, yield curves look slightly more symmetrical when the mature-unharvested phase is kept constant in duration. The value of MSY are similar in figure 5a and in figure 5c.

### *3.4. Sensitivity of stability domain to the seasonality of recruitment and maturing*

The domain of viability and of stability of the population in the $r \times F$ plan is also affected when $\Delta_{mat}$ and/or $\Delta_{rec}$ vary, although the first one has a much larger effect (figure 4c and 4d). Indeed, sensitivity index of $\Delta_{mat}$ is of 0.99 for the surface of viability domain and of 0.92 for the surface of stability domain in the considered section of $r \times F$ plan, which means that most of the variance in those surfaces are explained by variations of $\Delta_{mat}$.

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




(a) $\Delta_{rec}$ fixed (b) $\Delta_{rec}$ fixed (c) $\Delta_{rec} - \Delta_{mat}$ fixed

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 $\Delta_{mat}$ and/or $\Delta_{rec}$ 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 the right panel. 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) $\Delta_{mat}$ vary and $\Delta_{rec} = 44$ ; (b) $\Delta_{rec}$ vary and $\Delta_{mat} = 28$ ; (c) both $\Delta_{mat}$ and $\Delta_{rec}$ vary and their difference is constant and equals 14 ($\Delta_{mat} = 25, \ldots, 28$ ; $\Delta_{rec} = 39, \ldots, 42$).

When $\Delta_{mat}$ only varies (figure 6a), as was seen before, an increase in $\Delta_{mat}$ value reduces the viability surface of the population. Indeed for a same value of parameter $r$, a lower $F$ brings population to extinction when $\Delta_{mat}$ is high. Moreover, as was stated above, a difference of one or very few months can have large consequences in terms of viability. For example, take a species with a $r$ value around 0.2M (which is the order of magnitude of the Bay of Biscay sole), it will be able to sustain a fishing mortality of 0.2 if $\Delta_{mat}$ equals 26 whereas it will be extinct with an $F$ lesser than 0.01 if $\Delta_{mat}$ is greater than 27.

Variations of $\Delta_{mat}$ also have important consequences concerning the position of the stability frontier. Quite surprisingly, for a given $r$ the value of $F$ necessary to destabilise inter-annual equilibrium is higher when $\Delta_{mat}$ is high. This suggests that a long immature phase has a stabilizing effect on the population, probably a consequence of spreading in time density-dependent processes (as illustrated in figure 1).

As was also stated before, the value of $F_{MSY}$ is extremely sensitive to variations of $\Delta_{mat}$ with a decreased value when $\Delta_{mat}$ is high. By superimposing curves for $F_{MSY}$ with stability domain, we can see that MSY can in fact, at least theoretically, be associated to an unstable *i.e.* non-sustainable state. Once again position of crossings between $F_{MSY}$ curves and stability frontier is highly dependent of $\Delta_{mat}$. However considering realistic values for $r$ (of the same order of magnitude as the sole of the Bay of Biscay, say 0.2M), it is clear that the population is much more likely to become extinct than to get his equilibrium destabilised, given the respective positions of the stability and viability frontiers (figure 6).

The fact that intra-annual variations of $\Delta_{rec}$ have little effect on viability frontiers and on $F_{MSY}$ is confirmed by the stability analysis (figure 6b. The effect of these variations on stability frontiers is visible but appears to be lesser than the effect of $\Delta_{mat}$ variations. The direction of variation is the same as with $\Delta_{mat}$ variations given that for a fixed value of $r$, the higher $\Delta_{rec}$, the higher the value of $F$ needed to destabilise the equilibrium. Within the ranges of $r$ and $F$ investigated here, $F_{MSY}$ is always associated to a stable inter-annual equilibrium.

When $\Delta_{mat}$ and $\Delta_{rec}$ are varied jointly so that the mature unharvested phase is constant in duration (figure 6c), differences with the pattern observed for $\Delta_{mat}$ (figure 6a) concerning stability frontiers exist, even if viability frontiers are very similar. In particular, the stability domain is smaller (*i.e.* the equilibrium is easier to destabilise) when $\Delta_{mat}$ only varies. Indeed, for a given

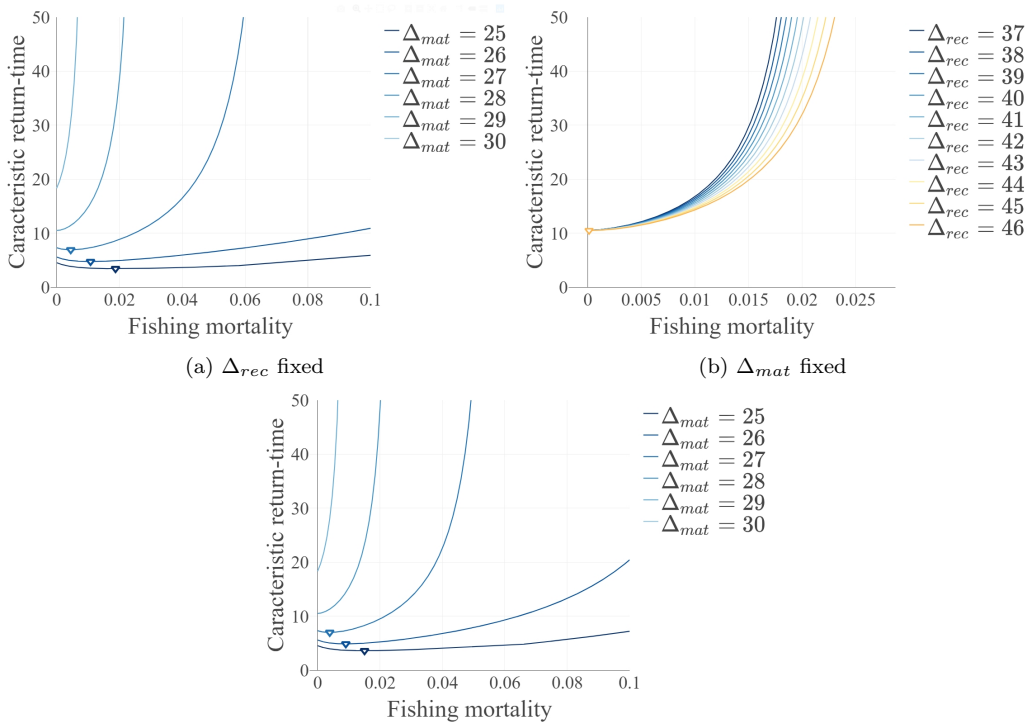
$r$, the fishing mortality necessary to destabilize the population is less than in figure 6a. Differences also exist on $F_{MSY}$ curves. By contrast to the pattern observed for $\Delta_{mat}$ variations only (figure 6a), they are interrupted when $r$ is increased beyond a certain threshold. This interruption is due to a modification of the yield curve's shape, the optimum being replaced by a plateau (see figure E.10 in appendices). In this configuration the MSY strictly speaking (*i.e.* the optimum) can either be (i) always stable (*e.g.* with $\Delta_{mat} = 25$) or (ii) stable or unstable depending on $r$ (*e.g.* with $\Delta_{mat} = 28$).

### *3.5. Sensitivity of the resilience to the seasonality of recruitment and maturing*

Resilience and $MiRT$ also are affected by intra-annual variations of $\Delta_{mat}$ and $\Delta_{rec}$. Once again, the influence of $\Delta_{mat}$ ($SI = 0.64$ for $MiRT$, and $SI = 0.65$ for $F_{MiRT}$, total effects) is much more pronounced than the influence of $\Delta_{rec}$ ($SI = 8.3 \times 10^{-4}$ for $MiRT$, and $SI = 0.02$ for $F_{MiRT}$, total effects), as shown in figures 4e and 4f). For the position of $F_{MiRT}$, interestingly, the parameter $r$ has a very low main effect but a strong interaction effect (more than 0.36) with $\Delta_{mat}$ (figure 4f). This suggests that $\Delta_{mat}$ is a major driver of the variations of the position of $F_{MiRT}$ but that it is likely to act very differently depending on $r$.

It appears that, as for yields, small variations of $\Delta_{mat}$ have a large effect on resilience curves (figure 7a). When $\Delta_{mat}$ is minimum, $MiRT$ is also minimum and resilience is high for a large range of fishing mortality. When $\Delta_{mat}$ increase, *i.e.* when the density-dependent phase increase in duration, $F_{RMY}$ decrease to reach zero for $28 \leq \Delta_{mat}$. Moreover, characteristic return-time increases faster when $\Delta_{mat}$ is higher. These elements suggest that populations with longer immature phase tend to be less resilient than populations with shorter ones and that small intra-annual variations in maturation process can have a decisive effect on their inter-annual resilience.

On the contrary, variations of $\Delta_{rec}$ within a year has little influence on resilience curves (figure 7b). In particular, $F_{RMY}$ is constant and equals 0 in our example. $MiRT$ is to be constant as well. This observation is strengthened by the fact that the first two cases, namely where (i) $\Delta_{mat}$ alone varies (figure 7a), and (ii) $\Delta_{mat}$ and $\Delta_{rec}$ vary jointly (figure 7c) present very similar patterns. This result suggests that resilience curves are mainly modified by small variations of maturation lag, rather than by variations of recruitment lag.




(a) $\Delta_{rec}$ fixed

(b) $\Delta_{mat}$ fixed

(c) $\Delta_{rec} - \Delta_{mat}$ fixed

Figure 7: Caracteristic return-time to inter-annual equilibrium as a function of fishing mortality (by month) and position of RMY when $\Delta_{mat}$ and $\Delta_{rec}$ vary and the system is parameterized for the Bay of Biscay sole. Coloured triangles correspond to RMY (numerically solved) and different colours indicate different values of $\Delta_{mat}$ and/or $\Delta_{rec}$ depending on the case: (a) $\Delta_{mat}$ vary and $\Delta_{rec} = 44$ ; (b) $\Delta_{rec}$ vary and $\Delta_{mat} = 28$ ; (c) both $\Delta_{mat}$ and $\Delta_{rec}$ vary and their difference is constant and equals 14 ($\Delta_{mat} = 25, 26, \ldots, 30$ ; $\Delta_{rec} = 39, 40, \ldots, 44$).

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

## 4. Discussion and conclusion

Our aim in this study was to investigate the effect of processes occurring at intra-annual time scales on the amount and sustainability of long-term yields from a population, and on the widely used reference point known as MSY. We considered an idealised population submitted to three structuring processes namely reproduction, maturation and recruitment and described using a deterministic, structured dynamic population model in monthly discrete-time. The main originality of the modelling approach relies on structuring of the population dynamics that has to our knowledge, never been adopted in earlier studies. Most modelling approaches use structuring by age (Marchal et al., 2009; Tahvonen, 2009; Doyen et al., 2012; Nielsen and Berg, 2014), by size (Bartolino, 2011; Lindstrøm et al., 2009) or by stage (Zipkin et al., 2008; Wikström et al., 2012; Liz and Pilarczyk, 2012). In our modelling framework instead, the classes of the population are defined by combining (i) age (in year), (ii) maturity and (iii) accessibility to fishing characteristics. Thanks to this original structure we were able on the one hand, to simulate month by month the evolution of the population, and on the other hand, to resume the inter-annual dynamics to a first order difference equation system. This interesting result enabled us to compute analytically the inter-annual equilibrium and to assess numerically its stability and resilience as a function of the model parameters. This is in our sense one of the main innovation of our approach.

Application of the model was illustrated with parameters and data published for the Bay of Biscay sole, although we stress that our model is general and flexible enough to be applicable to any species whatever the ages of maturation and recruitment. In our model, we hypothesized that recruitment occurs after maturation but the reverse situation would constitute a straightforward generalisation. Moreover, we investigated wide ranges of variations

for selected parameters of interest (namely lags $\Delta_{mat}$ and $\Delta_{rec}$, and adult fecundity $r$) so that our conclusions could be applicable to a large number of species.

First, we found that yields curves shape was much more influenced by variations of maturation lag $\Delta_{mat}$ than by variations of recruitment lag $\Delta_{rec}$. In classical stock-recruitment modelling (Hilborn and Walters, 1992), all processes occurring before the age of first capture are synthesised into a single stock-recruitment relationship (Bjorkstedt, 2000). The advantage of our model is to separate explicitly maturation and recruitment as processes of different nature. As a matter of fact, maturation is a strictly biological process on which no control is possible whereas recruitment is in part dependent of fishing behavior and gear (Laurec and Le Guen, 1981) so that it could be considered as a control variable.

In practice, for most exploited species, these information on maturation and recruitment are known, if at all, on a yearly basis only Committee (2018) and the specific uncertainty related to timing and duration of processes on intra-annual time-scales is generally ignored. The application of our model to the Bay of Biscay sole is in line with other studies (Kokko and Lindström, 1998; Tang and Chen, 2004; Xu et al., 2005; Cid et al., 2014) concerning the fact that intra-annual time-scales matter and that neglecting them can lead to important errors. Here, we argue that timing of biological processes have wider consequences than harvesting. With this example we show that ignoring the seasonality of maturation can have a large impact on the computation of classical reference points such as MSY. It is expected that these aspects could be even more critical if the seasonality of fishing was considered and F varied within the year as it is usually the case.

We aimed at evaluating the consequences of ignoring intra-annual time-scale or seasonality of maturation and recruitment processes which *in fine* translates into differences in mortality of individuals depending on their stage. Although we vary parameters $\Delta_{mat}$ and $\Delta_{rec}$ only, we are forced to recognise that the effect of these variations is confounded with the effect of changing the overall mortality , which limits the scope of our results.

The second aspect of our study was to quantify local stability of inter-annual equilibrium as a measure of sustainability of yields drawn from the population. There is a growing debate on whether the fish populations are stable or not, and on the role of fishing on their destabilisation (Anderson et al., 2008; Shelton and Mangel, 2011; Sugihara et al., 2011; Rouyer et al., 2012). Our results support after other studies (Hsieh et al., 2006; Anderson

et al., 2008; Cid et al., 2014; Liz, 2017) the fact that single population's equilibrium can be destabilised by increasing fishing mortality, especially for species with high fecundity. Our model allows us to investigate if change in reproduction could also lead to destabilisation of the equilibrium. When parameterised for the Bay of Biscay sole, the value of parameter $r$ required to effectively destabilise the inter-annual equilibrium is too high to be realistic and the population is more likely to become extinct than to have his inter-annual equilibrium destabilised.

Shelton and Mangel (2011) assessed the stability of a Ricker model parameterised for 45 exploited stocks and concluded that the presence of deterministic cyclic or chaotic behavior in real stocks was very unlikely. Our results are consistent with this prediction even if differences with their findings must be noticed. In particular, an important difference concerns the modification of the stability region when the time between birth and maturation increase. In our model, the stability region increases when $\Delta_{mat}$ increase, in the sense that a higher $F$ is necessary to destabilise the inter-annual equilibrium. In their study, on the contrary, the stability region decreases with each year added between birth and maturation. The explanation of this difference must rely on the different hypothesis concerning density dependence. Indeed, in our model immature individuals' mortality is made dependent of adult abundance at each month and not only on the abundance at birth-time as it is the case in Ricker model. Unfortunately, our model is too complex to get an analytical demonstration of this difference.

The fact that destabilisation seems to be unlikely in a realistic population does not imply that it should be excluded. In addition, our results demonstrate that the MSY can theoretically imply an unstable inter-annual equilibrium. This is in line with results obtained by Kokko and Lindström (1998). This eventuality was also known in predator-prey models (Beddington and Cooke, 1982) and in single species with Allee effect (Ghosh et al., 2014). Hence we argue after Beddington and Cooke (1982) that sustainability of $MSY$ reference points should not be taken for granted and that those should be redefined to take into account stability criterion. Moreover, even in case of a stable equilibrium, resilience measured by the return time to this equilibrium should also be considered. Indeed, as stated Beddington et al. (1976), in some cases, *"perturbations may take so long to die away that effectively the populations may never return to equilibrium within a biologically meaningful times-pan"*. Such a situation would result in the impossibility of managing properly an exploited system.

Assessment of resilience in exploited populations is a topic of growing interest among empirical (Britten et al., 2014; Mumby et al., 2016) and theoretical ecologists. Tromeur and Loeuille (2017) and Kar et al. (2019) investigated relationship between the objectives of resilience and yields in food chains and found a RMY distinct from the MSY, leaving room for a trade-off between these objectives. Lundström et al. (2019) also explored trade-offs between yields and a number of conservation objectives including resilience on two structured single population models. One of their key result is that resilience is highly correlated with biomass loss, suggesting to use this metrics as a proxy for resilience in practice. This is in line with our observation that return-time to inter-annual equilibrium increase dramatically near the viability frontier. Here, we predict that in most real exploited populations, resilience will be harmed by approaching this frontier due to a lowered equilibrium biomass, rather than by getting in an unstable region of parameter space.

Previous works proposed to manage the trade-off between yields and resilience by acting on the distribution of effort on trophic level (Tromeur and Loeuille, 2017; Kar et al., 2019) or on the stage development (juvenile *vs.* adults) inside the population (Lundström et al., 2019). Our model is not designed to answer these questions. Instead, we evaluated the effect of another control parameter which is the timing of recruitment. In our application for the Bay of Biscay sole, we found that variations within a year (and consequently corresponding to a seasonality) of recruitment time, although it had a non-negligible effect on the stability region of the parameter space, had little effect on the resilience curves. The resilience of the population was much more influenced by little variations of maturation lag, which is a purely biological parameter on which no control could be expected.

Our aim in this study was to propose a generalised and relatively simple model to shade light on the effect of seasonality in maturation and recruitment processes which are of key importance in fisheries management. Although we parameterised the model with published literature and data concerning a real stock, this was on a qualitative and illustrative purpose rather than to make quantitative predictions (*i.e.* to get possible rather than exact values). We stress that our model is far too idealised to make precise predictions and that available data are not designed for our model.

Our hypotheses concerning density-dependence could also be criticised. The choice here was to formulate as simply as possible a model of density dependence by cannibalism (or other induced mortality) of adults on juve-

niles. Cannibalism is known to be frequent in fish populations, is the most straightforward process of over-compensatory mortality and was the core hypothesis of development of Ricker historical stock and recruitment theory (Ricker, 1954). Moreover, Rindorf et al. (2022) recently showed that most of exploited stocks undergo density-dependence before recruitment and that overcompensation was more likely to occur in demersal stocks such as the Bay of Biscay of sole.

This is to our knowledge the first resilience analysis on a single exploited population subject to cannibalistic density-dependence, as well as the first evaluating the effect of seasonality of maturation and recruitment on resilience. We stress that in future studies, the model could be made more complex and realistic while keeping the proposed structuring in order to be able to study its dynamics easily as a first order system. In particular, different fishing regimes could be considered by applying different $F$ with respect to the month of the year. Also, the processes such as reproduction, recruitment and maturation were considered instantaneous while they are likely spread over several months in real populations.

Our results suggest that the overall importance of recruitment timing is weak relatively to timing of maturation. Unfortunately, no control is possible on that parameter. We think that improved knowledge on density dependent processes of early stages is a condition for the computation of relevant reference points. Based on that knowledge, monthly fishing recommendations could be formulated to follow more closely the population dynamics. We also recommend that stability and resilience of populations be taken into account when setting reference points and objectives, so that the sustainability of yields be guaranteed. A first step could be to modify the $F_{MSY}$-range framework (Hilborn, 2010; Rindorf et al., 2017) to include resilience objectives to be attained aside from high enough yields and including uncertainty due to seasonal processes.

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) |
| $\delta$ | 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 |
| $\Delta_{mat}$ | Lag between birth and maturation (in months) |
| $\Delta_{rec}$ | 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 $(h,\bar{h})$, *e.g.* $N_{a_{mat},d,\bar{h}}(t)$ is the number of immature, unharvested individuals of round age $a_{mat}$. |
| $\bullet$ | Union of groups, *e.g.* $(\bullet, \bar{d}, \bullet)$ 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) |
| $\mu$ | Density-dependence factor |
| $\omega$ | 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 $y$

$$\begin{cases} N_{0,d,\bar{h}}(m_{mat}, y+1) = r\, N_{\bullet,\bar{d},\bullet}(m_{rep}, y)\ \prod_{m=1}^{m_{mat}} S_d(m, y+1) \\ N_{a_1,d,\bar{h}}(m_{mat}, y+1) = N_{a_1-1,d,\bar{h}}(m_{mat}, y)\ \prod_{m=m_{mat}+1}^{m_{rep}} S_d(m, y)\ \prod_{m=1}^{m_{mat}} S_d(m, y+1) \\ N_{a_2,\bar{d},\bar{h}}(m_{mat}, y+1) = N_{a_2-1,\bar{d},\bar{h}}(m_{mat}, y)\, S_{\bar{d},\bar{h}}^{m_{rep}} \\ N_{>a_{rec},\bar{d},h}(m_{mat}, y+1) = N_{>a_{rec},\bar{d},h}(m_{mat}, y)\, S_{\bar{d},h}^{m_{rep}} \\ \qquad\qquad + N_{a_{rec},\bar{d},\bar{h}}(m_{mat}, y)\, S_{\bar{d},\bar{h}}^{m_{rec}-m_{mat}}\ S_{\bar{d},h}^{m_{rep}-(m_{rec}-m_{mat})} \end{cases} \tag{17}$$

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

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. $\mu$ and $\omega$ are the two constants in immature individuals' mortality function (2).

Number of spawners

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

with

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

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

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

with

$$\beta_1 = \mu \sum_{m=0}^{m_{mat}-1} S_{\bar{d},\bar{h}}^{m_{rep}-m_{mat}+m} \qquad \kappa_1 = \mu \sum_{m=0}^{m_{mat}-1} S_{\bar{d},h}^{m_{rep}-m_{mat}+m}$$

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

$$\theta_1 = \mu \, S_{\bar{d},\bar{h}}^{m_{rec}-m_{mat}} \sum_{m=0}^{m_{mat}-1} S_{\bar{d},h}^{m_{rep}-m_{rec}+m}$$

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

Other aggregated constants

$$\alpha_1 = e^{-\omega \, m_{mat}} \qquad \sigma = S_{\bar{d},\bar{h}}^{m_{rep}} \qquad \rho = S_{\bar{d},\bar{h}}^{m_{rec}-m_{mat}} \, S_{\bar{d},h}^{m_{rep}-(m_{rec}-m_{mat})}$$

$$\alpha_2 = e^{-\omega \, m_{rep}} \qquad \nu = S_{\bar{d},h}^{m_{rep}}$$

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 Committee (2018) |
| $F$ | fishing mortality (monthly) | 0.1/12 | | assumed equal to natural mortality |
| $\Delta_{mat}$ | maturation delay (in months) | 28 | $\{25, \ldots, 30\}$ | arbitrary value verifying $a_{mat} = 2$ (Committee, 2018) |
| $\Delta_{rec}$ | recruitment delay (in months) | 44 | $\{37, \ldots, 46\}$ | arbitrary value verifying $a_{rec} = 3$ (Committee, 2018) |
| $\mu$ | density-dependence constant | $2.40 \times 10^{-11}$ | | estimated |
| $\omega$ | density-dependence constant | 0.48 | | estimated |

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

The same way we deduced system (17) from equations (3-10) for the case when $m_{mat} \leq m_{rec}$, we can deduce from the same equations the system E.1, expressed in table E.6. As before, this system can be expressed as a first order difference equation (see Appendix B for proof):

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

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

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

and

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

where

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

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

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

The inter-annual equilibrium is solution of :

$$
\begin{cases}
N^*_{a_{mat},\bar{d},\bar{h}}(m_{mat}) = r\,\alpha_1\,\alpha_2^{a_{mat}}\,\Phi\left(\underline{N}^*_{\bar{d}}(m_{mat})\right) \\
\qquad\qquad\qquad\qquad\qquad\qquad \times e^{-\xi_1(\underline{N}^*_{\bar{d}}(m_{mat}))-a_{mat}\,\xi_2(\underline{N}^*_{\bar{d}}(m_{mat}))} \\
N^*_{a2,\bar{d},\bar{h}}(m_{mat}) = \sigma\, N^*_{a2-1,\bar{d},\bar{h}}(m_{mat}) \\
N^*_{a_{rec},\bar{d},h}(m_{mat}) = \chi\, N^*_{a_{rec}-1,\bar{d},\bar{h}}(m_{mat}) \\
N^*_{>a_{rec},\bar{d},h}(m_{mat}) = \nu\,\left[N^*_{>a_{rec},\bar{d},h}(m_{mat}) + N^*_{a_{rec},\bar{d},h}(m_{mat})\right]
\end{cases}
\tag{A.2}
$$

with
$\underline{N}^*_{\bar{d}}(m_{mat}) = {}^t\left(N^*_{a_{mat},\bar{d},\bar{h}}(m_{mat}), N^*_{a2,\bar{d},\bar{h}}(m_{mat}), N^*_{a_{rec},\bar{d},h}(m_{mat}), N^*_{>a_{rec},\bar{d},h}(m_{mat})\right)$
and $a2 = a_{mat}+1,\ \ldots,\ a_{rec}-1$.

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

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

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

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

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

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 $m_{mat} \leq m_{rec}$, we get after equations (3-10):

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

Else, we get:

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

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

We have, for all $y$:

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

with

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

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

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

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

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

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

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

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

and

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

Else we have:

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

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

and

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

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

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

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

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

see table 4 for exact formulation of $\alpha_1$, $\varphi_1$ and $\xi_1$.

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

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

$$\sum_{m=m_{mat}}^{m_{rep}-1} N_{\bullet,\bar{d},\bullet}(m,y)$$

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

$$+ \quad \ldots$$

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

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

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

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

and

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

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

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

and

$$\begin{aligned}\textstyle\sum_{m=m_{mat}}^{m_{rep}-1} N_{a_{rec},\bar{d},h}(m,y) = N_{a_{rec},\bar{d},\bar{h}}(m_{mat},y) \\ \times S^{m_{rec}-m_{mat}}_{\bar{d},\bar{h}} \textstyle\sum_{m=0}^{m_{rep}-m_{rec}-1} S^{m}_{\bar{d},h}\end{aligned} \tag{B.17}$$

Else we have:

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

and

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

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

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

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

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

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

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

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

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

$$j_{a1,a1-1} = \alpha_2\, e^{-\varphi_2(\underline{N}^*_{\bar{d}}(m_{mat}))}$$
$$j_{a1,a2} = -\alpha_2\,\beta_2\, N^*_{a1-1,d,\bar{h}}(m_{mat})\, e^{-\varphi_2(\underline{N}^*_{\bar{d}}(m_{mat}))}$$
$$j_{a1,a_{rec}} = -\alpha_2\,\theta_2\, N^*_{a1-1,d,\bar{h}}(m_{mat})\, e^{-\varphi_2(\underline{N}^*_{\bar{d}}(m_{mat}))}$$
$$j_{a1,a_{rec}+1} = -\alpha_2\,\kappa_2\, N^*_{a1-1,d,\bar{h}}(m_{mat})\, e^{-\varphi_2(\underline{N}^*_{\bar{d}}(m_{mat}))}$$

$$j_{a2+1,a2} = \sigma$$

$$j_{a_{rec}+1,a_{rec}} = \rho$$
$$j_{a_{rec}+1,a_{rec}+1} = \nu$$

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

$$
\begin{aligned}
&j_{0,a2} = -r\,\alpha_1\,[\beta_1\Phi(\underline{N}^*_{\bar{d}}(m_{mat})) - \psi_1]\;e^{-\xi_1(\underline{N}^*_{\bar{d}}(m_{mat}))}, \qquad a2 \neq a_{rec}-1\\
&j_{0,a_{rec}-1} = -r\,\alpha_1\,[\eta_1\Phi(\underline{N}^*_{\bar{d}}(m_{mat})) - \psi_1]\;e^{-\xi_1(\underline{N}^*_{\bar{d}}(m_{mat}))}\\
&j_{0,a_{rec}} = -r\,\alpha_1\,[\kappa_1\Phi(\underline{N}^*_{\bar{d}}(m_{mat})) - \psi_3]\;e^{-\xi_1(\underline{N}^*_{\bar{d}}(m_{mat}))}\\
&j_{0,a_{rec}+1} = -r\,\alpha_1\,[\kappa_1\Phi(\underline{N}^*_{\bar{d}}(m_{mat})) - \psi_3]\;e^{-\xi_1(\underline{N}^*_{\bar{d}}(m_{mat}))}
\end{aligned}
$$

$$
\begin{aligned}
&j_{a1,a1-1} = \alpha_2\,e^{-\xi_2(\underline{N}^*_{\bar{d}}(m_{mat}))}\\
&j_{a1,a2} = -\alpha_2\,\beta_2\,N^*_{a1-1,d,\bar{h}}(m_{mat})\,e^{-\xi_2(\underline{N}^*_{\bar{d}}(m_{mat}))}, \qquad a2 \neq a_{rec}-1\\
&j_{a1,a_{rec}-1} = -\alpha_2\,\eta_2\,N^*_{a1-1,d,\bar{h}}(m_{mat})\,e^{-\xi_2(\underline{N}^*_{\bar{d}}(m_{mat}))}\\
&j_{a1,a_{rec}} = -\alpha_2\,\kappa_2\,N^*_{a1-1,d,\bar{h}}(m_{mat})\,e^{-\xi_2(\underline{N}^*_{\bar{d}}(m_{mat}))}\\
&j_{a1,a_{rec}+1} = -\alpha_2\,\kappa_2\,N^*_{a1-1,d,\bar{h}}(m_{mat})\,e^{-\xi_2(\underline{N}^*_{\bar{d}}(m_{mat}))}
\end{aligned}
$$

$$
\begin{aligned}
&j_{a2+1,a2} = \sigma, \qquad a2 \neq a_{rec}-1\\
&j_{a2+1,a_{rec}-1} = \chi
\end{aligned}
$$

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

See table 4 for formulations of all the constants.

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

Assume that all the model parameters are known except $\mu$ and $\omega$. Here, we aim at fitting a custom stock-recruitment relationship compatible with our model formulation to estimate those parameters. Assume also that $\Delta_{mat}$ and $\Delta_{rec}$ verify $m_{mat} \leq m_{rec}$. Hence the population is governed by system (11). It comes immediately from the formulation of the system that:

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

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

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

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

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 table 4 for computations of these constants), and let us define:

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

then we can express:

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

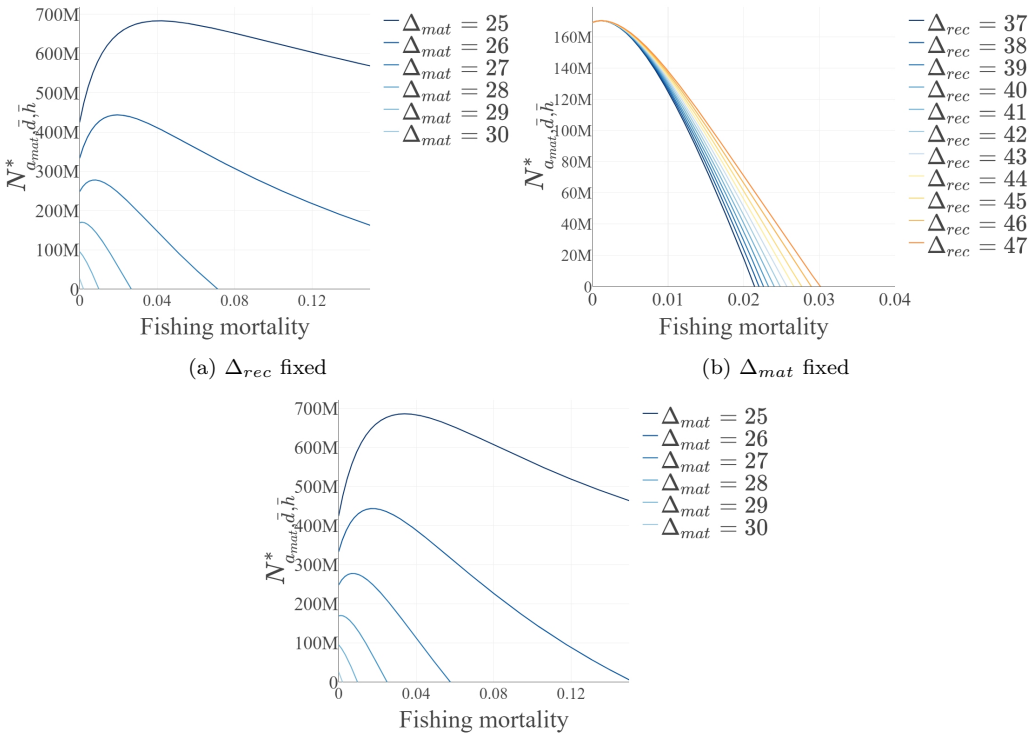
Finally, with $\alpha_1 \, \alpha_2^{a_{mat}} = e^{-\omega \, (m_{mat} + a_{mat} \, m_{rep})}$ we can write the custom stock-recruitment relationship as:

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

Hence, one can estimate parameters $\mu$ and $\omega$ by non-linear regression as long as sufficient temporal, age-structured data is available, assuming that assessment is effectively made at $m = m_{mat}$. The regression was performed using the `nls` function of R software.

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

## Appendix E. Supplementary outputs

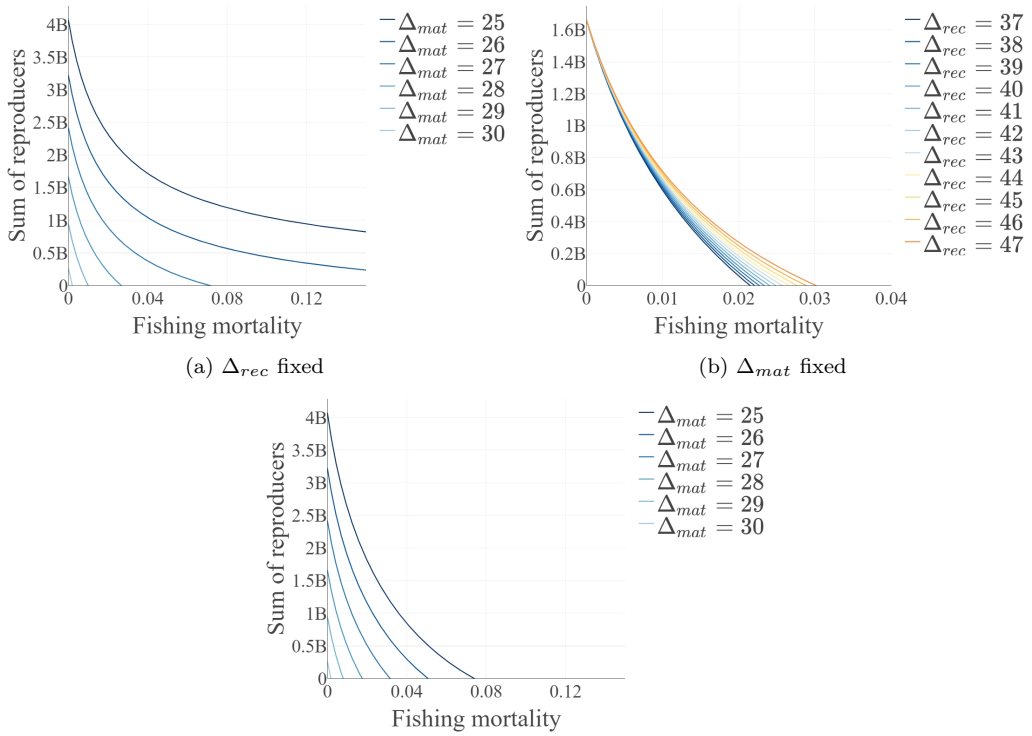



(a) $\Delta_{rec}$ fixed

(b) $\Delta_{mat}$ fixed

(c) $\Delta_{rec} - \Delta_{mat}$ fixed

Figure E.8: Number of mature individuals of round age $a = a_{mat}$ at equilibrium ($m = m_{mat}$) as a function of fishing mortality (by month) when $\Delta_{mat}$ and $\Delta_{rec}$ vary and the system is parameterized for the Bay of Biscay sole. Different colours indicate different values of $\Delta_{mat}$ and/or $\Delta_{rec}$ depending on the case: (a) $\Delta_{mat}$ vary and $\Delta_{rec} = 44$ ; (b) $\Delta_{rec}$ vary and $\Delta_{mat} = 28$ ; (c) both $\Delta_{mat}$ and $\Delta_{rec}$ vary and their difference is constant and equals 14.




(a) $\Delta_{rec}$ fixed

(b) $\Delta_{mat}$ fixed

(c) $\Delta_{rec} - \Delta_{mat}$ fixed

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

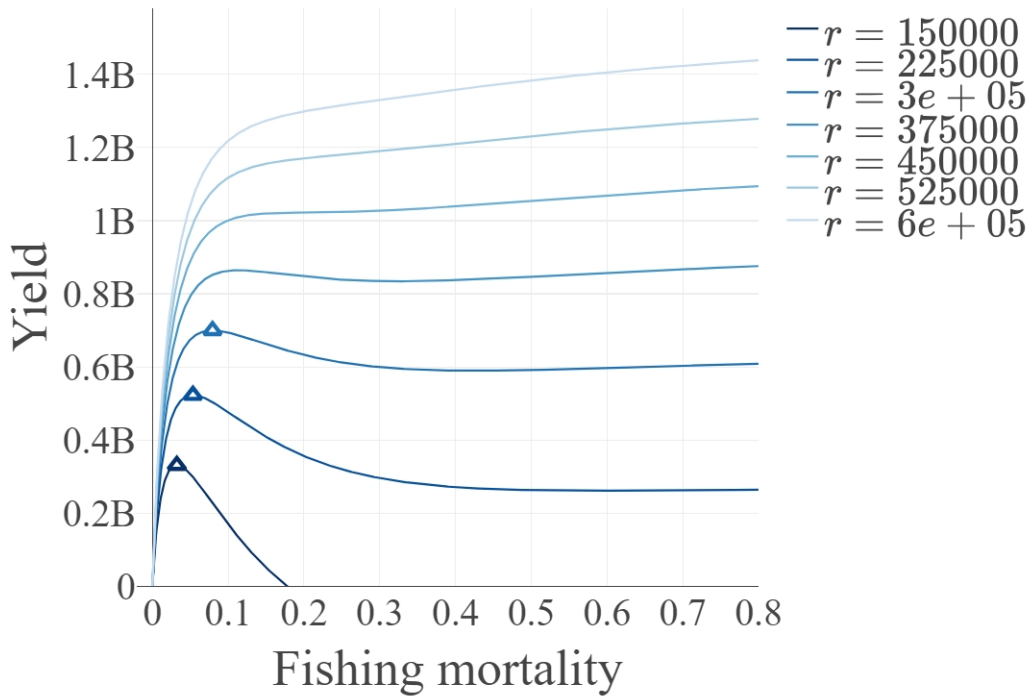



Figure E.10: Total annual yields at inter-annual equilibrium as a function of fishing mortality (by month) and position of MSY when $r$ varies, $\Delta_{mat} = 25$ and $\Delta_{rec} = 39$ (all other parameters being the same as in table 5). Coloured triangles correspond to MSY (numerically solved) and different colours indicate different values of $r$.

Table E.6: Expressions of the inter-annual dynamics of $\underline{N}(m_{mat}, y)$ when $m_{mat} > m_{rec}$:

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

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

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