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Fanny Ouzoulias

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Bayésien exploration of Surplus Production Models for cetaceans by-catch management, using strandings and abundance data

Par : Fanny OUZOULIAS



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This report is a pedagogical exercise that does not engage the responsibility of the host laboratories.

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Notations

Table 1.: Notations used in this study.

Notation	Meaning	Type
C_t^e	Observed (by-)catches (<i>e.g.</i> as strandings) at time t	Integer
C_t	(By-)Catches at time t	Integer
σ	Environmental stochasticity: the temporal variation in probabilities of vital rates due to random fluctuations in the environment (Burkhardt and Slooten, 2003).	Positive real
q	correction factor (<i>e.g.</i> proportion of dolphins dead from bycatch which float and can strand)	Percentage
r	Maximum intrinsic rate of population growth	Positive real between 0 and 1
ϕ	Extraction rate	Positive real between 0 and 1
K	Carrying capacity	Integer
γ	Shape parameter in the Pella Tomlinson model	Positive real
$\mathcal{N}(\mu, \sigma)$	Gaussian distribution of location parameter μ and scale parameter σ	Distribution
$\mathcal{LN}(\mu, \sigma)$	Log-normal distribution of location parameter μ and scale parameter σ	Distribution
$\mathcal{B}_e(a, b)$	Beta distribution of shape parameters a and b	Distribution

1. Introduction

Fisheries by-catch has an important impact on the marine fauna and has been responsible for the decline of many species of megafauna including seabirds, marine mammals or sea turtles (Lewison et al., 2004). Hall (1996) defines by-catch as "the portion of the capture that is discarded at sea dead (or injured to an extent that death is the most likely outcome), because it has a little or no economic value or because its retention is prohibited by law". Other factors than by-catch lead to the decrease of abundance or biomass, such as habitat modification, pollution, or competition for resources. In July 2020, the European Commission started an infringement procedure against three member states, including France, for failing to protect common dolphins (*Delphinus delphis*) in the Bay of Biscay (Eur, 2020). This infringement procedure resulted from the massive stranding events of bycaught dolphins along the Atlantic seaboard in France in the last few years. Dolphin by-catch is a conservation issue at the junction of environment, social and economic considerations: it remains complex and sensitive (Dolman et al., 2016). Stakeholders, including civil servants, professional fishermen and Non-Governmental Organizations (NGOs) have high expectations on science to propose efficient management measures that will help in decreasing current by-catch levels in the Bay of Biscay. The present study will focus on the development of a method for setting a by-catch limit, that is a number or biomass of animals that can be removed by anthropogenic activities, while meeting conservation objectives such as ensuring population viability in the long-term.

More precisely, Subsection 1.1 details the context of the study, highlighting the motivations behind this project and briefly summarizing the pros and cons of existing tools currently used to manage cetacean by-catch. This introduction of the technical aspects ends by explaining the outline of the work.

1.1. Context of the study

1.1.1. Overview of common dolphin ecology and protection status

Distribution, diet and trophic level

The short-beaked common dolphin (*Delphinus delphis*) is one of the most abundant cetacean species in the North-East Atlantic (Hammond et al., 2021) where this species is widely distributed from the Azores to Norway. In the Bay of Biscay, high density areas can be observed on the shelf break (Murphy et al., 2013). In winter (Laran et al., 2017b) and spring, common dolphins are more abundant close to the coasts (Certain et al., 2008). Common dolphins are also capable of very large-scale migration movements, depending on seasons and probably prey distribution: they are more likely to be on the continental shelf edge in summer and in the western English Channel, Celtic Sea or western Brittany in winter (Reid et al., 2003). There is currently a knowledge gap on possible migration patterns, especially seasonal ones within the North-East Atlantic.

Dolphins in general have different types of feeding strategies, such as "fish whacking" (whacking fish with their tails), digging in the substrate with their rostra or "kerplunking"

(movements of tail at the surface) (Burgess, 2006). Interactions with fishing gears have also been documented: dolphins take advantage of the confusion of the fish when they fall into the nets, which makes the hunt much easier (Pryor et al., 2006). A study analysing stomach contents shows that the diet of common dolphins in the Bay of Biscay is made of fish (84 % by number of prey items), mainly gobies, anchovy, sardine and sepiolids. The diet defines the trophic level of dolphins: it has been estimated at 4.2 by Pauly et al. (1998) within the scope of a global analysis on diet composition and trophic levels of marine mammals. Marine mammals in general occupy quite high trophic positions and have a key-role in the ecosystem (Kiszka et al., 2022). Declines of dolphin populations may cause modifications of biomass in the lowest levels (top-down effect, Carpenter et al. 1985).

Abundance/Biomass estimation

The abundance of common dolphins in the North-East Atlantic has been estimated in the SCANS/CODA surveys in 2005 and 2016 (Hammond et al., 2021). Abundance remained stable with $\approx 470,000$ (coefficient of variation 33%) common dolphins in 2005 and $\approx 487,000$ (coefficient of variation 25%) in 2016 (Figure 1).

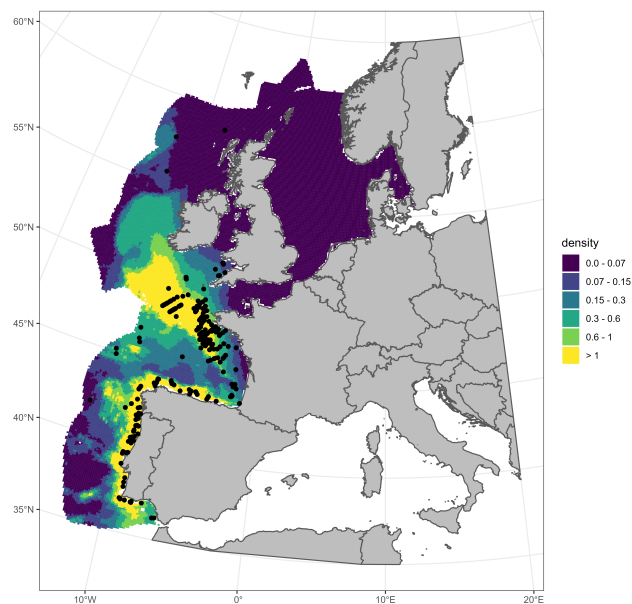


Figure 1.: Predicted surfaces of estimated density for common dolphins in 2016 (SCANS-III). Black dots represent the raw data (detections of common dolphins during the SCANS-III survey).

The common dolphin: a protected species

Many regulations have been promulgated to protect common dolphins, at different scales (national, European or international). These vary in scope and aim at improving knowledge, management and conservation to different degrees.

At the supra-national level, several conventions address the conservation of the marine life in general: it is the case, among others, of the United Nations Convention on the Law of the Sea, the Convention on Biological Diversity, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (regulates the trade of protected species such as dolphins), the Bonn convention (Convention on the Conservation of Migratory Species

of Wild Animals) (ICES, 2020). ASCOBANS (a sister instrument to the Bonn Convention under the aegis of the United Nations) promotes cooperation between countries to protect wild marine species.

A regional sea convention in the North-East Atlantic also covers cetaceans: the Oslo-Paris (OSPAR) convention. In its North-East Atlantic Environment Strategy, OSPAR aims at keeping this part of the ocean clean, healthy and biologically diverse as well as making it a productive area, used sustainably and resilient to both climate change and acidification. In particular, OSPAR will work with relevant competent authorities and other stakeholders to minimise and if possible eliminate incidental by-catch of marine mammals, birds, turtles and fish so that it does not represent a threat to the protection and conservation of these species. OSPAR will also work towards strengthening the evidence base concerning incidental by-catch by 2025 (OSPAR, 2021).

One of the most important European legislation on the conservation of wildlife is the Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora, also known as the Habitats Directive. Common dolphins are part of the Annex IV, "Animal and Plant Species of Community Interest in Need of Strict Protection". Species that are in this Annex have to be monitored to maintain a favourable conservation status. Also, according to the Marine Strategy Framework Directive (Directive 2008/56/EC of the European Parliament and of the Council of 17th June 2008 establishing a framework for community action in the field of marine environmental policy; MSFD), the priority "should be given to achieving or maintaining good environmental status in the Community's marine environment, to continuing its protection and preservation, and to preventing subsequent deterioration" (Dir, 2008, p. 20). Good Environmental Status (GES) is assessed with a suite of so-called descriptors covering biological diversity (including marine mammals), elements of marine food webs, eutrophication, contaminants, etc. Though utilitarian in philosophy, the MSFD is the current backbone of marine conservation in the European Union. The common dolphin was assessed as not at GES in 2018 in France (as well as in Spain and Portugal) due to by-catch. The next evaluation is due for 2024 with no expected improvement respecting GES because by-catch remains too high (ICES, 2021).

1.1.2. Fishing activity and the problem of by-catch

There are many possible threats which can impact cetaceans but it is clear that anthropogenic activities are the main cause of additional mortality (Avila et al., 2018).

Each year since 2016, over 1,000 strandings of cetaceans were registered along the French Atlantic seaboard (ICES, 2020). More than 800 common dolphins were estimated to be bycaught in fishing gears in 2020 in the Bay of Biscay (Peltier et al., 2020). Estimated at-sea by-catch of common dolphins using strandings highlights an increase in by-catch since 1990s (Peltier et al., 2016a, Figure 2).



Figure 2.: Time series of estimated common dolphin by-catch in the Bay of Biscay from stranding data collected on the French Atlantic seaboard, Peltier et al. (2020). Note the y-axis is on a logarithmic scale.

The majority of strandings of bycaught dolphins come from the continental shelf of the Bay of Biscay and correlations have been evidenced between fishing activities (French gill-netters, especially those targeting hake (*Merluccius merluccius*), Spanish bottom trawlers, Danish sennes, etc.) and by-catch (Peltier et al., 2021). Details about these correlations are in Appendix A.1.

Dolphins are trapped into the gears and die from asphyxia. When released from gears, between one fifth and one fourth of carcasses remains afloat, with the remainder sinking. Floating carcasses drift and may eventually be washed ashore on the French Atlantic seaboard. A majority ($\approx 75\%$) of stranded common dolphins have evidence of by-catch (in winter) (Peltier et al., 2021). In France, the survey of the dolphin's strandings is conducted by the French Stranding Network (*Réseau National Échouages* in French). It was created in 1972 and is now operated by Observatoire Pelagis (UAR 3462 La Rochelle University - CNRS). It aims at registering all marine mammal strandings in France, at collecting data on the stranded species including a necropsy of the carcass, when possible, to assess the cause of death (among others pieces of information). Pelagis also carries out large-scale surveys (either ship-based or plane-based) to estimate marine mammal abundance and distributions in French waters (Laran et al., 2017a).

The ASCOBANS Conservation and Management Plan, under the heading "Habitat conservation and management" coined the term "unacceptable interaction". ASCOBANS defined, according to the best available scientific evidence, "unacceptable interactions" as being, in the short term, a total anthropogenic removal above 1.7% of the best available estimate of abundance (Res.3.3) and underlines the intermediate precautionary objective to reduce by-catch to less than 1% of the best available population estimate (Res.3.3 and Res.5.5)¹. The current rate of additional mortality due to fisheries by-catch exceeds 1%, much more than what is viable for small cetaceans (Peltier et al., 2019). Indeed, the survivorship of common dolphins is not high in the Bay of Biscay: only 31% of dolphins reach 12 years old (Mannocci et al., 2012).

¹https://www.ascobans.org/sites/default/files/document/AC22_4.1.c_UnacceptableInteractions_NextSteps.pdf

Common dolphins are very vulnerable to fishing activities, among other reasons, because they have a small population growth rate which results in a large population-level sensitivity to any additional mortality (Read, 2008). Potential solutions to address common dolphin by-catch include spatio-temporal closures, changes in gears or practices, or using deterrent devices such as acoustic pingers (Murphy et al., 2013). These acoustic deterrents can be useful to prevent dolphins from interacting with gears during a fishing operation, but their efficacy is not well established.

Since 2019, fishing boats (over 12 meters) with bottom-set gillnet and entangling nets must be equipped with pingers (Eur, 2019) and since 2017, a dedicated national working group (including fisheries, Non-Governmental Organisations, scientists and other stakeholders) addresses the issue of by-catch. One of its program² aim's is to limit common dolphin's by-catch in the Bay of Biscay, by developing new acoustic deterrents.

1.1.3. Current management of cetacean by-catch

Management procedures for cetaceans have been developed, in particular within the work of the International Whaling Commission. A management strategy is a set of rules which aim at making agreed-upon objectives achievable (Punt, 2006; Bunnefeld et al., 2011). This strategy defines management objectives in the form of not-to-be exceeded thresholds that managers can track from available data. The process of evaluating a management strategy (Management Strategy Evaluation, MSE) relies on modeling and computer simulations (Cooke, 1994; Hilborn and Mangel, 1997): it is commonly used to compute biological reference points or, in the context of by-catch, removal limits. A complication in the management of by-catch stems from the fact that by-catch, unlike catch, is not usually monitored (no log-book). Data on by-catch is not systematically collected by onboard observers: these data, if not collected systematically and in a dedicated scheme, are usually of low quality and biased (Basran and Sigurðsson, 2021). This is especially true in European waters where there are no dedicated schemes to monitor by-catch at the relevant scales, especially marine mammal by-catch (Murphy et al., 2022).

There are two main harvest control rules currently used for managing marine mammal by-catch: the Potential Biological Removal (PBR; Wade, 1998) and the Removals Limit Algorithm (Cook, 1995). Both rules are evaluated with operational models that are *Surplus Production Model* (SPM; see § 2.2.1)

The calculation of the PBR, proposed by (Wade, 1998), is straightforward:

$$\text{PBR} = N_{\min} \frac{1}{2} R_{\max} F_R,$$

N_{\min} being an estimate of minimum population size, $\frac{1}{2} R_{\max}$ one half of the maximum theoretical net productivity rate of the stock and F_R a recovery factor chosen between 0.1 and 1. The computation of PBR does not require by-catch data, although by-catch data is necessary to gauge the level of by-catch against the PBR limit (that is to carry out an assessment). PBR is extensively used in the United States where it is enshrined in the US Marine Mammal Protection Act (MMPA). It has also been used in several cases, including dolphins, for example in New-Zealand (Slooten and Dawson, 2008)³. However,

²LICADO project: cf <https://www.observatoire-pelagis.cnrs.fr/pelagis-2/les-programmes/licado/>

³The so-called import rule provisions of the MMPA now requires a comparability finding for nations exporting sea products to the US (Bering et al., 2022). This comparability finding requires, among

the limits of the procedure are reached when there is a lack of stock-level abundance data, which is often the case when studying cetaceans (Robards et al., 2009). PBR is a number of dolphins, which could be used to set the maximum number of dolphins that can be removed by anthropogenic activities including but not limited to by-catch⁴. This number should not be reached (Parra et al., 2021).

The other harvest control rule currently in use is known as the Removals Limit Algorithm (RLA). It also aims at setting an upper limit to anthropogenic mortality of small cetaceans. The RLA requires both a time-series of abundance/biomass estimates (whereas PBR only requires one such estimate) and a time-series of by-catch estimates (whereas PBR requires none for its computation).

RLA is a variant of the Catch Limit Algorithm (CLA), formulated by Cook (1995). CLA algorithm is an *ad hoc* algorithm that uses historical series of captures and estimates of abundance, connected together through the use of a discretized (SPM) written as

$$B_{t+1} = B_t - C_t + rB_t \left(1 - \left(\frac{B_t}{B_0} \right)^2 \right), \quad (1.1)$$

where t indexes the time step (year) along a given period starting at $t = 0$, B_t is the population size (abundance) and C_t is the by-catch. The initial population size B_0 is often assumed to be equal to K (corresponding to an assumption of a population at carrying capacity before the impacts of anthropogenic activities). The features of SPM, which are key in this work, are introduced further in § 2.2.

The use of CLA can lead to stock depletion if there is imprecision concerning the spatial distribution (Boyce, 2000). The results of RLA are quite close from those provided by CLA, and are based on a simple dynamic of population, with density-dependent growth and fitted to time series of data on abundance (Hammond et al., 2019). The computation of the RLA control rule for setting a removal limit is:

$$\text{removals limit} = \hat{r} \times \max(0, \widehat{D}_t - \text{IPL}),$$

where IPL (Internal Protection Level) is the depletion threshold below which the limit is set to 0 (Punt, 1993) and D_t is the population depletion at year t :

$$D_t = \frac{B_t}{K}.$$

Both \hat{r} and \widehat{D}_t are estimated from data using Equation 1.1 in a Bayesian framework (Hammond et al., 2019; Genu et al., 2021).

The data used for PBR and RLA procedures are estimations of abundance/biomass and by-catch, which are usually scarce and can be imprecise, biased or both. Another complication arises from stochasticity (demographic and environmental, which are not taken into account in the previous models) and yet describe natural variability of the environment. Finally both the PBR and RLA control rules hinge on an estimate of r

other things, exporting nation to demonstrate a legislation and management similar to that of the MMPA, and in practice may necessitate to compute PBR.

⁴PBR is akin to a maximum quota, although it is inappropriate to use "quota" for a protected species whose intentional killing or harming is forbidden by law. For this reason, it is more appropriate to speak of a removals limit.

(or R_{\max} as an input) which is unknown in practice for most species. This knowledge gap may be exploited to argue against the use of either of the rules (M. Authier personal observation). Devising a new rule to set a removal limit, a rule that does not hinge on knowledge of this input is thus desirable.

1.2. Motivations of this work

The preceding paragraphs encourage improving the formalization of a decision-making framework for recommending removals limit for cetaceans⁵, and linking this decision-making framework to information or conclusions from ecological, ecosystem, and socio-economic studies.

Basic formalization of abundance

Let $\{B_t\}_{t \in [t_0, T]}$ denote the abundance/biomass of a species during a given period $[t_0, T]$ and relative to a geographical area \mathcal{X} . Because of the small to moderate amount of data typically available, it is desirable to approximate the evolution of $\{B_t\}_{t \in [t_0, T]}$ by a discrete, parametric Markov model of order s :

$$\frac{dB_t}{dt} \simeq B_t - B_{t-1} = h(B_{t-1}, \dots, B_{t-s}, \theta, \phi_t), \quad (1.2)$$

where h is a deterministic function, involving two sets of low-dimensional parameter vectors:

- θ is a set of parameters that provide a summary description of the main characteristics of the species which can be reasonably assumed not to evolve with time (*e.g.*, reproductive rate, carrying capacity, etc.);
- $\{\phi_t\}_{t \in [t_0, T]}$ is a set of parameters related to pressure on the population at time t . In particular, in the framework of the first-order Markovian models (SPM) detailed in § 2.2.1, each ϕ_t is assimilated to an *extraction rate* summarizing the anthropogenic pressure related to the fishing activity. Details are provided in Appendix A.3.1.

Considering $(B_t)_{t \in [t_0, T]}$ as a stochastic process gives:

$$B_{t+1} = h(B_t, B_{t-1}, \dots, B_{t-s}, \theta, \phi, \varepsilon_t) \quad (1.3)$$

where ε_t is a so-called *process noise* enhances realism.

Managing by-catch: a decision-analytic outlook

Let us then assume that we have chosen a model h that achieves an adequate trade-off between ecological realism and feasibility of estimation from the available data. Accordingly, let us assume that this model is statistically estimated. How can we formalize an appropriate management approach for a non-commercial species?

Since we have a stochastic model of the evolution of B_t , assumed to be relatively good, we can assess (either theoretically or by simulation) the predictive stochastic process of B_t in a future time period $[T + 1, T + \Delta_T]$:

$$\{B_t\}_{t \in [T+1, T+\Delta_T]} \sim \mathcal{P}_{T+1, T+\Delta_T}.$$

⁵or maximum extraction threshold(s) for commercial species

Taking advantage of the theory of stochastic processes (*e.g.* Grimmett and Stirzaker (2001)), the process $\mathcal{P}_{T+1, T+\Delta_T}$ can be :

- (i) *stationary*: $\mathcal{P}_{T+1, T+\Delta_T} = \mathcal{P}$;
- (ii) be *non stationary* and increasing;
- (iii) be *non stationary* and decreasing, leading eventually to population extinction.

In the case of cetaceans, two objectives motivate the management strategy:

1. obtaining at least the stationarity while meeting conservation objectives set by policy (*e.g.* "The population abundance of the species is not adversely affected due to anthropogenic pressures, such that its long-term viability is ensured" as required under the MSFD);
2. minimizing by-catch, which by definition is unwanted and maybe legally forbidden in the case of protected species (*e.g.* common dolphin under the Habitat Directive).

Any management strategy established on the basis of a model as (A.2) is therefore fundamentally related to the current estimate and possible forcings on the future values of the extraction parameter vector ϕ (see Appendix A.3.3 for further details). The nature of this new management rule, or forcing, can be quite varied: change in gears, closing of the fishing that affect the most the dolphins, regulations with onboard observers, move-on rules, pingers deployment, etc.

The use in simulation associated with statistical tests of stationarity and trend, such as those presented in § 2.1.2, make it possible to test strategies based on a choice of forcing on ϕ . Such simulations can also be used to test compliance with conservation objectives. To differentiate the historical and predictive analyses, T being the time at which the strategy is revisited, let us denote

- ϕ_{past} = the value of ϕ at time $t \leq T$ (estimated from available observations),
- ϕ_{new} = the value of ϕ wished for times $t \geq T + 1$, inducing a
(possibly) new management strategy

and accordingly rename $\{B_t\}_{t \geq T+1}$ in $\{B_t\}_{t \geq T+1}(\phi_{\text{new}})$ to denote the trajectory of abundance for the new strategy $\phi = \phi_{\text{new}}$.

A conservation objective proposed by the OSPAR Marine Mammal Expert Group (OMMEG) is for cetaceans to reach 80% of the carrying capacity (denoted K in the following) after 100 years with the probability of 0.8. (Genu et al., 2021). This objective is an operationalization of the ASCOBANS short-term practical subobjective "to restore and/or maintain stocks/populations to 80% or more of the carrying capacity" (Res.3.3). This objective necessarily requires K to be a dimension of θ . More generally, we can formalize the following objective, which encompasses the OMMEG proposal (with $\Delta_T = 100$ years and $\alpha = \beta = 0.2$).

Definition 1. Given two orders $0 < \alpha \ll 1$ and $0 < \beta \ll 1$, the species managed from time $T + 1$ under the policy ϕ is assumed to be sufficiently protected if

$$P(\mathcal{F}_{T+\Delta T}(\phi)) > 1 - \alpha \quad (1.4)$$

where \mathcal{F}_t is the probabilistic event of interest

$$\mathcal{F}_{T+\Delta T}(\phi) = \left\{ \frac{B_{T+\Delta T}(\phi)}{K} > 1 - \beta \right\}. \quad (1.5)$$

It should be possible to give a decision-theoretic interpretation of this criterion, based on an economic rationale by linking the protection of a non-commercial species to the ecosystem on which it depends. A possible rationale is detailed in Appendix A.3.2. Roughly speaking, α can be interpreted as a ratio of socio-economic costs or gains related to ecosystem services. Our explanation remains circumstantial and would merit further developments but is beyond the scope of the present work.

1.3. Internship objectives

The two existing management rules (PBR and RLA) have some limitations. Ideally, we would like to propose new management rules to handle cetaceans bycatch but in this study we will focus on exploring the use a specific type of models, Surplus Production Models (SPM) to manage bycatch, in the conservation context discussed above (80% of the carrying capacity (K) after 100 years with the probability of 0.8).

One innovation of our study is to focus on the use of strandings of common dolphins on the Atlantic seaboard of France (Peltier et al., 2016a) as a data in-put, which is new when assessing management rules for cetaceans. An obvious advantage of stranding data is that it does not rely on dedicated onboard observer schemes, which are lacking in Europe for monitoring cetacean by-catch.

We therefore need a model with few parameters because the data are few, and which incorporates environmental variability (stochasticity). The choice of a Bayesian framework therefore seems appropriate, as it allows us to manage uncertainty, the small amount of data and the precautions to be taken in a decision-making framework (Harwood and Stokes, 2003). It provides interesting and applicable management options (Carlin and Louis, 2010). It is then interesting to evaluate the feasibility of such a model to estimate parameters and project abundance. The use of stochastic SPM models have already been made in several studies and have shown good results for providing estimations of stochastic MSY (Polacheck et al., 1993; Millar and Meyer, 2000; Bousquet et al., 2008; Bordet and Rivest, 2014). In this study we will be focusing on the common dolphin, which is a cetacean species heavily affected by by-catch, particularly in the Bay of Biscay⁶.

⁶On the 20th of July 2022, during the writing of this report, the European Commission issue a Reasoned Opinion against France for, *inter alia*, (ii) not having entirely transposed the obligations of the Habitats Directive related to the establishment of system to monitor by-catch and to take the necessary conservation measures; and (ii) not having taken the necessary measures advised by science to reduce by-catch; and (iii) having failed to ensure effective control and inspection. France now have two months to respond and take the necessary measures. Otherwise, the Commission may decide to refer the case to the Court of Justice of the European Union. France already asks for an extra month to prepare its

Materials and methods required to propose and study new management rules for cetaceans are detailed in Section 2. Especially, a major part of this section is devoted to a simulation model generating by-catch and abundance data. Another key part is dedicated to estimation of reference points, such as the carrying capacity, the extraction rate, the intrinsic growth rate and the environmental stochasticity. Finally, these estimations feed 100 years-simulations of abundance of dolphins that provide information on the evolution of the population level to inform by-catch management (Section 3). A discussion follows and points to further work (section 4). Finally, several technical appendices are provided.

2. Materials and Methods

2.1. Available data for the motivating case study

There are two types of data available that we will use for the present study: data on strandings and abundance estimations. These two are collected with different methods and by different organisations.

2.1.1. Abundance estimates

Abundance estimations are outputs of the international SCANS surveys. SCANS' objective is to estimate abundance of small cetaceans, with plane and boat surveys. The 2016 SCANS survey covered the North-East Atlantic waters, from the Lofoten islands off Norway to the strait of Gibraltar (Figure 1). Abundance data are summarized in Table 2. Interested readers are referred to Blanchard et al. (2021); Hammond et al. (2021) and Lacey et al. (2021) for further information.

Table 2.: Conventional Distance Sampling estimates of common dolphin abundance in the North-East Atlantic (Hammond et al., 2021).

Survey	Season	Date	Estimation of common dolphin's abundance	Coefficient of variation
SCANS-II/CODA	Summer	July 2005 & July 2007	468356	33,3
SCANS-III	Summer	July 2016	473461	26,1

2.1.2. Strandings

Data on strandings are collected by the the French Stranding Network (RNE) coordinated by Observatoire Pelagis (UAR 3462 CNRS-La Rochelle Université) which is in charge of registering every strandings occurring on the French coasts. Each stranded carcass

response.

has to be examined following a precise protocol¹. Each year, a report on strandings is published², with information concerning the spatial distribution and intensity of marine mammal strandings in France. The RNE is a network of more than 400 trained professionals and citizen dedicated to the monitoring of marine mammals strandings in France. The data set we will be using is a chronological series of 31 years of strandings recorded by Pelagis (Figure 3).

Stationary condition was tested on the data set, using three different tests: the KPSS test (Kwiatkowski-Phillips-Schmidt-Shin test), the ADF test (augmented Dickey–Fuller test) and the Philips-Peron test. They all rejected the hypothesis of a stationary time-series: there are significant changes in strandings since 1990. Details of the results are in Appendix A.2.1 A linear regression model has also been fitted to the data to explore trends. As expected, the coefficient of determination is moderate ($R^2 = 0.50$) and the trend (slope coefficient) is positive (Figure 3). The stationary tests and linear regression were undertaken as part of an exploratory analysis of the available data to provide very basic descriptive information on the behaviour of the time-series data.

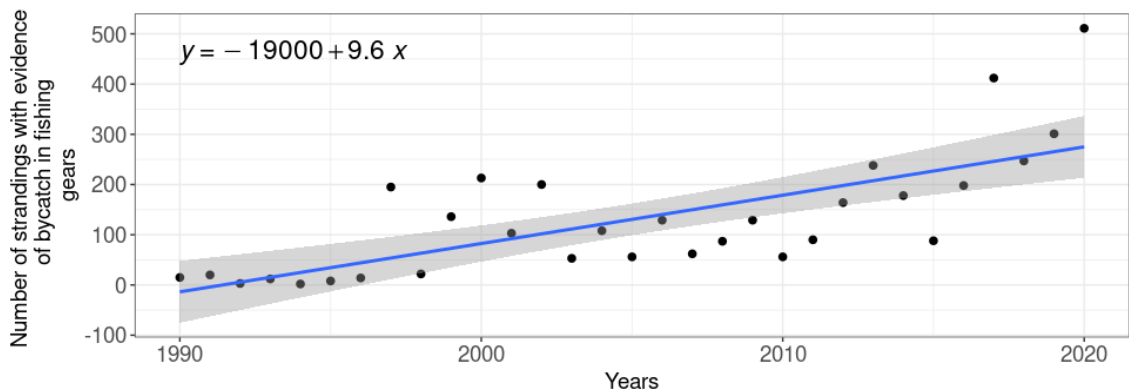


Figure 3.: Linear regression with stranding data of common dolphins.

Stranding data have information on parameters we are interested in (carrying capacity, extraction rate, etc.). Therefore, the next section details the development of a (simulation) model appropriate for these data to learn on these parameters.

2.2. Surplus production models (SPM)

Surplus production models (SPM) are standard models of population dynamics in situations of strong uncertainty and low information and can be used with the data available for this study (10 years of strandings and a handful of abundance estimations). First, we will develop a deterministic SPM, without taking into account stochasticity. Then, a stochastic SPM will be used to better take into account variability in abundance.

2.2.1. Deterministic SPM and biological reference points

The models described in § 1.1.3 are based on *Surplus Production Models* (SPM), which can be written with a very simple expression (Hilborn and Walters, 1992):

$$\text{next biomass} = \text{last biomass} + \text{recruitment} + \text{growth} - \text{catch} - \text{natural mortality}$$

¹<https://www.observatoire-pelagis.cnrs.fr/stranding/stranding-surveys/?lang=en>

²<https://www.observatoire-pelagis.cnrs.fr/rapports-rne/>

They are often used in management because they can provide management quantities directly estimated from survey data (Hilborn, 2001). In particular, the model proposed by Schaefer (1954) then generalized by Pella and Tomlinson (1969), Equation 2.1 is often used in this context:

$$B_{t+1} = B_t + r \left(\frac{\gamma + 1}{\gamma} \right) B_t \left(1 - \left(\frac{B_t}{K} \right)^\gamma \right) - C_t \quad (2.1)$$

$\gamma = 1$ refers to the Schaefer model, and B_t and C_t are respectively the biomass and capture at time t (in number of individuals typically), K being the carrying capacity and r the intrinsic rate of population growth, which modifies the shape of the population growth (Figure 4).

Equation 2.1 is the result of a discretization of the dynamics equation:

$$\frac{dB_t}{dt} = rB_t \left(1 - \left(\frac{B_t}{K} \right)^\gamma \right) - C_t.$$

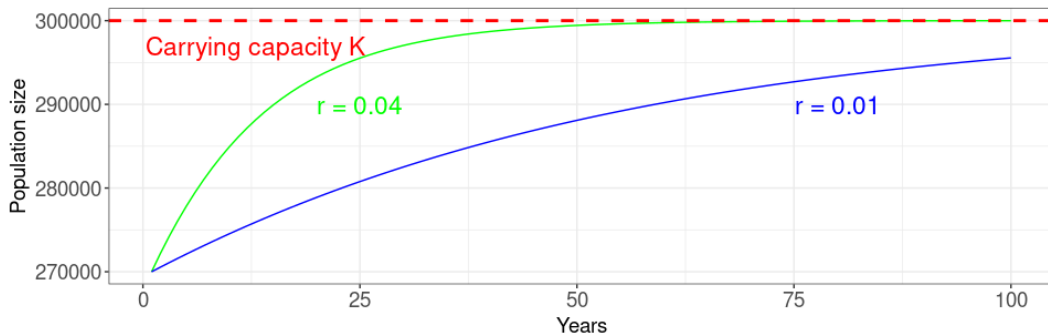


Figure 4.: Examples of population growth according to a Schaefer model, with different values of the intrinsic growth r .

The models presented before can generate reference points such as the maximum sustainable yield (MSY), which is the highest theoretical equilibrium yield that can be continuously taken (on average) from a stock under existing (average) environmental conditions without affecting significantly the reproduction process (FAO, 2011).

The use of this kind of aggregated model can be justified by the scarcity of available data (*e.g.*, population structure by age, stage or length) that has been (or that can realistically be) collected on some species. Equation 2.1 accommodates density-dependence, the corner-stone of population dynamics, which is certainly a major factor explaining its enduring use in practice. When applied to exploited populations (*e.g.* fish), Pella-Tomlinson (and other SPM) models offer the practical benefit of simplifying the derivation of these biological reference points. MSY is a harvest rule, calculated in a context of fishery management. In the case of a protected species (such as cetaceans), the catch is incidental and unwanted: by-catch should be minimized, that is lower than the MSY were it a commercial species. Other considerations come into play here such as conservation objectives.

In the frame of the present study, motivated by the fact that we dispose mainly of by-catch data to estimate the unknown parameters common to all SPM (growth rate, carrying capacity), we focus on the specific Pella-Tomlinson model (2.1), for which the by-catch C_t

is assumed to be related to the abundance B_t through by the expression:

$$C_t = \phi B_t \quad (2.2)$$

where $\phi \in [0, 1]$ has the sense of an extraction rate. This choice was defended in Bousquet et al. (2008) and then in Bordet and Rivest (2014) to study how to improve the assessments of biological reference points. The extraction rate is a constant here (see Equation A.2). It allows to build a model with few parameters, which is quite a necessity regarding data scarcity. It means that $\phi_t = \phi$. Then:

$$B_{t+1} = B_t + \left(\frac{\gamma + 1}{\gamma}\right) r B_t \left(1 - \left(\frac{B_t}{K}\right)^\gamma\right) - \phi B_t \quad (2.3)$$

with $B_t < K$ and $0 < r < 1$.

Now denote C_t^e the observed by-catch at time t . For example, we can observe only a fraction of by-catch via the strandings of carcass:

$$C_t^e = q C_t \quad (2.4)$$

where q has the sense of a the fraction of by-catches that float and can strand. This fraction is estimated from drifting experiments at 20-25% (Peltier et al., 2016b). For simplicity, we will assume that, conditionally on floating, the carcass of by-caught dolphin will drift and eventually strand on the shore where it will be registered by the RNE³. Also, we choose q constant ($q_t = q$) to simplify the writing of the model and the following inference. From Equations 2.2 and 2.4, one has:

$$C_t^e = q \phi B_t. \quad (2.5)$$

Then one can rewrite Equation (2.3) on abundance into an equation on strandings:

$$C_{t+1}^e = C_t^e + \frac{\gamma + 1}{\gamma} r C_t^e \left(1 - \left(\frac{C_t^e}{K q \phi}\right)^\gamma\right) - \phi C_t^e. \quad (2.6)$$

2.2.2. Including environmental stochasticity

The deterministic approach of abundance or by-catch dynamics previously proposed remains however very crude. For example, the concept of deterministic MSY has been criticized because its (too optimistic) value use may lead to population-level extinction. MSY ignores the natural variability in abundance/biomass, for example caused by environmental conditions so that true MSY is much lower than computed under a model wherein environmental stochasticity is ignored (Singini et al., 2013). The inclusion of environment stochasticity (so-called "process noise") in MSY calculation results in a decrease (Hubley and Heaslip, 2018). Including environmental stochasticity is therefore necessary to propose a correct simulation model for abundance.

For this reason, many researchers working on population dynamics (*e.g.*, Millar and Meyer, 2000; Polacheck et al., 1993) have proposed to incorporate a process noise ε_t reflecting

³Equation 2.4 could be refined to accommodate a time-varying drifting probability π_t :

$$C_t^e = \pi_t q C_t$$

Importantly, the π_t are auxiliary data estimated from numerical experiments with physical drift models (*e.g.* Peltier et al., 2016a). For simplicity, we assume in the remainder that $\forall t, \pi_t = 1$.

environmental variability within the abundance Equation 2.1, in a multiplicative way:

$$B_{t+1} = \left\{ B_t + r \left(\frac{\gamma + 1}{\gamma} \right) B_t \left(1 - \left(\frac{B_t}{K} \right)^\gamma \right) - C_t \right\} \varepsilon_t. \quad (2.7)$$

The stochasticity of the Markov chain induced by the (ε_t) is chosen to be *unbiased*:

$$\mathbb{E} [\varepsilon_t | \mathcal{F}_{t_1}] = 1$$

and the conditional variance (unknown and to assess) is chosen homoskedastic:

$$V [\varepsilon_t | \mathcal{F}_{t_1}] = \sigma^2$$

to avoid a strong increase of dimensionality.

When this choice is applied to (2.3), the observed by-catch process (2.6) becomes

$$C_{t+1}^e = \left\{ C_t^e + \frac{\gamma + 1}{\gamma} r C_t^e \left(1 - \left(\frac{C_t^e}{K q \phi} \right)^\gamma \right) - \phi C_t^e \right\} \varepsilon_t. \quad (2.8)$$

2.2.3. Defining a stochastic SPM on strandings

The previous developments lead us to consider the next steps to investigate the assessment of the SPM model (2.8) assuming by-catch is observed via the perfect registering of carcass of by-caught animals washing ashore (strandings).

The set of parameters that can vary in our model is defined as $\theta = \{K, \sigma, \phi, r\}$. Denote $\Theta \in \mathbb{R}^4$ its support set, which will be precised later. γ is not part of the set of parameters to estimate because it is quite difficult to estimate and it is common to fix it (Best and Punt, 2020; Fletcher, 1978). Let us consider the following reparametrization of the abundance proposed by Bordet and Rivest (2014):

$$Z_t = \frac{B_t}{K} \left(\frac{r(\gamma + 1)}{\gamma - \phi\gamma + r(\gamma + 1)} \right)^{1/\gamma} \quad (2.9)$$

which is well defined under the assumption that $\gamma - \phi\gamma + r(1 + \gamma) > 0$, namely if

$$\phi < 1 + r(\gamma + 1)/\gamma.$$

Obviously, with $\gamma > 0$ this assumption is not limiting since $0 < \phi < 1$. Then (2.3) associated to the multiplicative noise ε_t becomes:

$$Z_{t+1} = \left(1 - \phi + r \frac{\gamma + 1}{\gamma} \right) Z_t (1 - Z_t^\gamma) \varepsilon_t, \quad (2.10)$$

and the observed by-catch via strandings in Equation 2.8 becomes:

$$C_{t+1}^e = \left(1 - \phi + r \frac{\gamma + 1}{\gamma} \right) C_t^e (1 - \{D(\theta) C_t^e\}^\gamma) \varepsilon_t, \quad (2.11)$$

since $Z_t = D(\theta)C_t^e$ where

$$D(\theta) = \frac{1}{Kq\phi} \left(\frac{r(\gamma+1)}{\gamma - \phi\gamma + r(\gamma+1)} \right)^{1/\gamma}. \quad (2.12)$$

Note that non-negative observed by-catch implies $C_t^e \leq 1/D(\theta)$. To avoid heavy notations and to adopt a more conventional Markovian writing, we can simply rewrite (2.11) as:

$$C_t^e = g(C_{t-1}^e, \theta)\varepsilon_t$$

where

$$g(C_t^e, \theta) = \left(1 - \phi + r\frac{\gamma+1}{\gamma} \right) C_t^e (1 - \{D(\theta)C_t^e\}^\gamma). \quad (2.13)$$

Note that g is non-linear and non-log-linear.

2.2.4. Adding data on abundance

Since one of the parameter to estimate is K , the carrying capacity, it is needed to incorporate data on abundance. Data on abundance of common dolphins comes from SCANS campaigns (see § 2.1.1). Historically, there has been a SCANS campaign every decade: it means that data on cetacean abundance can be assumed to be updated every ten years.

More generally, we denote \mathcal{I} the years for which an abundance estimate B_t^* , observed with noise, can be collected. We denote \mathcal{J} the years for which (unnoisy) strandings are observed, with $\mathcal{I} \subset \mathcal{J}$. According to the model, the true abundance at year $t \in \mathcal{I}$ can be written as

$$B_t = \frac{C_t^e}{q\phi}.$$

We make here the traditional and customary assumption⁴ (*e.g.* Best and Punt (2020), Genu et al. (2021), or Cook (2013)) that for $\forall t \in \mathcal{I}$,

$$B_t^*|C_t^e, \theta = B_t \exp(\epsilon'_t) \text{ with } \epsilon'_t \sim \mathcal{LN}\left(-\frac{\tau^2}{2}, \tau\right),$$

where

$$\begin{aligned} \tau &= \sqrt{\log(1 + cv^2)} \quad \forall cv \\ \tau &\simeq cv \quad \text{if } cv^2 \ll 1 \end{aligned}$$

cv being the coefficient of variation associated with the estimated abundance B_t^* ; or similarly

$$B_t^*|C_t^e, \theta \sim \mathcal{LN}\left(\log C_t^e - \log q\phi - \frac{\tau^2}{2}, \tau\right). \quad (2.14)$$

⁴The choice of log-normal distribution could appear irrelevant considering the type of data, which is discrete, but it is a practical choice made by many authors, which makes computations more practical.

2.2.5. Likelihoods

Being assumed to be observed without noise, using the order-1 Markovian writing proposed in the precedent Section, a sequence of observed by-catch (C_0^e, \dots, C_T^e) yields a statistical information about θ embodied by the following likelihood:

$$f(C_0^e, \dots, C_T^e | \theta) = \prod_{t=1}^T f(C_t^e | C_{t-1}^e, \theta) \quad (2.15)$$

where each conditional density function $f(C_t^e | C_{t-1}^e, \theta)$ is determined by a choice on the distribution of ε_t .

When adding data on abundance, we can then define the complete statistical likelihood of the available data (abundances and observed by-catch):

$$f_\theta(\{B_t^*\}_{t \in \mathcal{I}}, \{C_t^e\}_{t \in \mathcal{J}}) = f(\{B_t^*\}_{t \in \mathcal{I}} | \{C_t^e\}_{t \in \mathcal{J}}, \theta) f(\{C_t^e\}_{t \in \mathcal{J}}, \theta) \quad (2.16)$$

where $f(\{C_t^e\}_{t \in \mathcal{J}}, \theta)$ is given by (2.15) and (A.14), and (under the assumption that abundances are observed independently), given (2.14),

$$f(\{B_t^*\}_{t \in \mathcal{I}} | \{C_t^e\}_{t \in \mathcal{J}}, \theta) = \prod_{t \in \mathcal{I}} \frac{1}{\sqrt{2\pi} B_t^* \tau} \exp\left(-\left(\log\left(\frac{q\phi B_t^*}{C_t^e}\right) - \frac{\tau^2}{2}\right)^2 \frac{1}{2\tau^2}\right) \quad (2.17)$$

2.2.6. Simulation model

The goal of defining a simulation model is to generate abundance and observed by-catch conditional on parameters θ . Assessing population viability under different sets of values of parameters θ is straightforward. The simulation model also allows to generate longer time-series of data than currently available on the common dolphin (31 years). A Pella Tomlinson SPM model was chosen for the simulation model (see § 2.2.2). This stochastic model depends on several variable parameters: the carrying capacity K , the extraction rate ϕ , the intrinsic growth rate r , the environmental stochasticity σ , the shape parameter γ (fixed at 2.4, (Genu et al., 2021)), the fraction of by-caught dolphins which float q (fixed at 24%, (Peltier et al., 2016b)), the initial depletion D_0 and the coefficient of variation for the observed abundance cv . Two different choices for the environmental stochasticity involved in the definition of the Pella-Tomlinson model have been made. The first choice is assuming a Beta distribution on the reduced abundance variable Z_t :

$$Z_t | \mathcal{F}_{t-1} = D(\theta) C_t^e \sim \mathcal{B}_e(a_t, b_t) \quad (2.18)$$

where $\mathcal{B}_e(a, b)$ is the Beta distribution on $[0, 1]$, with $(a, b) > 0$. This gives us an indirect elicitation of ε_t . The second choice of a log-normal distribution for ε_t is more traditional (McAllister and Kirkwood, 1998; Meyer and Millar, 1999; Hammond and Trenkel, 2005). Implications on likelihoods definition regarding the two options and more details of calculations are examined in Appendix A.4. The simulation model can be described as follow:

-
1. Initialisation of the abundance ($B_0 = D_0 \times K$) and the corresponding reduced abundance Z_0
 2. Simulation of the Z_t for each year, with a log-normal or beta distribution for process noise.

3. Calculation of the observed by-catch (C_t^e) corresponding to the Z_t
4. Calculation of the abundance:

$$B_t = \frac{C_t^e}{\phi q}$$

5. Generation of the observed abundances:

$$B_t^* \sim \mathcal{LN}(\log(B_t) - \frac{\tau^2}{2}, \tau)$$

with $\tau = \sqrt{\log(1 + cv^2)}$.

The three main outputs of the simulation model are the observed by-catch time-series C_t^e , the true abundance time-series B_t ; and the observed abundances B_t^* .

A simulation study was carried out to assess whether parameters can be estimated given available data. The accurate and consistent estimation of θ by maximum likelihood was performed using the `optim` function (with `method = "L-BFGS-B"`, see also Appendices A.4 in R version 2021.09.2+382 (R Core Team, 2021)). The results obtained either with a Beta or log-normal distribution for the process noise were similar (see Appendix A.4, Figures 24 and 23). Since the use of a log-normal distribution is more customary, this choice was retained.

2.3. Bayesian inference

Simulation model is precious to better understand the influence of certain parameters on data, in terms of extinction or monotony. Given a context of data scarcity, Bayesian inference is attractive to estimate the set of parameters $\{r, \sigma, \phi, K\}$ with a careful choice of priors. It is also recommended by many researchers to take into account uncertainty accurately (Millar and Meyer, 2000).

2.3.1. Prior elicitation

A bibliographic review was first conducted to look for similar cases of study that used SPM in a Bayesian framework. There is a variability of priors for K : uniform (Cook et al., 2021), log-normal (Meyer and Millar, 1999; Hammond and Trenkel, 2005) or non-informative (Millar and Meyer, 2000; McAllister and Kirkwood, 1998). We began with uniform priors for all the parameters and then tested more relevant priors, for example a gamma or an inverse gamma prior for the intrinsic growth r . The simulation model gives us the possibility to explore different trajectories of abundance, depending on chosen parameters (carrying capacity, intrinsic growth, etc). Some of these trajectories are implausible regarding the data at hand for the case study on common dolphins in the Bay of Biscay: for example cases where the population dies out or decrease are not consistent with the current data. Therefore, we excluded sets of parameters that conducted to these cases. Preliminary experiments have been conducted on triplets of values (σ, r, ϕ) within the support space $\Omega = [0, 0.7] \times [0, 0.1] \times [0, r]$. For each triplet of values, time-series of a period of 31 years (similarly to the real observations) of observed by-catch were simulated and assessed against two simple indicators :

- the probability for a population of "dying out" before 30 years;
- the average similar monotonicity of the simulated and observed by-catch time-series, computed by the mean of Kendall's tau ⁵ (an alternative could be to use the Spearman correlation coefficient). A triplet of value is considered as relevant a priori if this similar monotonicity is positive. It means that the real data and the simulated one have the same monotony, *i.e.*, in our case, the simulated by-catch are increasing over the study period.

Simulation tests only involve σ , r and ϕ . Indeed, the parameters K and q are only related to the magnitude of the abundance and do not play a role in the relative dynamics of the population. It is possible to graphically represent the sampling, by rejection, of the parameters respecting the constraints (Figure 5). The areas in the lightest colors correspond to sets of parameters that fulfill the conditions of monotony and extinction. The same figure but considering only the extinction condition is provided in Appendix A.5.1.

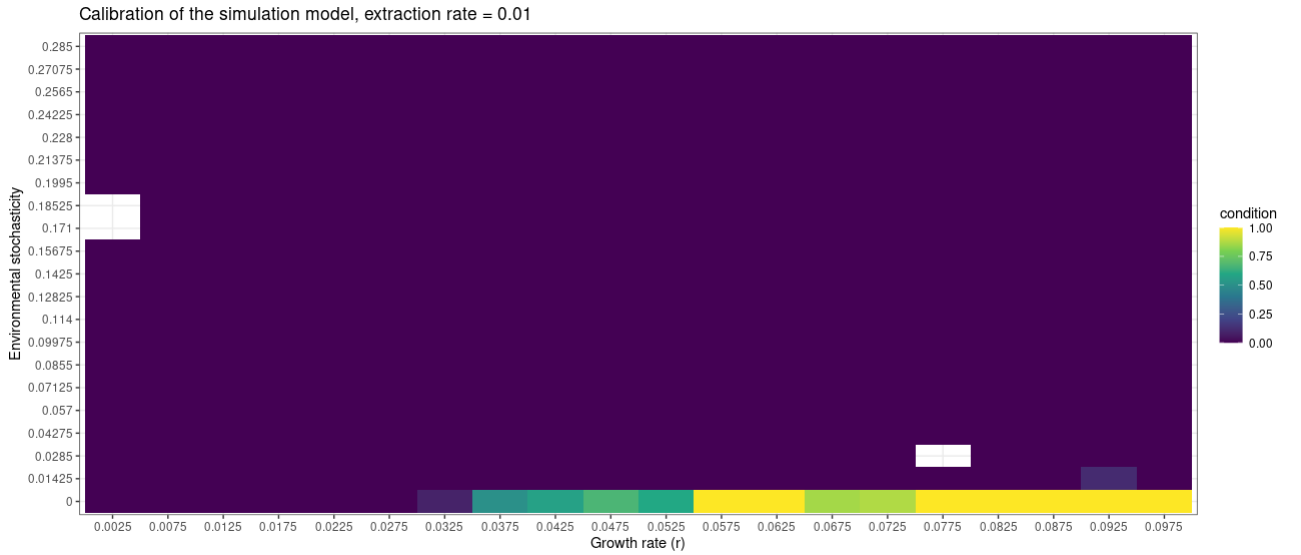


Figure 5.: Correlated sampling (by rejection) of (σ, r) such that the prior constraints (non-extinction and similar monotonicity) are simultaneously respected. The extraction rate was fixed at 0.01. Condition = 1 involves that the monotony and extinction constraints are respected (same monotony as the real data, with an error of 0.05 and probability of extinction < 0.1).

Theses "calibration" tests were the first steps that guided us towards relevant choice of priors. It also indicated the need to link the different priors, because of the correlated relations between the environmental stochasticity σ , the intrinsic growth r and the extraction rate ϕ . One of the most used tool to write joint priors is modelling with copulas.

2.3.2. 3D Prior copula modelling

Consider an input parameter θ . Denote

$$D(\theta) = \{ \{C_t^e(\theta)\}_t \text{ does not decrease on } [t_0, T] \text{ and probability of extinction is inferior to } 0.1. \}$$

⁵Kendall's tau measures the ordinal association between two quantities. The use of Kendall's tau or Spearman correlation coefficient implies to work on the ranks of real and simulated values, not on their magnitude. Therefore this should not threaten to increase artificially data information within the Bayesian inference, unlike empirical Bayesian approaches (Robert, 2007)

the criterion chosen to define *prior relevance* of a simulation depending on θ .

3D prior copula modelling aims at finding a correct joint prior which respects the conditions listed above, while taking into account correlations between the three parameters (σ, r, ϕ) . Details about details of calculations and numeric trials are in Appendix A.5.2.

A vine decomposition of the underlying 3D copula (see Appendix A.5.2) was conducted using the R package `Vinecopula` Schepsmeier (2016). The decomposition in so-called trees (see for instance Benoumechiara et al. (2020) for detailed explanations) with the best AIC criterion is described in Table 3.

Table 3.: Tree-based decomposition of the selected prior vine copula for (σ, r, ϕ) . Useful references on the nature of these bivariate copulas can be found in (Brechmann and Schepsmeier, 2013), and these distributions and their parameters are detailed in Appendix A.5.2.

Tree 1: unconditional pair copulas	
ϕ, σ	\sim Rotated Gumbel 90 degrees copula with parameter $\theta_{RG} = -1.21$
ϕ, r	\sim Gaussian copula with parameter $\theta_G = 0.39$
Tree 2: conditional pair copula	
$r, \sigma \phi$	\sim Rotated Tawn type 2 180 degrees copula with parameters $(\theta_{RT,1}, \theta_{RT,2}) = (2.97, 0.18)$

The full writing of the prior joint density of (σ, r, ϕ) is in Appendix A.5.2. Prior simulation in the rank space, realized using the same R `Vinecopula` package and plotted on Figure 6, highlights a good matching with the original design on Figure 27b (Appendix A.5.2) from which the copula was fitted. The detail of formulation (A.26) is necessary to incorporate the use of the underlying copula within Bayesian computational software tools, like `Stan` (Carpenter et al., 2017).

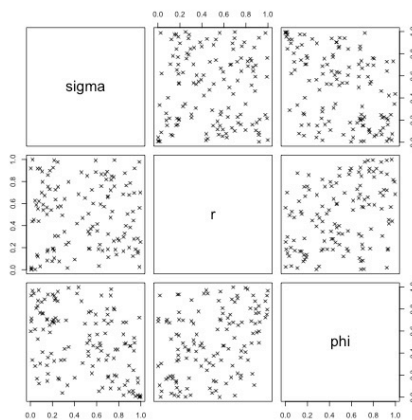


Figure 6.: Prior simulations of (σ, r, ϕ) in the rank space using the selected vine copula.

2.3.3. Bayesian estimation

For practical reasons, the initial depletion D_0 , instead of K , will be estimated. This choice is convenient as $D_0 = \frac{B_0}{K}$. In practice B_0 is unknown and the first abundance estimate available may not match the start of the observed by-catch time series. This will affect the interpretation of parameter D_0 . This will not affect K on the other hand. An additional advantage is that it may be easier to elicit a prior on depletion (a quantity expected to be bounded between 0 and 1) than on K . The set of parameters to estimate is now: $\pi(\theta) = \{r, \sigma, \phi, D_0\}$. Given any prior choice $\pi(\theta)$, as the one considered in § 2.3.1, the Bayesian estimation of θ consists in updating $\pi(\theta)$ by conditioning on the sequence of observed stranding (C_0^e, \dots, C_T^e) , which gives the posterior probability density function (pdf), given by Bayes' formula:

$$\pi(\theta|C_0^e, \dots, C_T^e) = \frac{f(C_0^e, \dots, C_T^e|\theta)\pi(\theta)}{m_\pi(C_0^e, \dots, C_T^e)}.$$

Unfortunately, the integration constant (or *evidence*, or *expected likelihood*)

$$m_\pi(C_0^e, \dots, C_T^e) = \int_{\Theta} f(C_0^e, \dots, C_T^e|\theta)\pi(\theta) d\theta$$

is untractable. Besides, $\pi(\theta|C_0^e, \dots, C_T^e)$ does not belong to a closed-form family. For this reason, we make the usual choice to sample from $\pi(\theta|C_0^e, \dots, C_T^e)$, using Markov Chain Monte Carlo (MCMC) algorithms (Robert and Casella, 1999). More precisely, we first used a Gibbs scheme to sample iteratively from each dimension of θ , each sampling step being hybridized by a Hastings-Metropolis step. The details of this procedure are describe in Appendix A.6.1. Then, to simplify the process of estimation, we used the Markov chain Monte Carlo (MCMC) algorithms available in **Stan** (Carpenter et al., 2017): the Hamiltonian Monte Carlo (HMC) algorithm. More technical details on this algorithm are explained in Appendix A.7.

The simulation model outlined above in section 2.2.6 is useful to test the performance of the estimation, by knowing the parameters of the SPM model. It is then possible to compare the values obtained with the simulation model to the estimated values.

2.3.4. Tools

All codes were written in **R** version (R Core Team, 2021) using the Integrative Development Environment **Rstudio** (RStudio Team, 2020). Figures were produced with the package **ggplot2** (Wickham, 2016). Bayesian inference with Halmitonian Monte Carlo was carried out using **Stan** (Carpenter et al., 2017) called from **R** using the package **rstan** (Stan Development Team, 2022).

2.3.5. Summary of the work

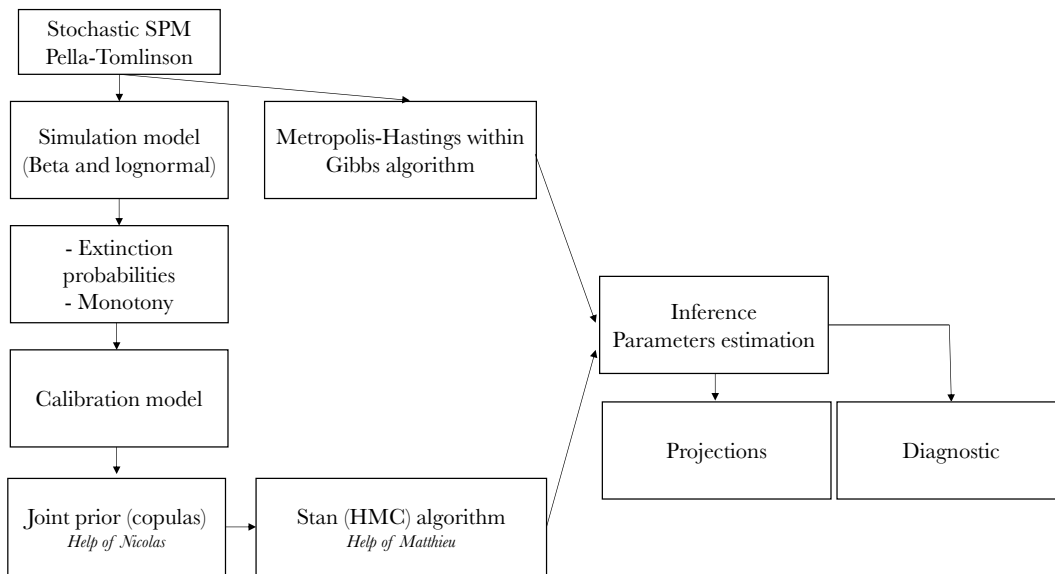


Figure 7.: Flowchart of the work undertaken during the project.

3. Results

3.1. Experiments conducted with the simulation model

3.1.1. Abundance trajectories

The different possible trajectories of abundance B_t obtained thanks to the simulation model vary a lot, depending on the values of the parameters, for example the extraction rate ϕ , *cf* Figure 8 or the environmental stochasticity, *cf* Figure 9 .

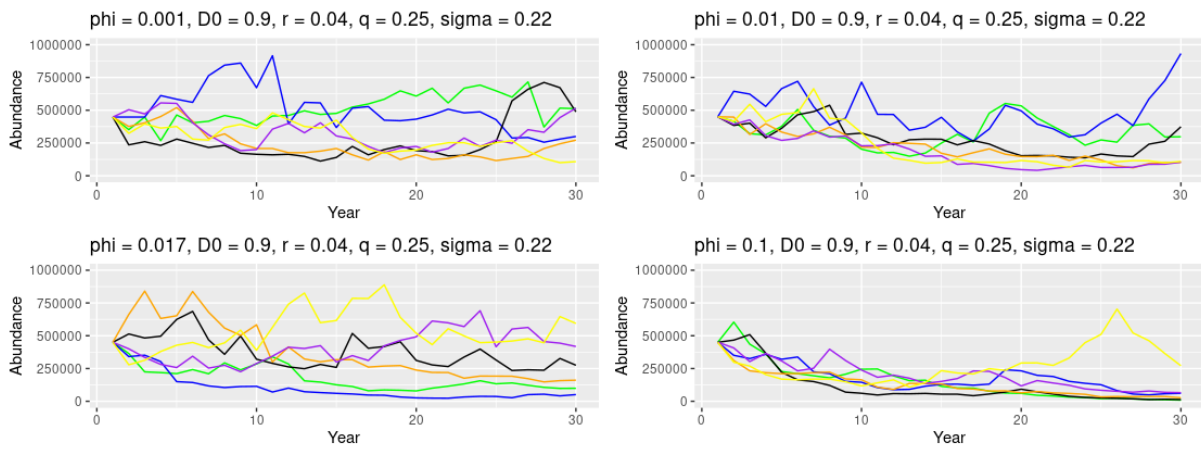


Figure 8.: Various trajectories depending on the value of the extraction rate ϕ .

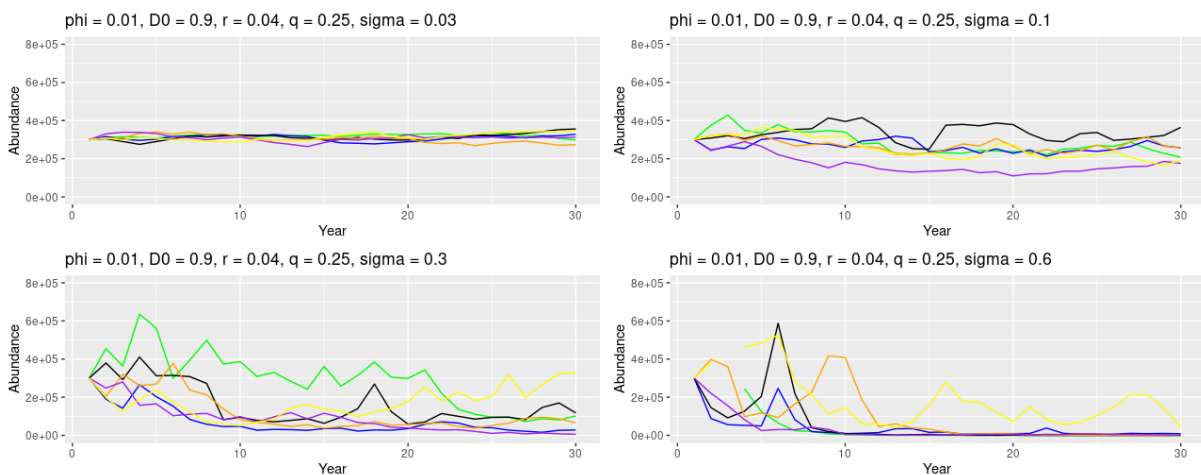


Figure 9.: Various trajectories depending on the value of the environmental stochasticity σ .

The extraction rate ϕ seems to have a small influence on the decreasing of abundance, but it is only visible if the extraction rate is very high (10%). If by-catch is important, the risk of extinction of the population is high. It is obvious when looking at Figure 8, especially for $\phi = 0.1$. Also, high values of environmental stochasticity (σ) cause important variations of abundance one year to another, which can lead to extinction (see last graph of Figure 9).

3.1.2. Extinction probability

One of the main risks for the common dolphin's populations is to go extinct, that could occur in particular conditions. The simulation model allows to test different sets of parameters and the corresponding abundance trajectories. Then, extinction probabilities can be calculated, considering a given set of parameters, for example the couple (environmental stochasticity σ , intrinsic growth r), Figure 10. We consider that there is extinction if abundance is null at the end of the chronological series.

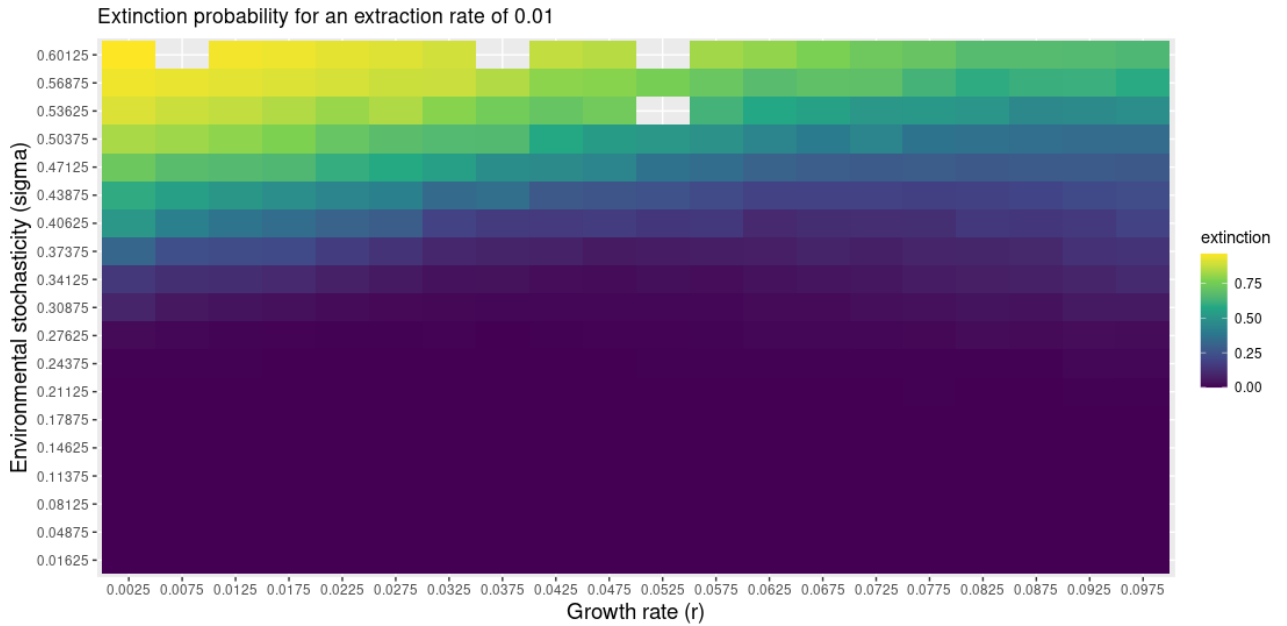


Figure 10.: Extinction probabilities for an extraction rate of 0.01, a for 100-years chronological series of abundance.

Considering the situation above, *i.e* for an extraction rate of 1%, which corresponds to the current interim management objective of ASCOBANS (Res.3.3 and Res.5.5), the extinction probability increases with increased environmental stochasticity and decreases with an increasing intrinsic growth (Figure 10). Also, for a situation where the intrinsic growth is $r = 0.04$ (the typical value assumed for a small cetacean species; Wade, 1998), the extinction probability increases with the environmental stochasticity. For an environmental stochasticity superior to 0.4, the extinction probability is superior to 0.5. Moreover, it is also possible, using the simulation model, to calculate the maximum environmental stochasticity that avoids extinction (probability of extinction $< 5\%$), see Figure 11. More discernible results were obtained assuming a Beta distribution for process noise (Beta distribution on the reduced abundance variable Z_t , *cf* § 2.2.6) than with a log-normal distribution. Figure 11 therefore shows the results with a Beta distribution.

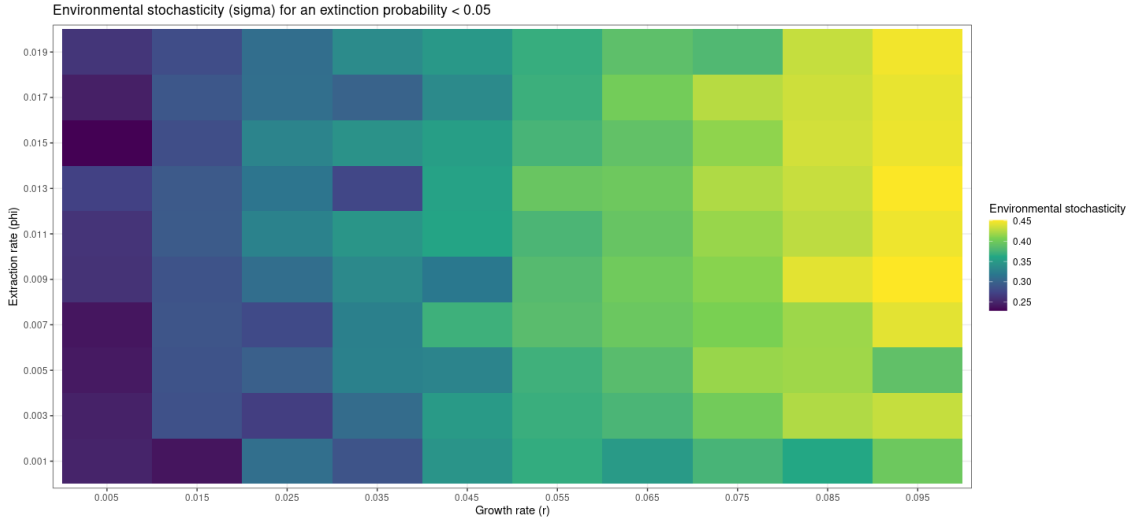


Figure 11.: Maximum environmental stochasticity corresponding to a probability of extinction < 0.05 (for a 100-years chronological series of abundance), with a beta distribution.

The extraction rate does not seem to have an influence on the maximum maintainable environmental stochasticity (σ_{max}). The growth rate does: for a low growth rate, σ_{max} must be low (< 0.25). For $\phi = 0.01$ and $r = 0.04$, maximum environmental stochasticity must be moderate: $\sigma_{max} \simeq 0.32$.

3.2. Bayesian estimation

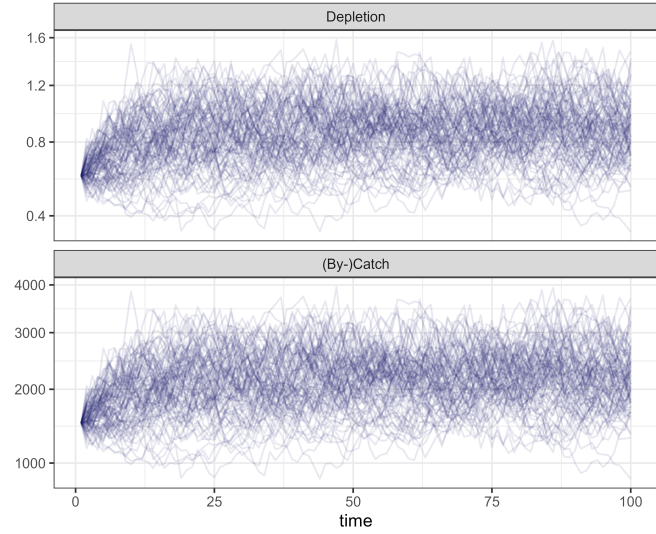
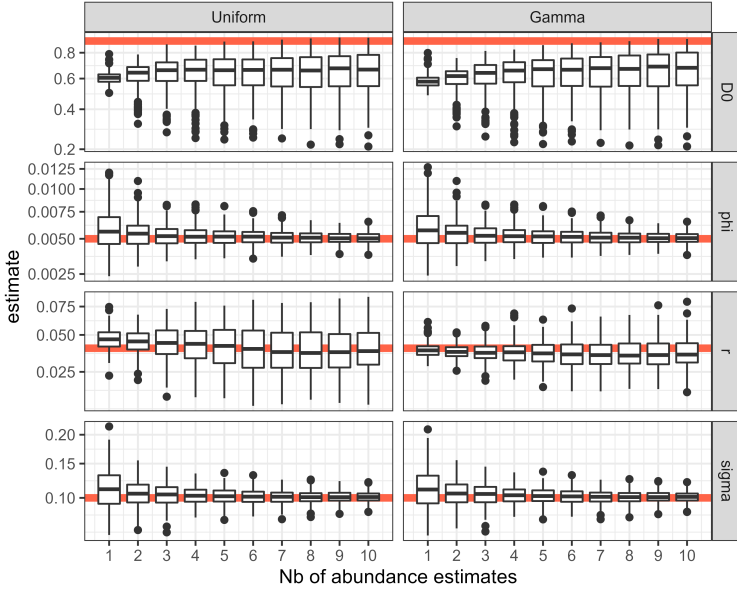
3.2.1. Tests with the simulation model

Running MCMC chains with the Metropolis-Hastings algorithm, compared to HMC algorithm with `Stan`, provides worse results and there are important auto-correlation in the MCMC chains (*cf* Appendix A.6.2). It could be explained by the length of the MCMC chains, that are longer with `Stan` and the computational performance of the HMC algorithm, which is higher than Metropolis-Hasting. It vindicates our choice to estimate the parameters with `Stan`.

Running `Stan` HMC algorithm with simulated data allows to control the parameters of the population's dynamics and to modify the monotony of the abundance and by-catch trajectories. Moreover, it enables to choose the size of the data set, which means the number of abundance estimation (for realism), since usually one abundance estimation is produced every 10 years. Therefore, in the following paragraphs, three simulation cases are tested, corresponding to different trajectories of by-catch and abundance.

Case 1: Stationary population

The first case tested is the the case of a stationary population, with an initial depletion close to 1, which means that the carrying capacity is almost reached. Figure 12 summarises the results for 300 simulations and the corresponding trajectories of depletion (B_t/K) and by-catch.



(a) Results of the MCMC with Stan HMC algorithm. Red line represents the true parameter values used for simulating data. One abundance estimate is collected every 10 years. Boxplots are based on 300 simulations.

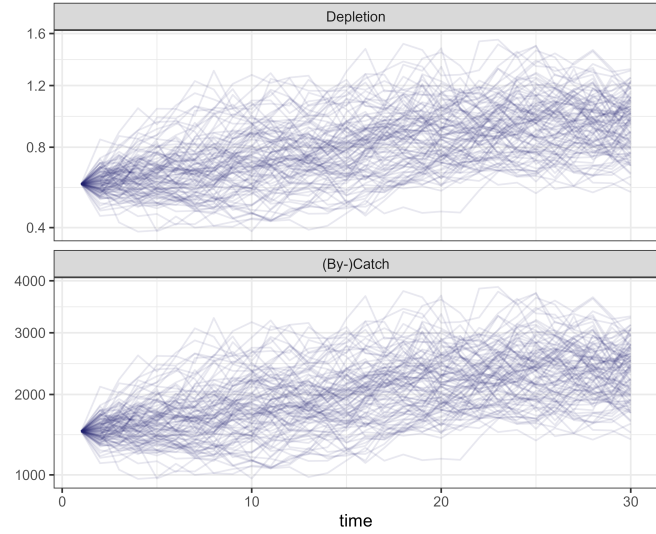
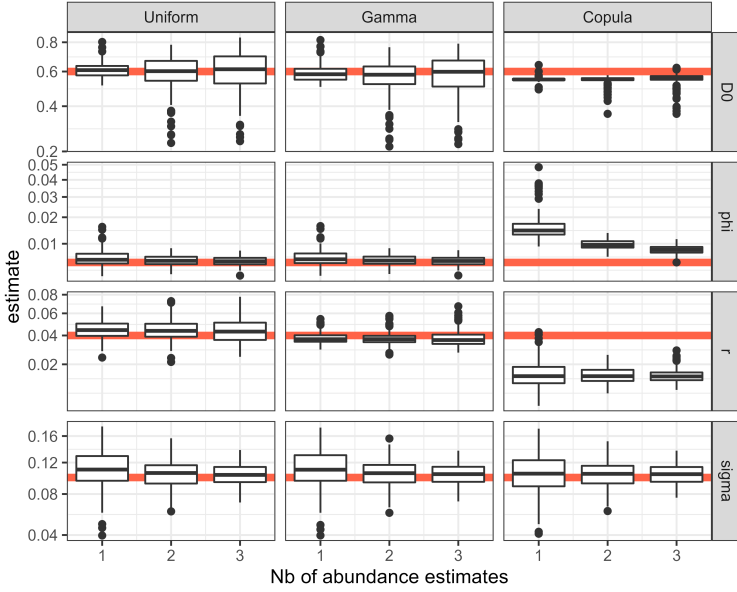
(b) Corresponding abundance trajectories

Figure 12.: Stan model with simulated data, in a case of stationary population.

The initial depletion D_0 is underestimated, both with a uniform or gamma prior, but also seems to converge slowly to the true value as more data on abundance is added. The initial depletion was set to 0.9, reflecting a population not depleted. In this setting, estimation of D_0 (and K) is difficult as there are little variations in abundance over the population trajectory to learn from. For the environmental stochasticity σ or the extraction rate ϕ , estimation is very close to the true values, which suggests accurate estimation. Moreover, a larger period of abundance estimations generates more precise estimations (reduction of the sizes of the boxplots for ϕ and σ). On the contrary, it is less visible for the intrinsic growth: uncertainty seems to increase when the number of abundance estimation is high but the estimation is still very close to the simulation value.

Case 2: Increasing population

The second case tested is the case of an increasing population, with an initial depletion much lower than case 1, which means that the carrying capacity is not reached. Figure 13 summarises the results for 300 simulations and the corresponding trajectories of depletion (B_t/K) and by-catch. In this case, we only tested three different sizes of abundance data (corresponding to a time-series of by-catch of 30 years similar to the case study), since we also run the model with a 3D copula as a prior.



(a) Results of the MCMC with Stan HMC algorithm, with three types of prior. Red line represents the true parameter values used for simulating data. One abundance estimate is collected every 10 years. Boxplots are based on 300 simulations.

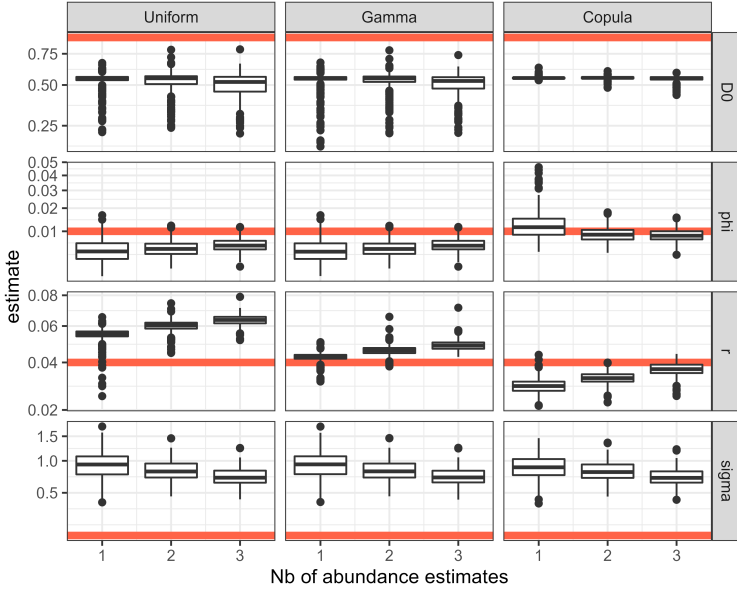
(b) Corresponding abundance trajectories

Figure 13.: Stan model with simulated data, in a case of a increasing population.

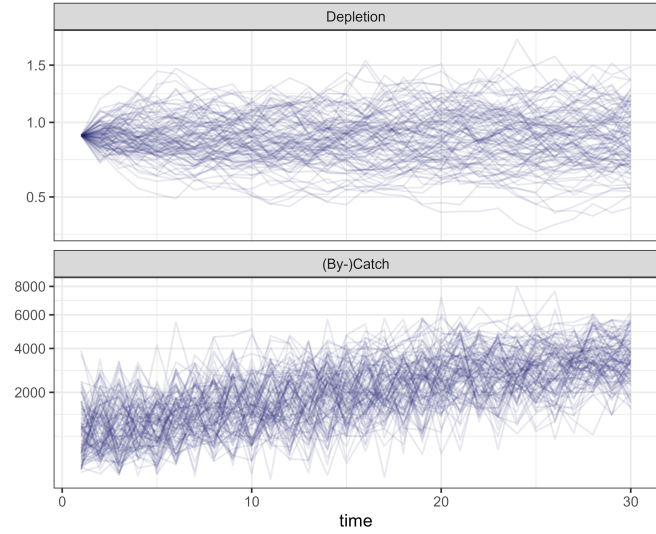
Since the carrying capacity is not reached, initial depletion is much better estimated than in case 1. Estimation is also very good for σ . Surprisingly, the use of the 3D copula diminishes the quality of the estimation for ϕ and r : the former is over-estimated and the latter is under-estimated. It may be caused by a conflict between the data and the 3D copula prior, which is supposed to be more informative than the uniform one (that models prior independence).

Case 3: Decreasing population and increasing by-catch

In this case, there is a negative correlation between abundance and by-catch: abundance decreases and by-catch increases. To generate such a situation, abundances were produced according to Equation 2.7 and by-catch was generated with an increasing trend over 30 years so that abundance remains stable or decreases (Figure 14(b)). This pattern corresponds to a plausible scenario for our case study on common dolphin where no decline in abundance is apparent yet (Table 2) and strandings are increasing (Figure 3). It is noteworthy that in this case, the model used to analyze the data is misspecified as it is different from the true data-generating process.



(a) Results of the MCMC with `Stan` HMC algorithm, with three types of prior. Red line represents the true parameter values used for simulating data. One abundance estimate is collected every 10 years. Boxplots are based on 300 simulations.



(b) Corresponding abundance trajectories

Figure 14.: `Stan` model with simulated data, in a case of a decreasing population.

In this case, the model has difficulty correctly estimating the initial depletion D_0 and the environmental stochasticity σ , maybe because data on by-catch and on abundance do not bring the same information, due to the mismatch between them. However, the extraction rate ϕ is well estimated with the 3D copula but is underestimated with the other priors. Both the uniform and gamma priors tend to overestimate r , especially as sample size increases, whereas r is initially underestimated with the 3D copula prior and seems to converge to the true value with 30 years of data.

3.2.2. Case study: common dolphins in the North-East Atlantic

As a reminder, two types of data are used to estimate the parameters: data on strandings (31 years, Figure 3) and abundance estimations (2 estimations, in 2005 and 2016; Table 2). The results of Figure 15 are obtained with `Stan`. Posterior summaries are provided in Appendix A.8.1, MCMC convergence assessments in Appendices A.8.2 (trace plots), A.8.3 (auto-correlation) and A.8.4 (Gelman-Brooks-Rubin \hat{R} statistics).

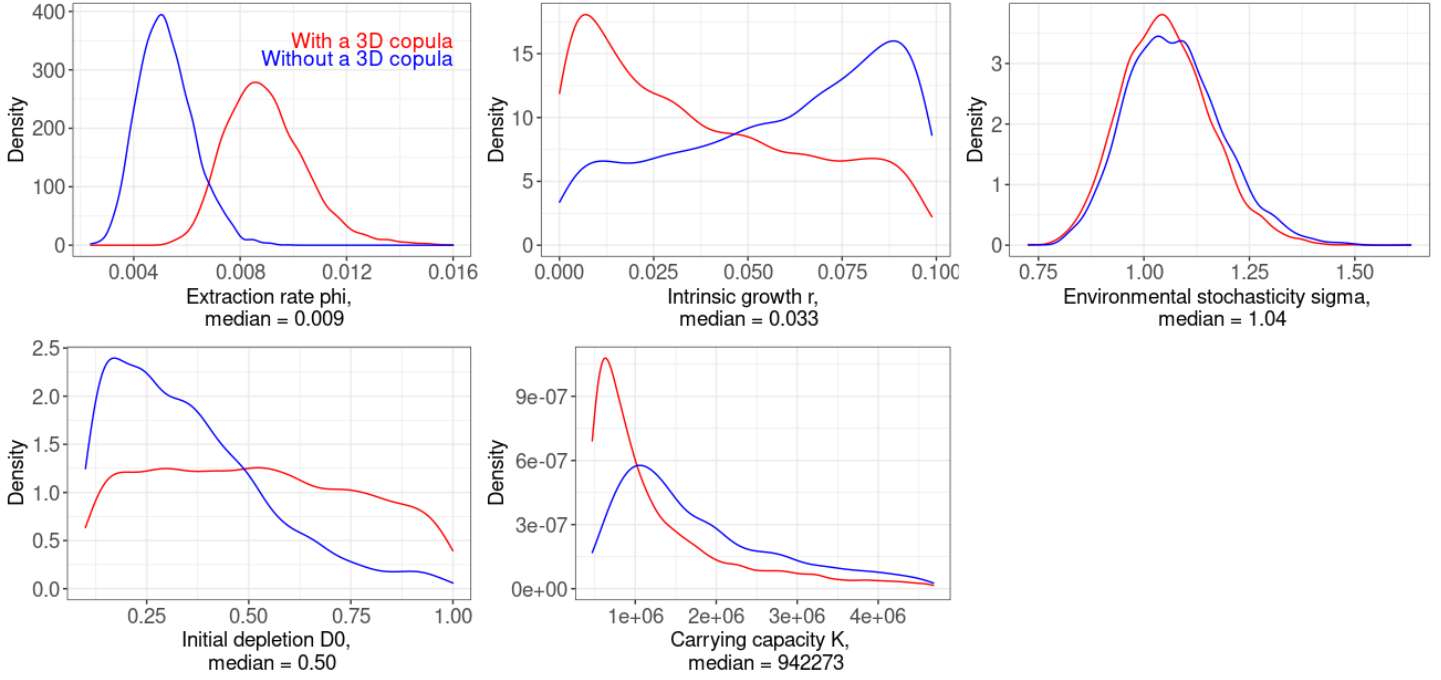


Figure 15.: Posteriors with (red curve) out without (blue curve) the 3D copula. The medians are indicated for the posterior with the 3D copula.

First of all, there are quite important differences of estimation when using a 3D copula (the red curve) and independent uniform priors. Estimation of ϕ doubles with the 3D copula. It seems coherent since the 3D copula prior selects sets of parameters which conduct to an increasing of by-catch and no extinction (conditions which fit the most the real data). Also, the posterior distribution of ϕ is narrow, which suggests a precise estimation (coefficient of variation of 16%). Variations of estimation are very large for the intrinsic growth r . In both cases, the posterior is diffuse, which suggests that the data does not really seem to contain information about this parameter. It can be explained by the few abundance estimations (two abundance estimations). The same remark can be formulated for the initial depletion D_0 : with the 3D copula, estimation is vague and imprecise whereas the posterior distribution obtained from independent uniform prior suggests a heavily depleted population. Only the environmental stochasticity's estimation does not differ from the model including the 3D copula or not, but the estimation seems high compared to what we would expect (*cf* Section 4 for further discussion).

Projected abundance trajectories can be obtained by running the simulation model (*cf* Section 2.2.6) with the estimated parameters showed above. These abundance trajectories are represented in Figure 16.

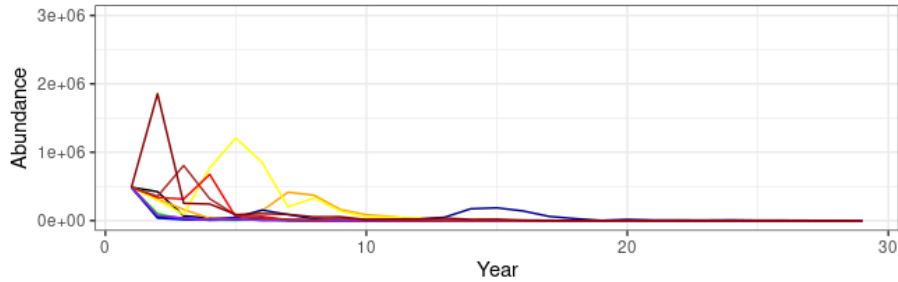


Figure 16.: Abundance trajectories using the simulation model with the estimated parameters.

The simulated abundance trajectories show that the population dies out in less than 20 years, largely because of the important environmental stochasticity, which cause massive variations and then depletion. This result will be discussed in Section 4.

4. Discussion

In our study we first discussed the regulatory framework about common dolphin's by-catch, by listing the current management procedures and discussing their limits. A formalization of a decision-making framework for recommending removals limit for cetaceans was also outlined. One class of models was studied, stochastic SPM models, in order to estimate the population's dynamics parameters. Using both abundance data and strandings (by-catch) data is one important innovation of our study. More than a final set of management rules, this report proposes an exploratory approach to use stochastic SPM in a Bayesian framework by using data on by-catch. It includes methodological choices, such as the priors distribution, the writing and the statistical distribution of abundance, the distribution laws for abundance and strandings, the formalization of the likelihoods. It partly explains the length of the Section Material and Methods: the main objective of the internship was not necessarily to produce new management rules but to work on a generalizable model that could be used in other cases of by-catch management.

4.1. Major results

The simulation model allowed to show that the extinction risk depends on the intrinsic growth and the environmental stochasticity, more than on the extraction rate. The extinction risk increases with the environmental stochasticity, for this class of models, which is coherent: it induces important variations of abundance, which can, at the end, lead to extinction (Lande, 1993; Foley, 1994). The opposite trend can be observed for the intrinsic growth: a high intrinsic growth reduces the risk of extinction. This is also biologically coherent (Giles Leigh, 1981). Custom R code to simulate data from the posited model (Section 2.2.6) was written and tested. Custom R code to implement a Metropolis-Hasting sampler and Stan code were also written to estimate, in a Bayesian framework, parameters underlying the posited model. Parameter estimability from data was validated in simulation studies: ϕ , r and σ can be accurately estimated with uniform priors and realistic amounts of data (Figures 12(a) and 13(a)). Estimation of initial

depletion (and carrying capacity) is possible if abundance estimates are available (see Supplementary Figure 25 in Appendix A.4). Accurate estimation of these parameters was possible under restrictive conditions in practice: a population recovering from a depleted state with low enough levels of additional anthropogenic mortality that still allows growth at maximum potential rate for some time, and then a slowdown due to density dependence effects (Figure 13; Punt et al., 2020). For a stationary population close to carrying capacity, estimation of initial depletion appeared possible under unrealistic long time-series of data (Figure 12).

Applying the model to an empirical dataset on common dolphins in the North-East Atlantic led to some surprising results (Figure 15). In particular, the estimated intrinsic growth rate was large, and bouncing on the upper bound of the assumed uniform prior (Figure 15). More worryingly, estimated environmental stochasticity was huge (posterior mean > 1) and beyond realistic values for a K-selected species such as the common dolphin (and marine mammals more generally). Our simulations (Figures 10 and 11) clearly showed that such a large environmental stochasticity would quickly lead to extinction, a result confirmed by projections (Figure 16). This lack of realism led to re-thinking the prior used and to design a more complex joint prior for parameters ϕ , r and σ by means of copula. This joint prior encapsulate information via its posited correlation structure between these parameters. In particular, the prior was built to reflect a situation of increased by-catch and no extinction over a specified time horizon.

Estimating under the joint 3D copula prior was substantially different: the extraction rate ϕ doubled (estimated median = 0.009), the intrinsic growth r decreased to a more realistic value for small cetaceans (estimated median = 0.033): Wade (1998) recommend 0.04 as an *omnibus* value for a cetacean species). Environmental stochasticity σ remained extremely large (estimated median = 1.04). Initial depletion D_0 was not precisely estimated (estimated median = 0.50). The latter parameter is linked to the carrying capacity, estimated at 942,273 animals.

Environmental stochasticity was largely overestimated irrespective of which prior was used. Common dolphins are long-lived and may only produced one calf per year (K-selected species): the very large variations of abundance, as represented in Figure 16, are unrealistic. This overestimation may be caused in part by observation error in by-catch (reconstructed from observed strandings). One other reason could come from the initial abundance B_0 in 1990, which is assumed to be the same as the the first abundance estimate available (2005 SCANS campaign). When simulating abundance using the estimated parameters of ϕ , r , D_0 and $\sigma = 0.2$, abundance trajectories are very different from Figure 16: the risk of extinction is lower and variations of abundance less important (Figure 17), but yet still somewhat unrealistic large for a cetacean species.

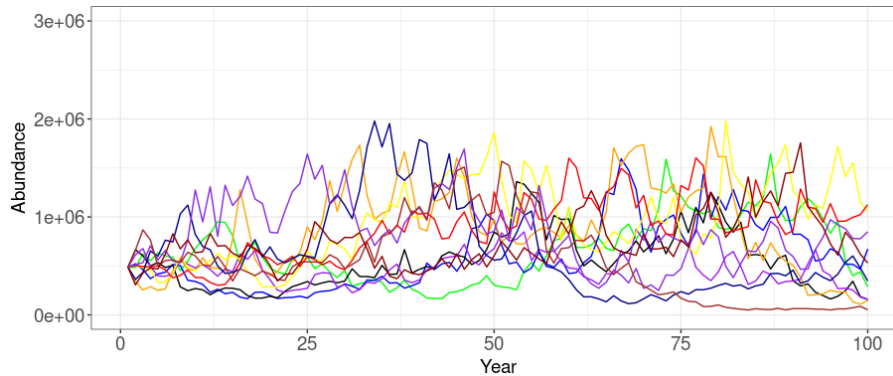


Figure 17.: Abundance trajectories using the simulation model with the estimated parameters under the joint 3D copula prior and assuming $\sigma = 0.2$.

Overestimation of environmental stochasticity betrays a deeper problem with the model, which led us to consider model misspecification. Specifically, we simulated data to generate a mismatch between by-catch data that are increasing over time and abundance data that remains stable (or decreases) over time. The data-generating mechanism is thus different than the posited model. Results from these simulations evidenced that overestimation of σ was pervasive under such model misspecification (Figure 14). Assuming independent priors led to bias in estimates of r and ϕ with the former being overestimated and the latter underestimated. Using the joint 3D copula prior attenuated these biases, especially with respect to ϕ (Figure 14). Reasonable estimates of ϕ were recovered with the joint 3D copula prior and the assumed model, even when the latter was misspecified compared to the true data-generated mechanism.

It is important to note that there is, to the best of our knowledge, no model for cetaceans management which provides direct estimations of the extraction rate ϕ . PBR and RLA are control rules whose computation hinges on an estimate for r (Genu et al., 2021), which is difficult to come by for most cetacean species (Wade, 1998). Selecting a default value for r is common practice but is often met with resistance in practice (personal observation from M. Autthier). Our model allows to estimate a parameter ϕ that is akin to an extraction rate ϕ which can be estimated from data (even when estimation of r is difficult or biased; *cf* Figure 14). This feature opens the ground to explore devising new control rules for managing by-catches using estimates of ϕ . This development is beyond the scope of the current work, but would represent a straightforward extension.

4.2. Main limitations and perspectives

4.2.1. Estimating the extraction rate ϕ

In the model, ϕ , the extraction rate, is constant through time. This hypothesis seems maybe correct when considering small chronological series, but this choice is more questionable when dealing with 100 years of time series. But choosing ϕ_t dependent on time would have led to much more complexity in the model. Also, our model does not take into account possible management decisions that could affect fishing activities and influence the extraction rate (for example the effect of pingers, the closing of some fishing spots during particularly vulnerable moments for dolphins, modification of the fishing practices, etc). Future developments may include defining more realistic processes for generating

time-varying ϕ_t .

4.2.2. Value of q and B_0

The model requires a pristine abundance (B_0) which is unusually unknown. Worse, the first abundance estimate may only be available long after by-catch started to be recorded. In the case of common dolphins in the North-Sea Atlantic, the time-series of strandings starts in 1990 while the first abundance estimate is provided by the SCANS-II survey in 2005. In practice, the pristine abundance needs to be estimated or set at some historical value. It could be possible to consider it as another parameter to estimate (and choose a prior for it). The profile likelihood with respect to this parameter B_0 shows a maximum (the maximum likelihood exists), *cf* Appendix A.4.1, Figure 25. The simulations we carried out during this work showed that estimation of B_0 is possible under some settings that may be rarely met in practice for cetaceans (see also Punt et al. 2020).

Accurate estimation of the parameters ϕ , r and σ depended also on correct knowledge of q (the proportion of dead dolphins (by-caught) which float and can strand) in the operationalization equations for strandings: $C_t^e = q\phi B_t$. We ran a few numerical experiments with **Stan** to assess the sensitivity of results to q : we fixed $q = 0.5$ to simulate data. This is twice the empirical value estimated from drifting experiments with carcass at sea (0.24; Peltier et al., 2016b). Data were generated with $q = 0.5$ but analyzed assuming $q = 0.24$ in the **Stan** code. This setting imitates a scenario whereby the correct value of q is not known and the one used in practice is incorrect. We compared the results with a situation where the value of q is correctly known, by setting $q = 0.24$ when simulating the data (Figure 18).

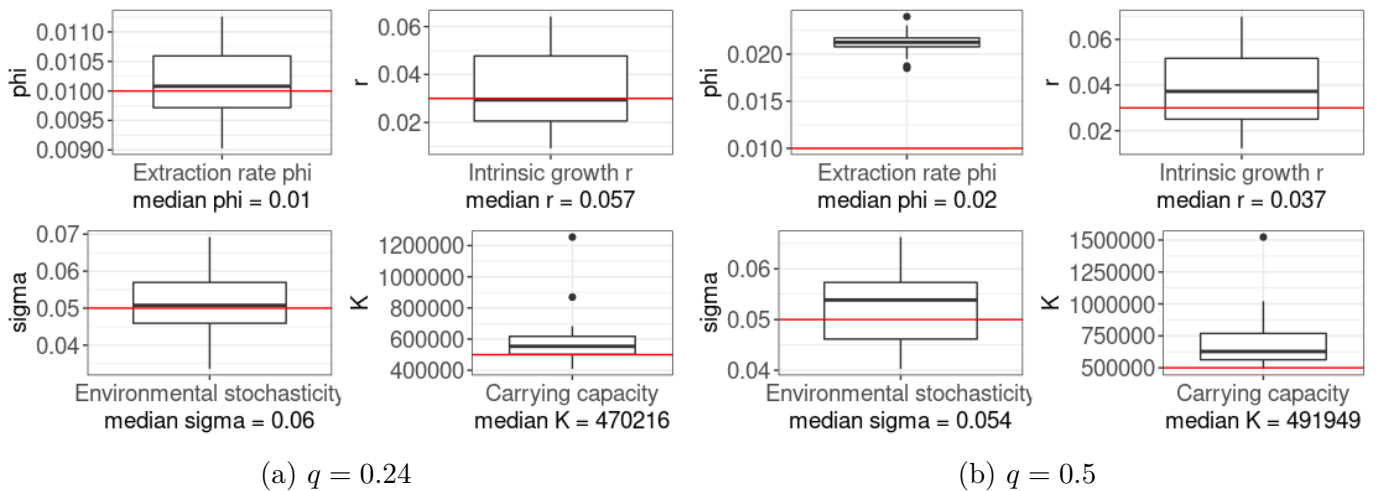


Figure 18.: **Stan** model with simulated data, with $q = 0.24$ (left) and $q = 0.5$ (right). 30 simulations were conducted and the median was calculated for each simulation. The boxplots summarise information about the medians.

Figure 18 shows that a wrong value of q in the model results in biased parameter estimates, especially (and unsurprisingly) with respect to ϕ . Accurate knowledge of q appears paramount for efficient management.

Finally, q , was assumed constant although it may be affected by various parameters. In particular, Peltier et al. (2016b) used physical drift models (MOTHY) to predict the drift trajectory of a dolphin dead from by-catch. These models allow to compute a stranding

probability for floating carcass, which is different one month to another because of meteorological conditions. These probabilities could be included as data in our model to scale up observed strandings into by-catch estimates instead of using the inferred by-catch estimates as it was done in the present work. The important point is that drift and buoyancy probabilities are auxiliary data to be included in the model to account for variations in observed strandings and to allow for accurate estimation of by-catch at sea. More generally, these data may be replaced by a proxy of effort in the case of commercial species. The model developed in this work may be used in data-poor context and is not necessarily restricted to cetaceans.

4.2.3. Environmental stochasticity and the need to improve data on by-catch

It is very likely that the environmental stochasticity (σ) is overestimated in our case study (*cf* Section 4.1). One of the reason could be the noise and the uncertainty linked to the by-catch data, that affects the estimation of the parameter. Another reason, non mutually exclusive, could be model misspecification with respect to the true data-generating process behind the data. We proved, thanks to the simulation model, that the extinction risk depends on the estimation of σ : with high values of σ the risk of extinction is very high. A management rule that would be established relying on this estimation would be very (too) severe. It highlights, indirectly, the need of precise and accurate data on by-catch to be able to propose fair management rules. It could be an argument to encourage the monitoring on by-catch, so that data is produced without error.

Finally, one limit is that the model needs data on by-catch to be fitted. For protected species, it means that if there is a complete ban on by-catch and no dedicated monitoring of bycatch, there is no guarantee to obtain non-zero values for by-catch in official statistics. A zero value in the time-series of by-catch would be understood as extinction of the population in the current model set-up.

This study sets out to investigate with simulations the sensitivity of SPM to environmental stochasticity for cetacean species. In practice, there are few species or populations of cetaceans for which long-enough time-series of abundance data are available to estimate environmental stochasticity. This parameter governs yearly variations in abundance. Given the low productivity of cetacean (one calf per female), large values of environmental stochasticity are unlikely for a closed population or stock of cetaceans (even assuming $\sigma = 0.2$, there are large fluctuations, unrealistic for a cetacean species; Figure 17). The projections on Figure 16 all result in a rapid projected extinction of common dolphins everything else being equal. This probable overestimation of σ may be the result of model misspecification with respect to the true data-generating mechanism. However, independent evidence from age-at-death data collected from stranded animals also projects extinction within the next 30 years everything else being equal (Figure 19, Rouby (2022)).

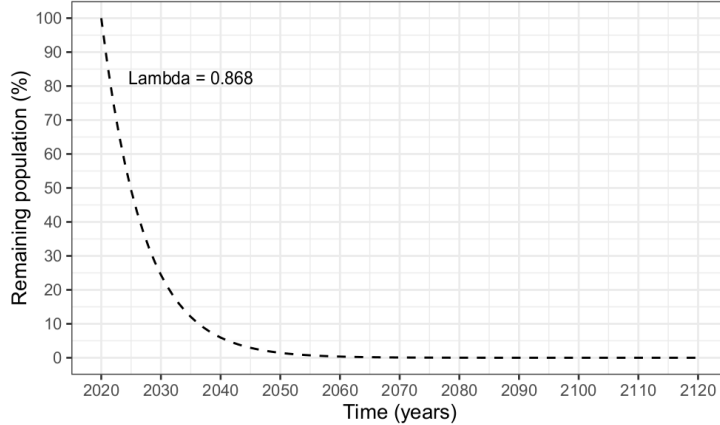


Figure 19.: Remaining population from 2020 to 2120, Rouby (2022)

The matrix population models underlying these projections are very different from SPM, yet they nevertheless projected extinction due to an increase in additional mortality over time. The extraction rate estimated with the joint 3D copula prior is of the order of 1% of abundance, which aligns with the ASCOBANS intermediate precautionary objective to reduce by-catches to less than 1% of the best available population estimate. Given the projections from matrix population models, and the expected increase in true environmental stochasticity (due for example to climate change effects), all these evidence points to increased pressure on common dolphins and a likely decreased population viability if current conditions remain unchanged.

4.2.4. Perspectives

First of all, the code of the model developed in this work will integrate the package `RLA` on `R`, to propose another simulation model that produces abundance trajectories. The codes developed in this work are operational and reusable, in order to be used to provide management rules, for common dolphin or for other species.

Also, the final aim of this work is to be included in management procedures for the cetaceans by-catch. Our model could be transposable to other species, such as harbor porpoise (*Phocoena phocoena*) in the North Sea (where by-catch data from fisheries may be available from onboard monitoring) or some fish species such as rays (*e.g.* in the Southern Ocean where rays are by-caught on toothfish longlines). Indeed, this work could be useful to deal with by-catch of some data-poor stocks of (protected) species. Important caveats remain around the reliability and accuracy of the data but the model developed during this study could be adapted to incorporate fishing effort were this piece of information is available.

With respect to dolphin by-catch, we could eventually consider the following procedure: the parameters can be re-estimated every 6 years, which corresponds to the aspirational frequency of the SCANS surveys. Then, the main goal is to find a tolerable extraction rate, ϕ_{opt} , and the corresponding removal limit, that respects the conservation objective (for example, 80% of the carrying capacity K over 100 years with a probability of 80%). The removal limit could be calculated as:

$$\text{Removal limit} = N_{\text{best}} \times \hat{\phi},$$

with N_{best} the last abundance estimation and $\hat{\phi}$. This control rule differs from both PBR and RLA as it does not need an estimate of r or current depletion. However, this rule

does not allow to set a null removal limit either: this may not need a drawback in theory as a removal limit is an upper limit not to be exceeded. It means in practice that some level of by-catch would always be expected, even under good management schemes.

ϕ_{opt} depends on the estimation of ϕ in the model and we could imagine an approach that rewards precise estimation (and hence accurate and reliable data): the more precise the estimation of ϕ , the more concentrated is its posteriori distribution. ϕ_{opt} could be chosen as a quantile of that distribution (inferior to the median, for example the 30% quantile). If the posteriori distribution is very tight, the median is close to this quantile and ϕ_{opt} is "fair". On the contrary, a bad estimation of ϕ (it may be the result of the uncertainty of the by-catch data) gives very low values of ϕ_{opt} . It may thereby encourage the production of high quality data on by-catch. This remains to be formally tested in a Management Strategy Evaluation.

We could also adjust ϕ_{opt} depending on the current abundance. For example multiply it by a factor $x \in]0, 1]$, $\simeq 0$ when the population is very low and 1 when it is in good status. The state of the population could induce a signal for the management decisions, such as $MSY B_{trigger}$: under this threshold, the fishing activity must be reduced to allow the stock to be restored. This factor x would be very much akin to the recovery factor used in the PBR control rule.

Finally, the production of a bio-economic model, in addition to the SPM model presented in this work, could be useful to integrate economic considerations and make the formalization a decision-making framework (Section 1.2) more practical.

4.3. Conclusion

This work demonstrated the interest of using by-catch data in order to estimate the parameters of the common dolphin's population dynamics, in particular the extraction rate. It can be concluded that the use of our model can provide a precise estimation of the extraction rate, in any case (increasing, stationary or decreasing population) and also for other species for which data on abundance is sparse. With further reflection on the decision-making process, the methodology proposed here could integrate management strategy evaluations, to handle cetacean's by-catch. This would be an improvement compared to the existing rules setting removal limits of by-catch.

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A. Appendix

A.1. Correlations between fishing activities and dolphins

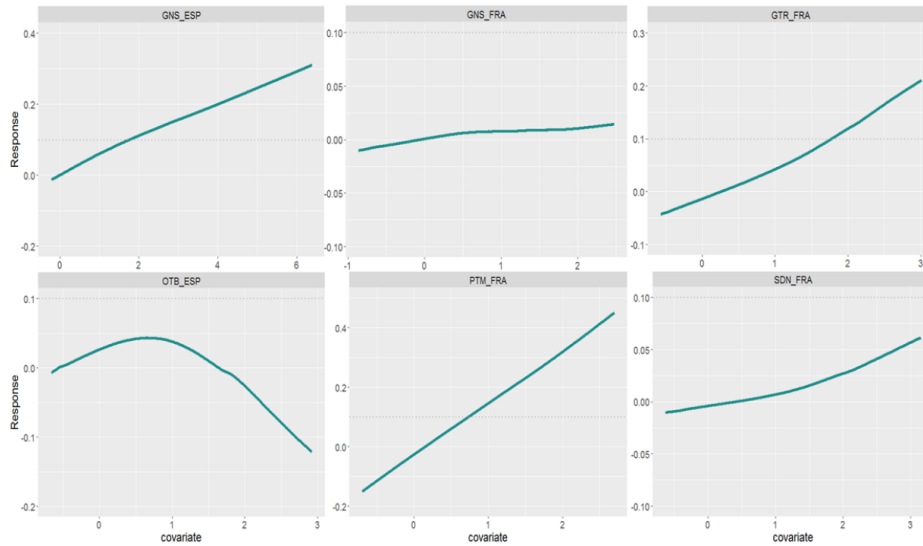


Figure 20.: Correlations between areas where common dolphin by-catch occurs and fishing effort of various métiers (Peltier et al., 2019). Correlation is positive for gill-nets flying the Spanish or French flag (GNS ESP and GNS FRA), trammel nets flying the French flag (GTR FRA), pelagic pair trawlers flying the French flag (PTM FRA) and Danish seiners flying th French flag (SDN FRA).

A.2. Data on strandings

A.2.1. Stationary tests

Table 4.: Results of the stationary tests

Test	Null hypothesis	Results	Minimum size of the sample for the test
KPSS	Stationary	p -value = 0.04	30
ADF	Non-stationary	p -value = 0.98	30
Phillips-Peron	Non-stationary	test-value = -0.97 (critical value - 2.96)	20

A.3. An economic rationale of management rules

A.3.1. Formalization of abundance: details

$\{B_t\}_{t \in [t_0, T]}$ denotes the abundance/biomass of a species during a given period $[t_0, T]$ and relative to a geographical area \mathcal{X} . In practice, when data are scarce, $\{\phi_t\}_{t \in [t_0, T]}$ should be assimilated to some process parameterized by a time-independent vector ϕ . Accordingly, we can replace (1.2) by

$$B_{t+1} = h(B_t, B_{t-1}, \dots, B_{t-s}, \theta, \phi) \quad (\text{A.1})$$

Finally, state-space models like (1.2) or (A.1) are crude, and replacing (A.1) by

$$B_{t+1} = h(B_t, B_{t-1}, \dots, B_{t-s}, \theta, \phi, \varepsilon_t) \quad (\text{A.2})$$

where ε_t is a so-called *process noise* enhances realism: $(B_t)_{t \in [t_0, T]}$ can be more relevantly interpreted as a *stochastic process*.

Very generally, each element $\phi_t(x)$ of a set of extraction rates $\{\phi_t(x)\}_{t,x}$ corresponds to the probability, at time step t and for the geographical position $x \in \mathcal{X}$, that a dolphin is captured during a fishery. This probability can be ideally explained by a fishing effort $E_{t,x}$ and a set ψ of parameters describing the main features of this fishery (e.g. net mesh size, practice, the potential pingers, etc.). Learning a model g such that

$$\phi_t(x) = g(\psi, E_{t,x})$$

remains however delicate since x can typically be not known and $E_{t,x}$ is difficult to define.

A.3.2. Interpretation of the criterion

In this appendix, we use the concepts and notations presented in § 1.2 to provide an interpretation of the criterion given in Definition 1, based on an economic rationale. It is based on the comparison between two strategies of forcings on the extraction features ϕ .

First, denote $\bar{\mathcal{F}}_{T+\Delta T}(\phi) = \left\{ \frac{B_{T+\Delta T}(\phi)}{K} \leq 1 - \beta \right\}$ the complementary event of $\mathcal{F}_{T+\Delta T}(\phi)$.

At time T , when examining a new proposal $\phi = \phi_{\text{new}}$ versus the historical situation $\phi = \phi_{\text{old}}$, then a binary decision $\delta_T \in \{0, 1\}$ has to be made:

$$\delta_T = \begin{cases} 1 & \text{if } \phi_{\text{new}} \neq \phi_{\text{old}} \text{ (strategic change),} \\ 0 & \text{if } \phi_{\text{new}} = \phi_{\text{old}} \text{ (no modification).} \end{cases}$$

Because the abundance simulation model is necessarily erroneous (and more generally because of the uncertainties related to model choice statistical inference and prediction), it is possible that, despite a model-based decision $\delta_T = 1$ is considered optimal for conservation, the actual event $\mathcal{F}_{T+\Delta T}(\phi_{\text{new}})$ might not occur:

$$1_{\{\mathcal{F}_{T+\Delta T}(\phi_{\text{new}})\}} = 0 = 1 - 1_{\{\bar{\mathcal{F}}_{T+\Delta T}(\phi_{\text{new}})\}}.$$

Then deciding wrongly $\delta_T = 1$ results in a cost $C_{T+\Delta T}^{(0)}(\phi_{\text{new}})$ that can aggregate ecosystem,

socio-economic and political losses. This aggregated cost depends certainly on the real abundance trajectory between $T + 1$ and $T + \Delta_T$. Nonetheless, it can be estimated as a first-order magnitude of the real cost. We deduce that the cost function associated to deciding wrongly $\delta_T = 1$ can be written as

$$L^{(0)}(\delta_T) = C_{T+\Delta_T}^{(0)}(\phi_{\text{new}})\delta_T 1_{\{\bar{\mathcal{F}}_{T+\Delta_T}(\phi_{\text{new}})\}}.$$

There is also an economic cost $C_{T+\Delta_T}^{(1)}(\phi_{\text{old}})$ resulting from deciding wrongly $\delta_T = 0$ (no change of strategy). The associated cost function is

$$L^{(1)}(\delta_T) = C_{T+\Delta_T}^{(1)}(\phi_{\text{old}})(1 - \delta_T) 1_{\{\bar{\mathcal{F}}_{T+\Delta_T}(\phi_{\text{old}})\}}.$$

Finally, two other costs $C_{T+\Delta_T}^{(2)}(\phi_{\text{new}})$ and $C_{T+\Delta_T}^{(3)}(\phi_{\text{old}})$ can be associated to the "good" decision of modifying or not the strategy, respectively. When doing nothing rightly (namely choosing $\delta_T = 0$), political costs are still probable. Possible ecosystemic benefits can be understood as negative costs. The associated cost functions are then

$$L^{(2)}(\delta_T) = C_{T+\Delta_T}^{(2)}(\phi_{\text{new}})\delta_T 1_{\{\mathcal{F}_{T+\Delta_T}(\phi_{\text{new}})\}}.$$

and

$$L^{(3)}(\delta_T) = C_{T+\Delta_T}^{(3)}(\phi_{\text{old}})(1 - \delta_T) 1_{\{\mathcal{F}_{T+\Delta_T}(\phi_{\text{old}})\}}.$$

Finally, the total additive cost function is

$$L(\delta_T) = \sum_{i=0}^3 L^{(i)}(\delta_T)$$

and an optimal decision should be

$$\delta_T^* = \arg \min_{\delta_T \in \{0,1\}} L(\delta_T). \quad (\text{A.3})$$

Nonetheless, since events $1_{\{\mathcal{F}_{T+\Delta_T}(\phi_{\text{new}})\}}$ and $1_{\{\bar{\mathcal{F}}_{T+\Delta_T}(\phi_{\text{old}})\}}$ are not known, it appears rational (following the same principles of rationality face to uncertainty than Bayesian decision theory) to replace (A.3) by

$$\delta_T^* = \arg \min_{\delta_T \in \{0,1\}} \mathbb{E}[L(\delta_T)] \quad (\text{A.4})$$

where the expectancy is taken with respect to the *predictive* joint distribution of $(B_{T+\Delta_T}(\phi_{\text{new}}), B_{T+\Delta_T}(\phi_{\text{old}}))$. One has

$$\mathbb{E}[L(\delta_T)] = \delta_T \ell_1 + (1 - \delta_T) \ell_2$$

with

$$\begin{aligned} \ell_1 &= C_{T+\Delta_T}^{(0)}(\phi_{\text{new}}) \left\{ 1 - P_{B_{T+\Delta_T}(\phi_{\text{new}})}(\mathcal{F}_{T+\Delta_T}(\phi_{\text{new}})) \right\} + C_{T+\Delta_T}^{(2)}(\phi_{\text{new}}) P_{B_{T+\Delta_T}(\phi_{\text{new}})}(\mathcal{F}_{T+\Delta_T}(\phi_{\text{new}})), \\ \ell_2 &= C_{T+\Delta_T}^{(1)}(\phi_{\text{old}}) \left\{ 1 - P_{B_{T+\Delta_T}(\phi_{\text{old}})}(\mathcal{F}_{T+\Delta_T}(\phi_{\text{old}})) \right\} + C_{T+\Delta_T}^{(3)}(\phi_{\text{old}}) P_{B_{T+\Delta_T}(\phi_{\text{old}})}(\mathcal{F}_{T+\Delta_T}(\phi_{\text{old}})). \end{aligned}$$

Finally, it is worthy to modify the strategy ($\delta_T = 1$) if and only if $\mathbb{E}[L(1)] \leq \mathbb{E}[L(0)]$, or

equivalently $\ell_1 \leq \ell_2$, which is similar to have

$$P_{B_{T+\Delta T}(\phi_{\text{new}})}(\mathcal{F}_{T+\Delta T}(\phi_{\text{new}})) \geq 1 - \alpha \quad (\text{A.5})$$

where:

$$\alpha = \frac{C_{T+\Delta T}^{(1)}(\phi_{\text{old}}) - C_{T+\Delta T}^{(2)}(\phi_{\text{new}}) + \{C_{T+\Delta T}^{(3)}(\phi_{\text{old}}) - C_{T+\Delta T}^{(1)}(\phi_{\text{old}})\} P_{B_{T+\Delta T}(\phi_{\text{old}})}(\mathcal{F}_{T+\Delta T}(\phi_{\text{old}}))}{C_{T+\Delta T}^{(0)}(\phi_{\text{new}}) - C_{T+\Delta T}^{(2)}(\phi_{\text{new}})}$$

Clearly, the costs of wrong decisions can be assumed to be strictly greater than costs of good decisions. A sufficient condition to have $0 < \alpha \ll 1$ is having

$$C_{T+\Delta T}^{(2)}(\phi_{\text{new}}) \leq C_{T+\Delta T}^{(3)}(\phi_{\text{old}}) \ll C_{T+\Delta T}^{(0)}(\phi_{\text{new}}).$$

The result (A.5) occurs when comparing two strategies of forcings on the extraction rate ϕ . But the rule (1.4) proposed in Definition (1) could be interpreted similarly: conservation efforts are declared sufficient (and the current policy may not be changed) if the negative cost of ecosystemic services (in a broad sense) counterbalance the costs due to catches and strandings, in the sense that $1 - \alpha$ remains close to the historical probability $p = P_{B_T(0)}(\mathcal{F}_T(0))$ (i.e. before anthropogenic pressure: $\phi_{\text{old}} = 0$ and assuming the stationarity of abundance).

A.3.3. Relation with the current abundance estimation

The strandings on the reachable coastline \mathcal{Y} , named C_t^e in the remainder of this document, can be theoretically expressed as (on average)

$$C_t^e = \int_{\mathcal{X} \times \mathcal{Y}} q_{x(t), y(t+\delta_t)} dy \phi_t(x) B_t(x) dx \quad (\text{A.6})$$

where:

- $B_t(x)$ is the abundance at position x ;
- $q_{x(t), y(t+\delta_t)}$ is the stranding probability at position $y \in \mathcal{Y}$ for a dolphin bycaught at position x ,

provided the mean time interval δ_t of drift between captures and strandings remains negligible in comparison to the chosen time step t .

Concerning the case study that motivates this work, numerical models of currentology have been developed and used in inversion by the PELAGIS team to estimate the starting locations x from the stranding locations y (Peltier et al., 2016b). However, these works are still very exploratory, and today numerical tools remain delicate to use because of their very high computational cost. Furthermore, such estimations can be submitted to large uncertainties, since after a variable number of days within sea water, a bycaught dolphin can be too decomposed to verify that its death was caused by fishing (Peltier et al., 2019). For these reasons, in addition to the arguments of information sparsity expressed before, which forbid to specify $B_t(x)$ in (A.6), it appears more suitable in the present work to define the global conditional stranding probability q_t such that

$$C_t^e = q_t \phi_t B_t. \quad (\text{A.7})$$

A.4. Assumptions on the environmental stochasticity

This section describes two choices for the environmental stochasticity involved in the definition of the Pella-Tomlinson model: a Beta distribution on the reduced abundance variable Z_t , or a lognormal distribution on strandings.

A.4.1. A Beta approach to environmental stochasticity

The versatility of the Beta distribution is well-known, which can explain the choice (Figure 21).

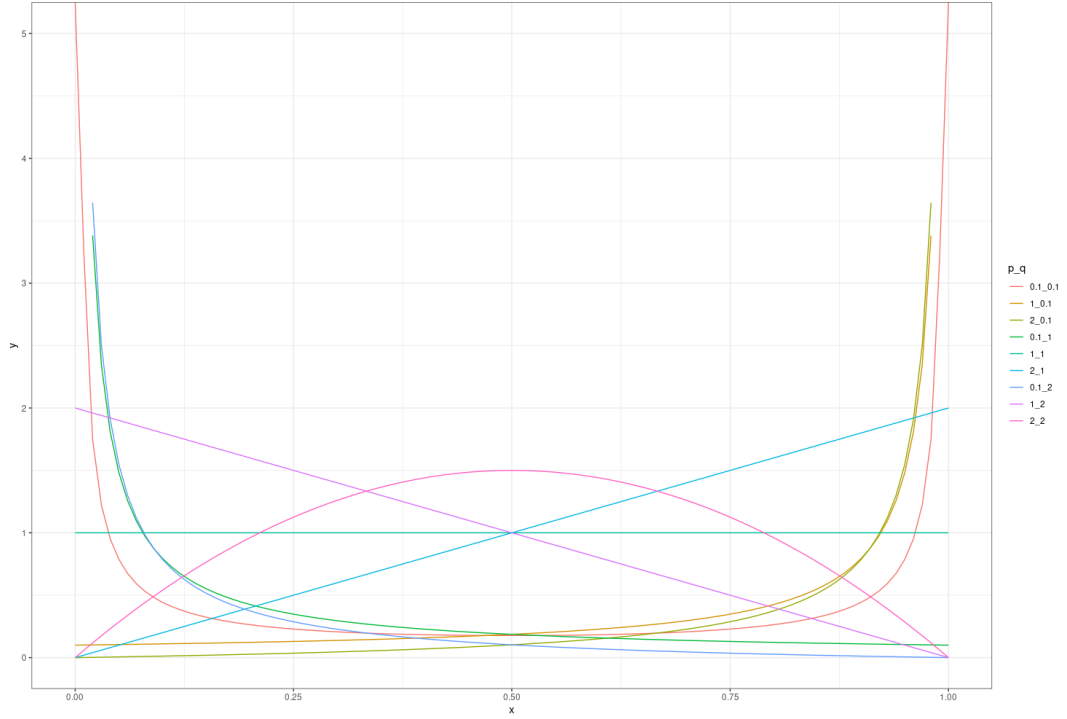


Figure 21.: Beta distributions with different parameters p and q

Accordingly, one has:

$$E[Z_{t+1}|Z_t] = \tilde{g}(Z_t, \theta)$$

and:

$$V[Z_{t+1}|Z_t] = \sigma^2 \tilde{g}^2(Z_t, \theta)$$

where

$$\tilde{g}(Z_t, \theta) = \left(1 - \phi + r \frac{\gamma + 1}{\gamma}\right) Z_t (1 - Z_t^\gamma), \quad (\text{A.8})$$

$$= D(\theta) g(C_t^e, \theta). \quad (\text{A.9})$$

From Lemma 1 (see after), the Beta distribution can be calibrated with:

$$p_t = \frac{1}{\sigma^2} \{1 - \tilde{g}(Z_t, \theta)\} - \tilde{g}(Z_t, \theta) \quad (\text{A.10})$$

$$q_t = \frac{1}{\sigma^2} \frac{\{1 - \tilde{g}(Z_t, \theta)\}^2}{\tilde{g}(Z_t, \theta)} - \{1 - \tilde{g}(Z_t, \theta)\}. \quad (\text{A.11})$$

Requiring p_t and q_t to be positive leads to:

$$\sigma^2 < \frac{\{1 - \tilde{g}(Z_t, \theta)\}}{\tilde{g}(Z_t, \theta)}. \quad (\text{A.12})$$

With $Z_t \in (0, 1)$, one has:

$$Z_t(1 - Z_t^\gamma) \leq \frac{\gamma}{(1 + \gamma)^{1+1/\gamma}}.$$

Then:

$$\tilde{g}(Z_t, \theta) \leq G(\theta) = \left(1 - \phi + r \frac{\gamma + 1}{\gamma}\right) \frac{\gamma}{(1 + \gamma)^{1+1/\gamma}} \quad (\text{A.13})$$

and:

$$\frac{\{1 - \tilde{g}(Z_t, \theta)\}}{\tilde{g}(Z_t, \theta)} \geq \sigma_1^2(\theta)$$

with

$$\sigma_1^2(\theta) = \frac{(1 + \gamma)^{1+1/\gamma}}{\gamma \left(1 - \phi + r \frac{\gamma + 1}{\gamma}\right)} - 1.$$

Then, from (A.9), a sufficient condition for (A.12) is to have:

$$\sigma^2 < \sigma_1^2(\theta).$$

However, an obvious requirement, that comes from the Beta choice, is that $\sigma_1^2(\theta) > 0$ or similarly that $G(\theta) < 1$. This condition can be determined on r , which is known to stay lower than an upper value $r_0 \leq 1$ for cetaceans. From Lemma 2 (see after), a choice of $r_0 = 0.5$, which is met for small cetaceans ensures that $\sigma_1^2 > 0$ for $\gamma \in (0, 5]$, a reasonably large sensitivity domain for γ .

Under the conditions of Lemma 2, from (A.10-A.11) reformulate

$$\begin{aligned} p_t &= p_t(C_t^e, \theta), \\ q_t &= q_t(C_t^e, \theta). \end{aligned}$$

Now, the conditional density $f(C_{t+1}^e | C_t^e, \theta)$ can be determined from (2.18) by variable change: reminding that

$$C_{t+1}^e = h(Z_{t+1}) = \frac{Z_{t+1}}{D(\theta)},$$

it comes

$$f_t(C_{t+1}^e|C_t^e, \theta) = \frac{f_u(h^{-1}(C_{t+1}^e|C_t^e, \theta))}{|h' \circ h^{-1}(C_{t+1}^e|C_t^e, \theta)|}.$$

We know that $h^{-1}(Z_{t+1}) = D(\theta)Z_{t+1}$, $h' \circ h^{-1}(C_{t+1}^e|C_t^e, \theta) = D(\theta)$ and

$$f_u(h^{-1}(C_{t+1}^e|C_t^e, \theta)) = \frac{\Gamma(p_t(C_t^e, \theta) + q_t(C_t^e, \theta))}{\Gamma(p_t(C_t^e, \theta)) \Gamma(q_t(C_t^e, \theta))} \{D(\theta)C_{t+1}^e\}^{p_t(C_t^e, \theta)-1} \{1 - D(\theta)C_{t+1}^e\}^{q_t(C_t^e, \theta)-1}$$

Therefore, denoting

$$A(C_t^e, \theta) = \frac{\Gamma(p_t(C_t^e, \theta) + q_t(C_t^e, \theta))}{\Gamma(p_t(C_t^e, \theta)) \Gamma(q_t(C_t^e, \theta))},$$

the conditional density of the stranding at time t is

$$f(C_{t+1}^e|C_t^e, \theta) = \frac{A(C_t^e, \theta)}{D(\theta)} \{D(\theta)C_{t+1}^e\}^{p_t(C_t^e, \theta)-1} \{1 - D(\theta)C_{t+1}^e\}^{q_t(C_t^e, \theta)-1}. \quad (\text{A.14})$$

The definition of the support set Θ arises from the various constraints previously expressed: assuming $\gamma \in (0, 5]$,

$$\begin{aligned} \Theta = \{ & \theta \in \mathbb{R}_{*+}^6, \\ & 0 < \phi < r, \\ & 0 < q < 1, \\ & r < 1, \\ & \sigma^2 < \sigma_1^2(\theta) \}. \end{aligned}$$

Lemma 1. *Let $X \sim \mathcal{B}_e(p, q)$ with $(p, q) > 0$ and assume the constraints*

$$\begin{aligned} \mathbb{E}[X] &= \mu \in [0, 1], \\ V[X] &= \tau^2. \end{aligned}$$

Then

$$\begin{aligned} p &= (1 - \mu) \frac{\mu^2}{\tau^2} - \mu, \\ q &= (1 - \mu)^2 \frac{\mu}{\tau^2} - (1 - \mu) \end{aligned}$$

provided that

$$\tau^2 < \mu(1 - \mu). \quad (\text{A.15})$$

Proof. (Lemma 1).

With $\mu = p/(p + q)$ and

$$\tau^2 = \frac{pq}{(p + q)^2(p + q + 1)} = \frac{\mu^2 q}{p(p + q + 1)},$$

it comes

$$p + q = \frac{1}{\mu}p = \frac{\mu^2}{\tau^2}(1/\mu - 1)$$

which proves the statement of the Lemma. Values of (p, q) are strictly positive under the condition (A.15). \square

Lemma 2. *Assume $r_0 = 1$ and $0 < \phi < 1$. Then $\sigma_1^2(\theta) > 0$ if and only if $\gamma \in (0, 2.235)$. Assume $r_0 = 0.5$ and $0 < \phi < 1$. Then if $\gamma \leq 5$ then $\sigma_1^2(\theta) > 0$.*

Proof. (Lemma 2). Assume $0 < r \leq r_0 \leq 1$. From (A.13), one has

$$G(\theta) \leq \kappa(r_0, \gamma) = \frac{(1 + r_0)\gamma}{(1 + \gamma)^{1+1/\gamma}} + \frac{1}{(1 + \gamma)^{1+1/\gamma}}.$$

As plotted in Figure 22, the function $(r_0, \gamma) \mapsto \kappa(r_0, \gamma)$ is increasingly monotonic with respect to both input variables, and especially remains lower than 1, when $r_0 = 0.5$, for a large range of values of γ . The results provided in Lemma 2 follows from simple numerical calculation. \square

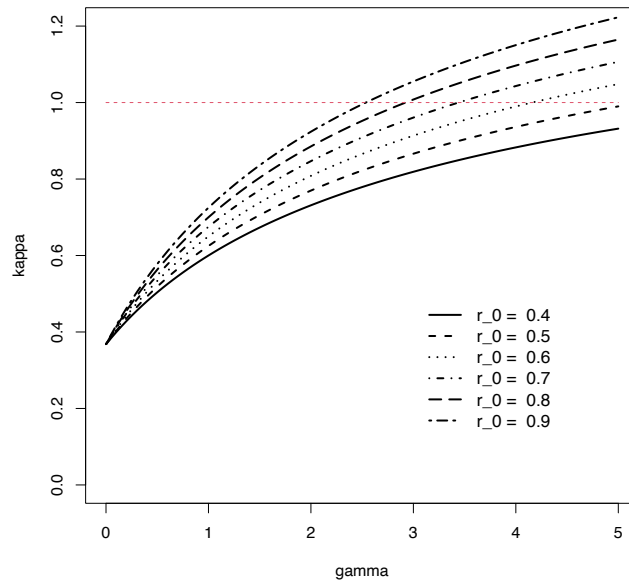


Figure 22.: Some plots of the mapping $\gamma \mapsto \kappa(r_0, \gamma)$ for several selected values of the upper bound r_0 for the growth rate r .

Maximum likelihoods estimations for beta stochasticity Maximum likelihood estimation of the complete likelihood, mixing strandings and one observed biomass per period of ten years, was tested using the classical L-BFGS-B optimization algorithm, constrained by the support boundaries for unknown parameters. Results computed over 500 replicates for various numbers of observation years are displayed on Figure 23.

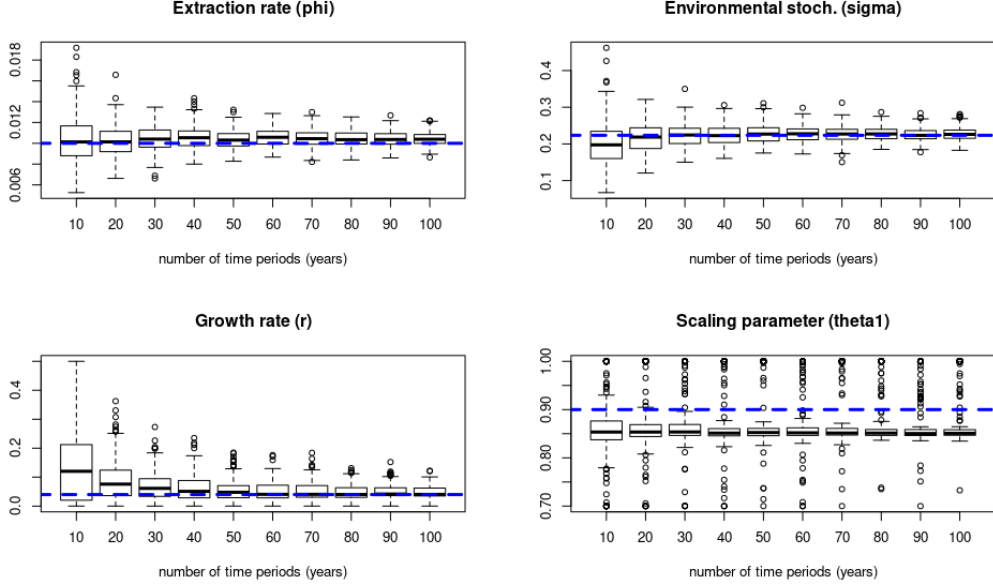


Figure 23.: Distributions of maximum likelihood estimators based on the lognormal model assumption for the unknown parameters, per number of observation years. Blue dotted lines highlight the simulation values. 500 replicates of abundance trajectories are generated for each number of years. These trajectories are generated using the lognormal assumption on environmental stochasticity.

A.4.2. A lognormal approach to environmental stochasticity

Alternatively to assume that the reduced abundance Z_t obeys to a beta distribution conditionally to the past, a more usual modelling hypothesis about the environmental stochasticity is to assume that, in Equation (2.8), that

$$\varepsilon_t \sim \mathcal{LN}(-\sigma^2/2, \sigma^2),$$

which implies that $\mathbb{E}[\varepsilon_t] = 1$ and σ is approximately the coefficient of variation of C_{t+1}^e given the past. Accordingly, the conditional density of C_{t+1}^e , involved in the likelihood of strandings defined in Equation (2.15), is

$$f(C_{t+1}^e | C_t^e, \theta) = \frac{1}{\sqrt{2\pi}\sigma C_{t+1}^e} \exp\left(-\frac{1}{\sigma^2} \exp\left\{\log C_{t+1}^e - \log g(C_t^e, \theta) - \sigma^2/2\right\}^2, \sigma^2\right).$$

Despite the fact that the lognormal distribution cannot sample discrete values (as the strandings), it often simplifies computations and allow to produce satisfying estimators, which participates in explaining its popularity in quantitative ecology for modelling uncertainty about positive magnitudes.

Maximum likelihoods estimations for lognormal stochasticity Maximum likelihood estimation of the complete likelihood, mixing strandings and one observed biomass per period of ten years, was tested using the classical L-BFGS-B optimization algorithm, constrained by the support boundaries for unknown parameters. Results computed over 500 replicates for various numbers of observation years are displayed on Figure 24.

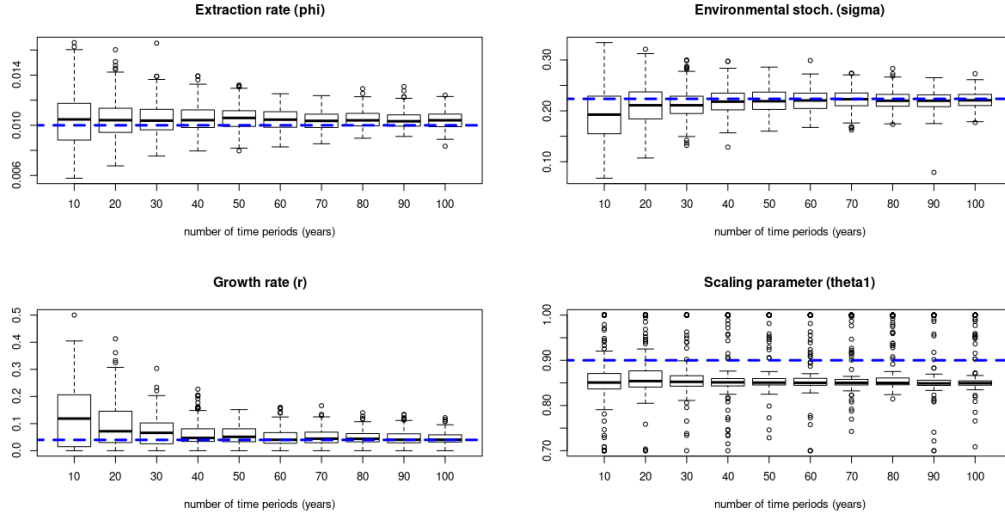


Figure 24.: Distributions of maximum likelihood estimators based on the lognormal model assumption for the unknown parameters, per number of observation years. Blue dotted lines highlight the simulation values. 500 replicates of abundance trajectories are generated for each number of years. These trajectories are generated using the lognormal assumption on environmental stochasticity.

Estimating B_0 . Available abundance data do not contain the first abundance value B_0 (up to an observational / reconstitution noise). For this reason, B_0 can be considered as an additional unknown parameter to assess. Noticing that conditionally to a given choice of B_0 , the maximum likelihood estimation of other parameters θ can be conducted, it is possible to provide the profile maximized negative log-likelihood of the model for a range of values of B_0 . Figure 25 highlights that for truly available data this function admits a unique minimum value around 9.2×10^5 individuals.

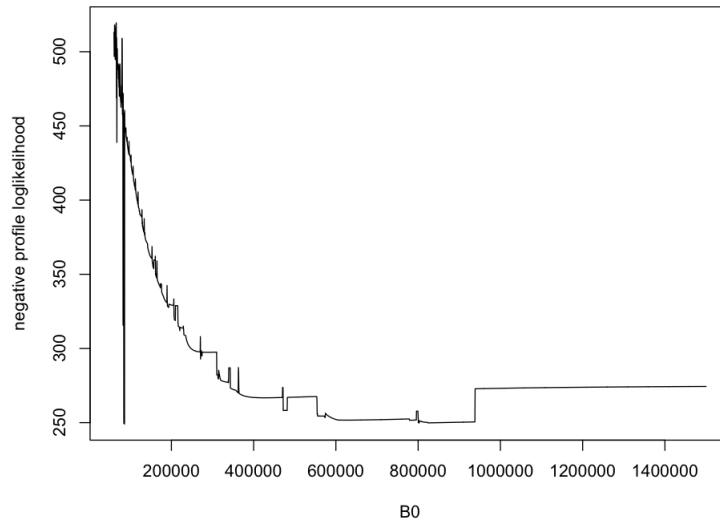


Figure 25.: Profile negative maximized log-likelihood of truly available observations, in function of B_0 .

A.5. Prior elicitation

A.5.1. Calibration tests

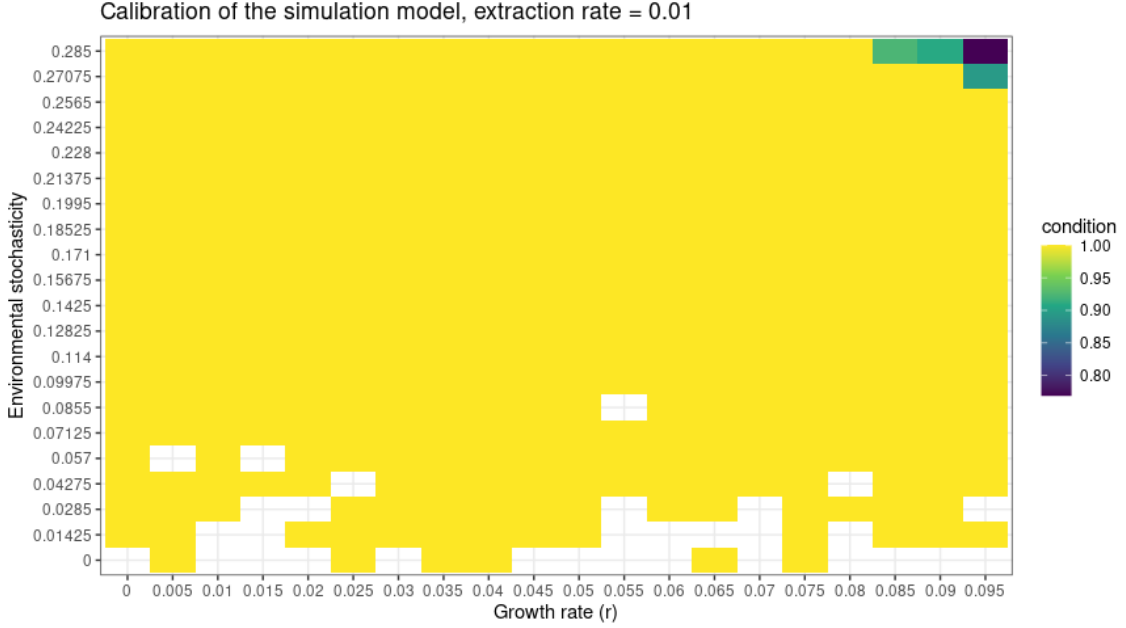


Figure 26.: Correlated sampling (by rejection) of (σ, r) such that the prior constraints (only non-extinction here) are respected. The extraction rate was fixed at 0.01. Condition = 1 involves that the extinction probability is < 0.02 .

A.5.2. Details about copulas

Description

Let P be a joint distribution of p random variables, composed by the marginal probability measures P_1, \dots, P_d , inducing a random vector $X = (X_1, \dots, X_d)^\top$. The copula C of X Nelsen (2006) can be defined by using the random vector

$$(U_{P_1}, \dots, U_{P_d})^\top = (F_{P_1}(X_1), \dots, F_{P_d}(X_d))^\top.$$

where F_{P_i} denotes the cumulative distribution function (cdf) of the probability measure P_i . The copula of X is the function defined as:

$$C_P(u_1, \dots, u_d) = \mathbb{P}(U_{P_1} \leq u_1, \dots, U_{P_d} \leq u_d). \quad (\text{A.16})$$

It can be noted that each U_{P_i} , $i = 1, \dots, d$ follows a uniform distribution over $[0, 1]$, and the copula can be interpreted as their joint cdf. A common interpretation of copulas is that they describe the intrinsic correlation structure between dependent variables, beyond the usual correlation matrices. The existence and unicity of copulas for continuous multivariate distributions, estimated from a multivariate sample, is ensured by Sklar's theorem (Sklar, 1959). Many computational tools in several languages are now well developed to fit a copula given this sample. In the present work, the R package `VineCopula` was used (Schepsmeier, 2016). It uses the so-called *vine structure* of copulas (Aas et al., 2009), which allows to write the joint density of any multivariate distribution using the following form (Czado,

2010):

$$f(x_1, \dots, x_d) = \prod_{j=1}^{d-1} \prod_{i=1}^{d-j} c_{i,(i+j)|(i+1),\dots,(i+j-1)} \cdot \prod_{k=1}^d f(x_k) \quad (\text{A.17})$$

where

1. $c_{i,j|i_1,\dots,i_k} = c_{i,j|i_1,\dots,i_k}(F(x_i|x_{i_1},\dots,x_{i_k}), F(x_j|x_{i_1},\dots,x_{i_k}))$ is a conditional bivariate copula, with i, j, i_1, \dots, i_k such that $i < j$ and $i_1 < i \dots i_k$;
2. the $f(x_k)$ are the marginal densities.

This decomposition, which simplifies handling and simulation, is not unique Joe (1997). However, a preference structure can be identified, by selecting the optimal Aikake score copula (AIC) (Akaike, 1998). This is the choice made in this study.

Bivariate copulas that are involved in the selection of the joint prior distribution described in § 2.3.2 are detailed beneath. These details are a summary of results provided in (Brechmann and Schepsmeier, 2013) and Cheng et al. (2020). In these paragraphs, parameter θ is the canonic parametrization used in the `VineCopula` package Schepsmeier (2016). The couple (u, v) denotes two variables defined on $[0, 1]^2$.

Rotated Gumbel copula. Given $\theta < -1$, the cdf (or so-called *copula function*) of the bivariate Rotated Gumbel 90 degrees copula is

$$F_{RG,\theta}(u, v) = v - F_{R,-\theta}(1 - u, v) \quad (\text{A.18})$$

where $F_{R,\theta}$ is the cdf of the usual Gumbel copula (with $\theta > 1$)

$$F_{R,\theta}(u, v) = \exp \left\{ -(\psi_\theta(u) + \psi_\theta(v))^{1/\theta} \right\}$$

with

$$\psi_\theta(u) = (-\log u)^\theta.$$

The corresponding probability density function (pdf) is

$$f_{R,\theta}(u, v) = F_{R,\theta}(u, v) [\psi_\theta(u) + \psi_\theta(v)]^{1/\theta-2} \left[\theta - 1 + (\psi_\theta(u) + \psi_\theta(v))^{1/\theta} \right] \left(\frac{\psi_{\theta-1}(u)\psi_{\theta-1}(v)}{uv} \right)$$

The boundary conditions on $[0, 1]^2$ for $f_{R,\theta}(u, v)$ are the following: for all $(u, v) \in (0, 1)$, $f_{R,\theta}(u, 0) = f_{R,\theta}(0, v) = 0$ and this density is not defined at $(0, 0)$ and $(1, 1)$.

Accordingly, the density corresponding to $F_{R,\theta}$ is

$$f_{RG,\theta}(u, v) = \frac{\partial^2}{\partial u \partial v} F_{RG,\theta}(u, v) = f_{R,-\theta}(1 - u, v). \quad (\text{A.19})$$

Gaussian copula. The density of the bivariate Gaussian copula is

$$f_{G,\theta}(u, v) = \det^{1/2}(R) \exp \left(-\frac{1}{2} \begin{pmatrix} \Phi^{-1}(u) \\ \Phi^{-1}(v) \end{pmatrix}^T (R^{-1}(\theta) - I_2) \begin{pmatrix} \Phi^{-1}(u) \\ \Phi^{-1}(v) \end{pmatrix} \right) \quad (\text{A.20})$$

where I_2 is the bidimensional identity matrix, Φ is the cdf of the standard reduced Gaussian distribution, and

$$R(\theta) = \begin{pmatrix} 1 & \theta \\ \theta & 1 \end{pmatrix}$$

is the correlation matrix (hence $\theta \in (-1, 1)$ is the usual correlation coefficient between u_1 and u_2). The corresponding cdf (or *copula function*) is

$$F_{G,\theta}(u, v) = \Phi_{R(\theta)}(\Phi^{-1}(u), \Phi^{-1}(v)) \quad (\text{A.21})$$

where Φ_R is the the joint cdf of a multivariate normal distribution with mean vector zero and covariance matrix R . This cdf is of no simple form but can be manipulated numerically.

Rotated Tawn type 2 copula. With $\theta_1 > 1$ and $0 \leq \theta_2 \leq 1$, the pdf of the Rotated Tawn type 2 180 degrees copula

$$F_{RT,\theta_1,\theta_2}(u, v) = u + v - 1 + F_{T,\theta_1,\theta_2}(1 - u, 1 - v) \quad (\text{A.22})$$

where F_{T,θ_1,θ_2} is the pdf of the Tawn type 2 copula, which is a generalization of the Gumbel copula:

$$F_{T,\theta_1,\theta_2}(u, v) = (1 - \theta_2)t + [\theta_2(1 - t)^{\theta_1} + t^{\theta_1}]^{1/\theta_1}$$

and $t = \log v / \log uv$. Then the corresponding pdf of $F_{RT,\theta_1,\theta_2}(u, v)$ is

$$f_{RT,\theta_1,\theta_2}(u, v) = f_{T,\theta_1,\theta_2}(1 - u, 1 - v) \quad (\text{A.23})$$

where

$$\begin{aligned} f_{T,\theta_1,\theta_2}(u, v) &= \frac{\partial^2}{\partial u \partial v} F_T(u, v | \theta_1, \theta_2), \\ &= (1 - \theta_2)t'' + \alpha_1 \beta(t'_u) \beta(t'_v) + \alpha_2 \alpha_3 \end{aligned}$$

with

$$\begin{aligned}
\alpha_1 &= \frac{1 - \theta_1}{\theta_1^2} [\theta_2(1 - t)^{\theta_1} + t^{\theta_1}]^{1/\theta_1 - 2}, \\
\alpha_2 &= \frac{1}{\theta_1} [\theta_2(1 - t)^{\theta_1} + t^{\theta_1}]^{1/\theta_1 - 1}, \\
\alpha_4 &= -t''\theta_1 (\theta_2(1 - t)^{\theta_1 - 1} - 1) + t'_u t'_v \theta_1 (\theta_1 - 1) (\theta_2(1 - t)^{\theta_1 - 2} + t^{\theta_1 - 2}) \\
\beta(x) &= -x\theta_1\theta_2(1 - t)^{\theta_1 - 1} + x\theta_1 t^{\theta_1 - 1}
\end{aligned}$$

and

$$\begin{aligned}
t'_u &= \frac{\partial}{\partial u} t = -\frac{\log v}{u (\log(uv))^2}, \\
t'_v &= \frac{\partial}{\partial v} t = \frac{(1/v) \log(uv) - (1/u) \log v}{(\log(uv))^2} \\
t'' &= \frac{\partial^2}{\partial u \partial v} t = -\frac{1}{uv} \frac{[\log(uv) - 2 \log(v)]}{|\log(uv)|^3}.
\end{aligned}$$

Conditional prior cdf. In Equations (A.27) and (A.28), the computation of conditional prior cdf $\Pi_r(r|\phi)$ and $\Pi_\sigma(\sigma|\phi)$ require to compute the partial derivatives

$$\frac{\partial F_{G,\theta_G}}{\partial u}(u, v), \quad \frac{\partial F_{RG,\theta_{RG}}}{\partial u}(u, v)$$

where $(u, v) \mapsto F_{G,\theta_G}(u, v)$ and $(u, v) \mapsto F_{RG,\theta_{RG}}(u, v)$ are the copula functions given by (A.21) and (A.18). Noticing that

$$\frac{\partial F_{G,\theta_G}}{\partial u}(u, v) = P(Y \leq \Phi^{-1}(v) | X = \Phi^{-1}(u))$$

when $(X, Y) \sim \mathcal{N}(0, R(\theta))$, it is well known (e.g., Bertsekas and Tsitsiklis (2002), Section 4.7) that

$$Y | X = \Phi^{-1}(u) \sim \mathcal{N}(\theta \Phi^{-1}(u), 1 - \theta^2).$$

Then it comes

$$\frac{\partial F_{G,\theta_G}}{\partial u}(u, v) = \Phi \left(\frac{\Phi^{-1}(u) - \theta \Phi^{-1}(v)}{\sqrt{1 - \theta^2}} \right). \quad (\text{A.24})$$

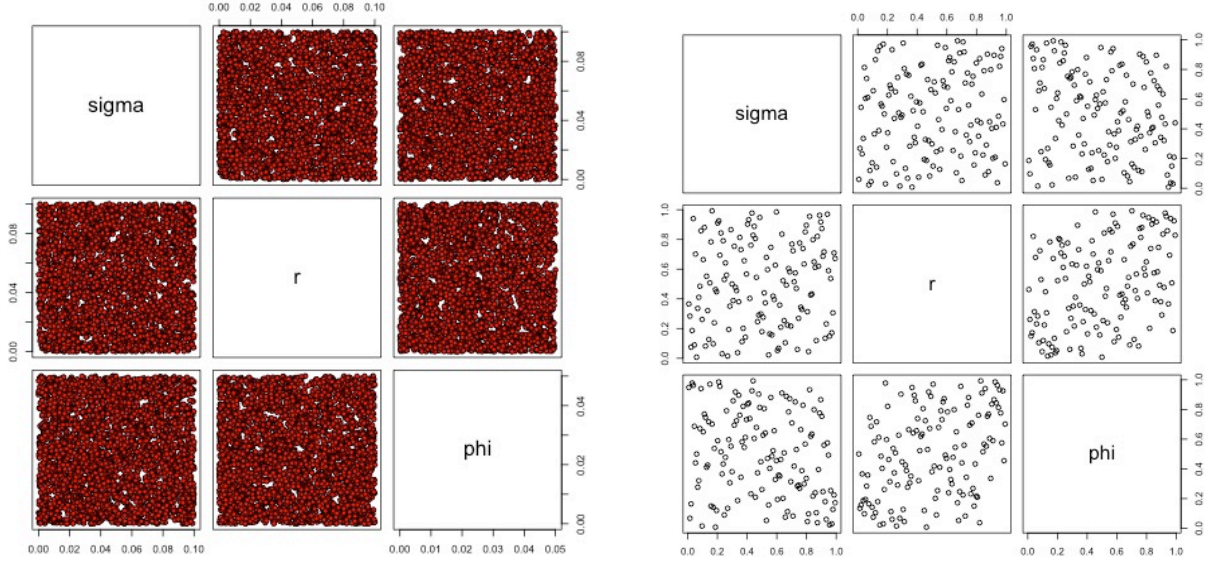
Furthermore, by simple derivation from (A.18), it comes

$$\frac{\partial F_{RG,\theta_{RG}}}{\partial u}(u, v) = F_{R,-\theta}(1 - u, v) [\psi_\theta(1 - u) + \psi_\theta(v)]^{1/\theta - 1} \frac{(-\log u)^{\theta - 1}}{u}. \quad (\text{A.25})$$

3D configurations

When considering simultaneously 3D configurations (σ, r, ϕ) sampled uniformly in Ω , Figure 27a displays the configurations respecting criterion (2.19). While the scatter plots on this figure does not seem to show any particular correlation structure, the same scatter

plot applied to the ranks (Figure 27b) lets this underlying correlation structure appear more clearly.



(a) Prior configurations of (σ, r, ϕ) selected according to criterion (2.19). (b) Prior configurations of (σ, r, ϕ) in the rank space, selected according to criterion (2.19).

Figure 27.: Prior configurations

Writing of the prior joint density

From Formula (A.17) and the explanations provided in Brechmann and Schepsmeier (2013) (Section 3.1), the full writing of the prior joint density of (σ, r, ϕ) is

$$\begin{aligned} \pi(\sigma, r, \phi) = & f_{RG, \theta_{RG}}(\Pi_\phi(\phi), \Pi_\sigma(\sigma)) \times f_{G, \theta_G}(\Pi_\phi(\phi), \Pi_r(r)) \times \\ & f_{RT, \theta_{RT,1}, \theta_{RT,2}}(\Pi_r(r|\phi), \Pi_\sigma(\sigma|\phi)) \times [\pi_\sigma(\sigma)\pi_r(r)\pi_\phi(\phi)] \end{aligned} \quad (\text{A.26})$$

where:

1. $(\pi_\sigma, \pi_r, \pi_\phi)$ are the marginal prior densities of (σ, r, ϕ) , respectively;
2. $\Pi_\phi(\phi)$, $\Pi_\sigma(\sigma)$ and $\Pi_r(r)$ are the marginal prior cdf of (ϕ, σ, r) ;
3. the copula densities $(f_{RG, \theta_{RG}}, f_{G, \theta_G}, f_{RT, \theta_{RT,1}, \theta_{RT,2}})$ are provided in Appendix A.5.2 (Equations A.19, A.20 and A.23);
4. $\Pi_r(r|\phi)$ and $\Pi_\sigma(\sigma|\phi)$ are *conditional* prior cdf (given ϕ), defined as follows: from Darsow et al. (1992)

$$\Pi_r(r|\phi) = \Pi(R < r|\phi) = \frac{\partial F_{G, \theta_G}}{\partial u}(\Pi_\phi(\phi), \Pi_r(r),), \quad (\text{A.27})$$

$$\Pi_\sigma(\sigma|\phi) = \Pi(\Sigma < |\sigma|\phi) = \frac{\partial F_{RG, \theta_{RG}}}{\partial u}(\Pi_\phi(\phi), \Pi_\sigma(\sigma)) \quad (\text{A.28})$$

where $(u, v) \mapsto F_{G, \theta_G}(u, v)$ and $(u, v) \mapsto F_{RG, \theta_{RG}}(u, v)$ are the copula functions with

respective densities f_{G,θ_G} and $f_{RG,\theta_{RG}}$ on $[0, 1]^2$. The expressions for the derivatives (A.27) and (A.28) are provided in A.5.2 (Equations A.24 and A.25).

A.6. Metropolis Hasting within Gibbs algorithm

A.6.1. Description of the algorithm

The algorithm can be described as follow:

(1) Parameters are initialized (in the same way than a classic MCMC). The group of parameters we want to estimate can be defined as θ_0 .

(2) A candidate $\tilde{\theta}_k$ is generated, so that $\tilde{\theta}_k \sim \rho(\theta|\theta_{k-1}, \dots, \theta_0)$. ρ is called the instrumental and can have different possible forms, such as a random walk $\mathcal{N}(\theta_{k-1}, \sigma^2)$. There is obviously a dependence between the new candidate and the previous one (θ_{k-1}).

(3) The new candidate $\tilde{\theta}_k$ is accepted regarding a probability which is the acceptance ratio α . Otherwise, the last candidate is kept, with a probability of $1 - \alpha$. α is the Metropolis ratio and is defined as:

$$\alpha = \frac{\pi(\tilde{\theta}_k|C_t^e) f(C_t^e|\tilde{\theta}_k) \rho(\theta_{k-1}|\tilde{\theta}_k, \theta_k, \dots, \theta_0)}{\pi(\theta_{k-1}|C_t^e) f(C_t^e|\theta_{k-1}) \rho(\tilde{\theta}_k|\theta_{k-1}, \dots, \theta_0)}, \quad (\text{A.29})$$

π are priors' density of the parameters and ρ the instrumental densities.

The steps of acceptance and reject are inserted in a Gibbs Sampling (MCMC). Three Markov chains are launched in parallel. It means that for each step, three new candidates are generated. The iteration ends when the different chains mix and when the estimation of the parameters is stable (convergence).

The next part describes the algorithm in the case of the strandings data. We can suppose that these are partially caused by bycatch. These data are simulated with a Pella Tomlinson model on biomass. We then calculate the corresponding catches ($C_t = \phi B_t$). We have (Bordet et Rivest 2014):

$$B_{t+1} = (B_t + \left(\frac{\gamma + 1}{\gamma}\right) r B_t (1 - (\frac{B_t}{K})^\gamma) - \phi B_t) \varepsilon_t, \quad (\text{A.30})$$

with $\varepsilon_t \sim \mathcal{LN}(-\frac{\sigma^2}{2}, \sigma^2)$.

More formally, the Metropolis-Hasting algorithm can be described as follow (M is the number of iterations):

Step k :

-
1. Parameters initialisation $\theta = \{r, \phi, K, \sigma^2\}$
 2. Simulation of the candidates within the instrumental (for each parameter):
 $i\theta \sim \rho(\tilde{\theta}|\theta_{k-1})$.

3. Calculation of the probability (Metropolis ratio)

$$\alpha_i = \left(\frac{f(\mathbf{C}_n|\tilde{\theta})\pi(\tilde{\theta})}{f(\mathbf{C}_n|\theta_{k-1})\pi(\theta_{k-1})} \right) \cdot \left(\frac{\rho(\theta_{k-1}|\tilde{\theta})}{\rho(\tilde{\theta}|\theta_{k-1})} \right).$$

\mathbf{C}_n is a vector with all the simulated data.

4. $\left. \begin{array}{l} \text{Simulate } U \sim \mathcal{U}_{\text{unif}}[0, 1]. \\ \text{If } U \leq \alpha_i \text{ choose } \theta_k = \tilde{\theta}. \\ \text{Otherwise choose } \theta_k = \theta_{k-1}. \end{array} \right\} \text{Accept } \tilde{\theta} \text{ within } \alpha_i.$

A.6.2. Estimation with simulated data using a Metropolis-Hastings within Gibbs algorithm

Results

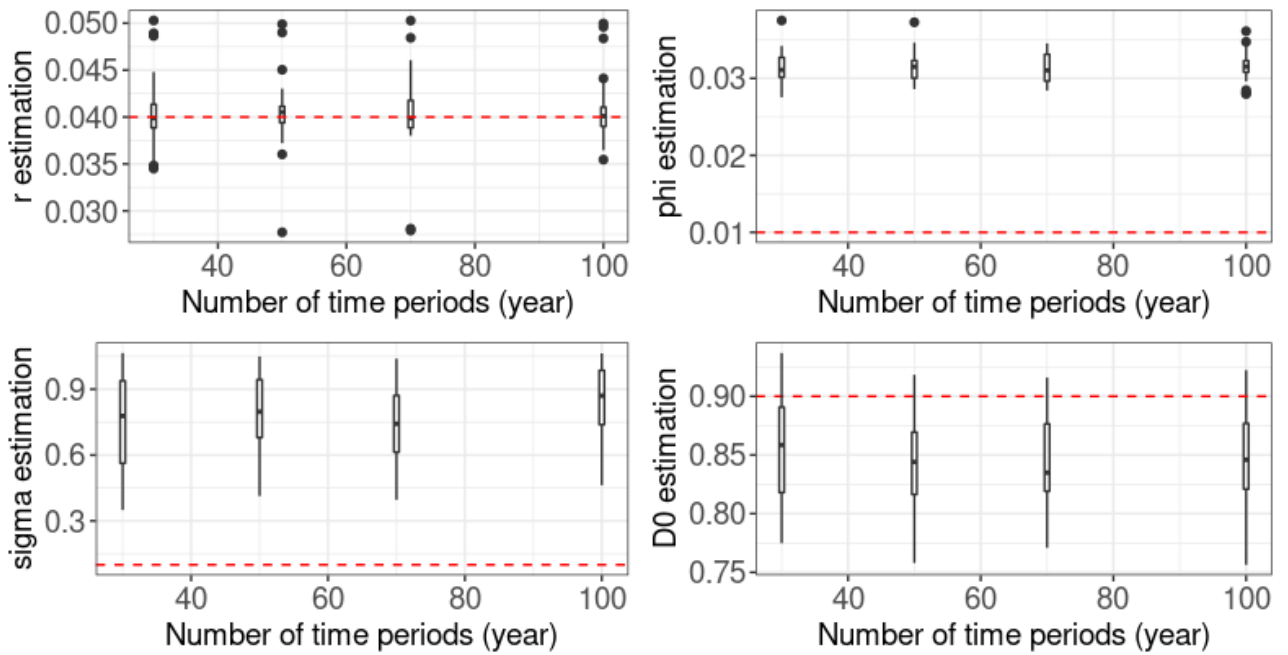


Figure 28.: Estimation of the parameters with a Metropolis-Hastings within Gibbs algorithm. The dashed red line represents the simulation values.

Auto-correlation diagnostics

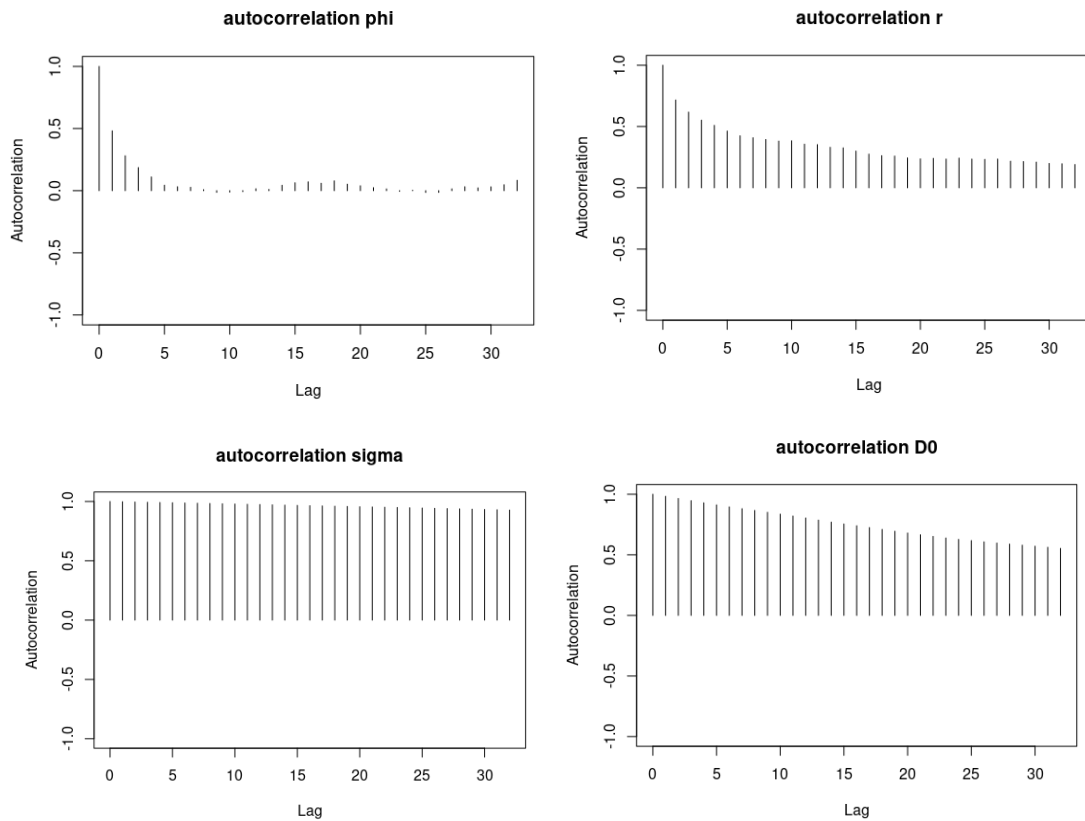


Figure 29.: Auto-correlation diagnostics with the Metropolis-Hastings algorithm.

A.7. HMC algorithm in Stan

Markov chain Monte Carlo algorithms approximate the posterior distribution (a.k.a. the target) by sequentially drawing and proposing samples from an instrumental distribution, resulting in a finite number of autocorrelated samples. For example, the Metropolis Hasting within Gibbs algorithm sketched in Appendix A.6.1 uses a first-order random walk process, centered at the current sample to draw a candidate value. This candidate value is accepted as a sample from the target with a probability proportional to the density ratio of the proposed to current sample values. If tuned correctly and run for a sufficiently long time, the algorithm will eventually explore the parameter space and converge to the target. 'Sufficiently long' is a vague description and hinges on the choice of the instrumental distribution. A poor choice may result in an impractically long computation time. For instance, with a first-order random process as the instrumental distribution, multiple draws may be needed to move away from a current region in parameter space, leading to high autocorrelation between samples and slow mixing of chains (inefficiency), especially in high-dimensional problems.

A Metropolis-Hastings algorithm with Gaussian updates does not usually scale well to high dimensions: the probability of selecting a random point with a high enough density under the target gets lower as the dimensions of the parameter space increases. This is because in

a high-dimensional space, much more volume lies outside any given neighborhood (centred on the current value in the sample) than inside of it. The principles of Hamiltonian dynamics underlying the Hamiltonian Monte Carlo algorithm provides a way to generate efficient proposal to move the sampler across the high-dimensional space. This is achieved by

1. introducing auxiliary position and momentum parameters for each parameter, expanding the D-dimensional parameter space into a 2D-dimensional phase space; and
2. using gradient information on the log of the density function of the target distribution to propose moves in parameter space that follow contours of high probability density (and have a high acceptance probability).

Briefly and schematically, starting from any position, a new proposal for a parameter is drawn from a probability distribution by giving the position some momentum and then updating the position and momentum according to a system of differential equations called Hamilton's equations. Solving these differential equations is costly but allows to preserve the target density, that is to propose new samples that have a high acceptance probability, thereby generating a sample from the target with little autocorrelation. This allows to explore efficiently the potentially high-dimensional parameter space. The computational cost in solving Hamilton's equations for generating a new proposal is usually more than offset by the reduction in autocorrelation: with a HMC algorithm, each iteration is more costly (compared to a Metropolis-Hasting algorithm), but few iterations are needed to reach the target (small burn-in).

This brief and non technical description only sketches the surface of HMC and the interested is referred to Neal (2011) and Betancourt (2017) for in-depth treatments, and to Monnahan et al. (2017) for ecological applications and examples.

The probabilistic programming language **Stan** (Carpenter et al., 2017) implements the No-U-Turns (NUTS) algorithm which is an adaptive HMC algorithm. **Stan** allows the user to focus on model specification and development rather than technical implementation of the algorithm. **Stan** allows ecologists to use state-of-the-art modeling techniques without the hurdle of writing custom algorithms (Monnahan et al., 2017).

A.8. Bayesian estimation on real datasets

A.8.1. Results

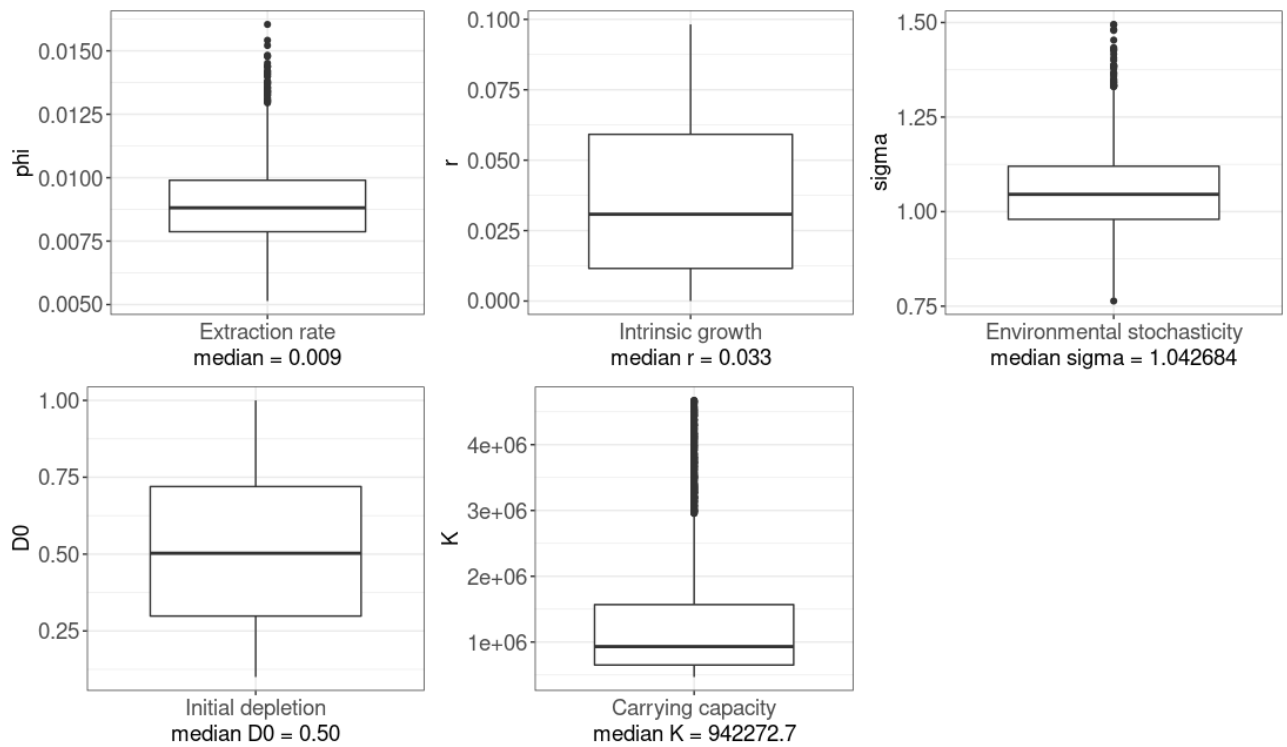


Figure 30.: Estimation of the parameters with Stan.

A.8.2. MCMC chains

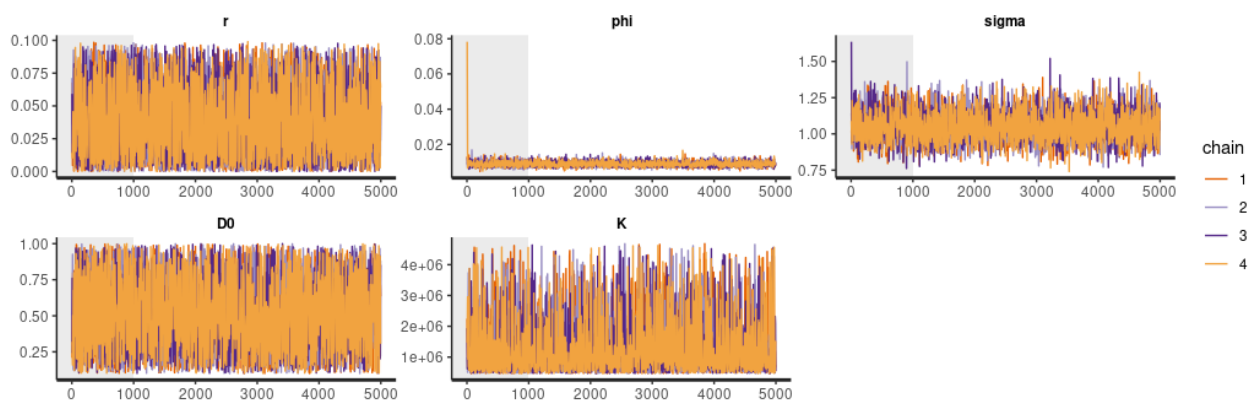


Figure 31.: MCMC chains of the different parameters

A.8.3. Auto-correlation diagnostics

Function `plotAuto` from the package `plotMCMC` was used to test auto-correlation of the MCMC chains.

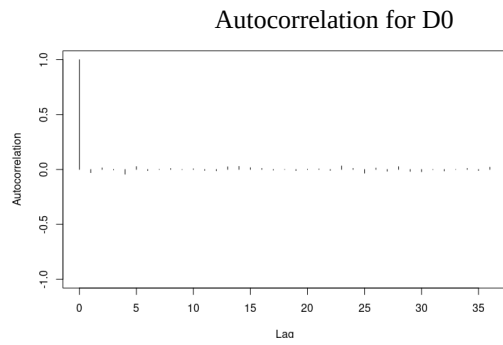
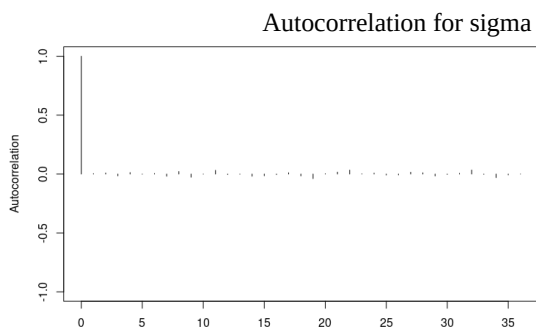
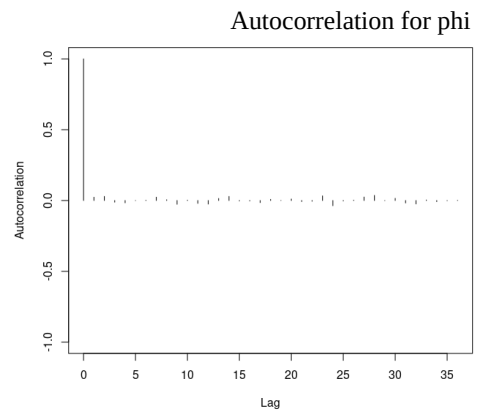
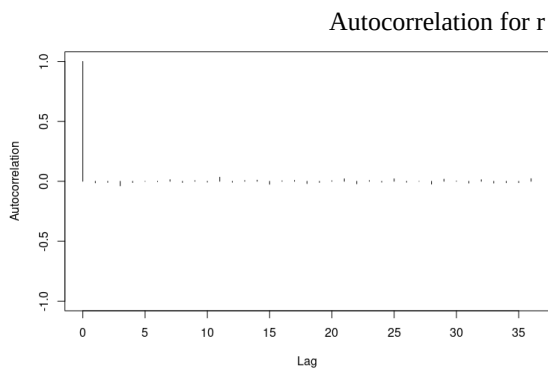


Figure 32.: Auto-correlation diagnostics

A.8.4. Convergence diagnostics

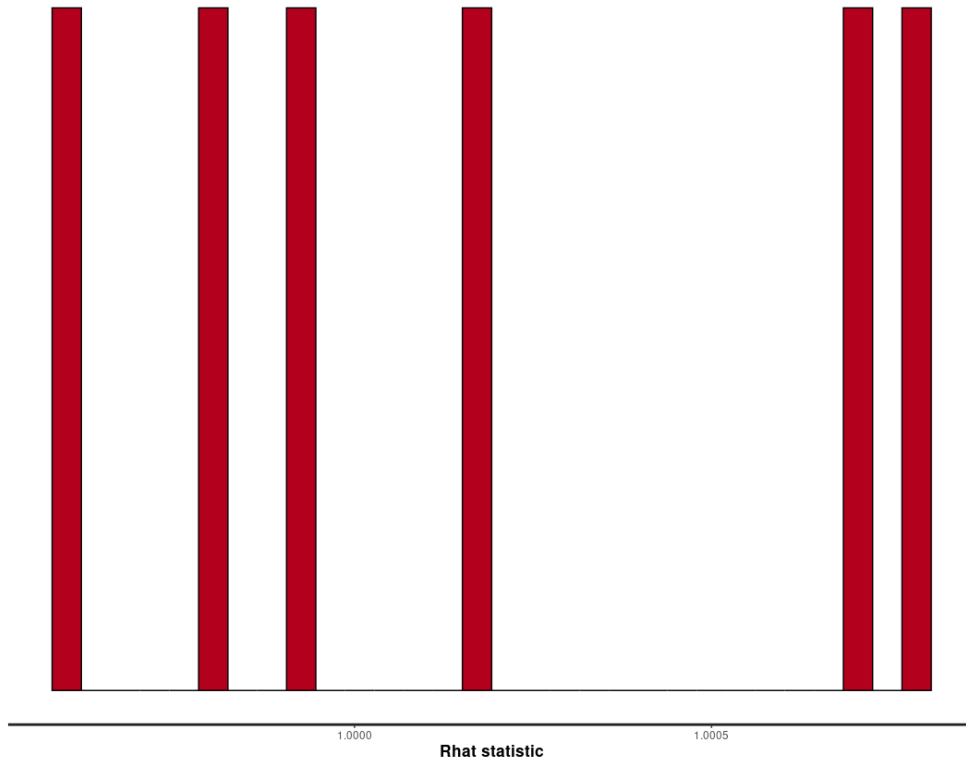



Figure 33.: Convergence diagnostic

	Diplôme : Master 2 Spécialité : SML-Biologie Spécialisation / option : Sciences halieutiques et aquacoles, option REA (Ressources et écosystèmes aquatiques) Enseignant référent : Étienne Rivot
Auteur(s) : Fanny Ouzoulias Date de naissance* : 28/06/1998	Organisme d'accueil : Pelagis (La Rochelle Université), Laboratoire LPSM (La Sorbonne) Adresse : Campus Pierre et Marie Curie, 4 place Jussieu, 75252 PARIS CEDEX 05
Nb pages : 35 Annexe(s) : 29	Maîtres de stage : Matthieu Authier et Nicolas Bousquet
Année de soutenance : 2022	
Titre français : Exploration bayésienne de modèles de surplus-production pour la gestion des prises accidentelles de cétacés, en utilisant des données d'échouage et d'abondance. Titre anglais : Bayesian exploration of Surplus Production Models for cetaceans by-catch, using strandings and abundance data.	
Résumé (1600 caractères maximum) : Les prises accidentelles dans les engins de pêches menacent de nombreuses espèces de cétacés, dont le dauphin commun. En 2020, plus de 800 dauphins, pêchés accidentellement dans le golfe de Gascogne, se sont échoués sur le littoral Atlantique. Dans ce contexte, nous avons cherché à développer un nouveau modèle permettant d'améliorer les règles de gestion existantes pour le dauphin commun. En particulier, nous avons exploré l'usage de <i>surplus production models</i> (SPM), dans un cadre bayésien et en intégrant une stochasticité (variabilité) environnementale. Ce modèle peut être estimé à partir de données d'abondance mais aussi des données d'échouage, ce qui est innovant pour un modèle de ce type. Captures et abondances sont reliées par un taux d'extraction (ϕ), correspondant à la proportion de dauphins capturés accidentellement par la pêche. Le but de l'étude est notamment d'estimer ce paramètre, ainsi que trois autres intervenant dans les modèles de dynamique des populations : la croissance intrinsèque (r), la capacité biotique (K) et la stochasticité environnementale (σ). Un modèle de simulation a d'abord été développé, permettant de générer des trajectoires d'abondance en faisant varier les quatre paramètres cités plus haut. Ce modèle permet notamment d'évaluer des probabilités d'extinction et de comprendre l'influence des paramètres sur ces probabilités. Une seconde partie du travail est dédiée à l'estimation des paramètres ϕ , r , K et σ , réalisée dans un cadre bayésien. L'estimation de ϕ peut notamment permettre d'améliorer la gestion des captures accidentelles, en proposant des limites de captures.	
Abstract (1600 caractères maximum) : Bycatch is one of the main threat looming on cetacean species, including the common dolphin. In 2020, more than 800 dolphins that were by-caught in the Bay of Biscay were washed ashore on the Atlantic seaboard of France. In this context, we developed a new model to improve existing management rules for common dolphin. In particular, we explored the use of surplus production models (SPM), in a Bayesian framework and integrating environmental stochasticity . This model integrates abundance data but also stranding data, which is innovative for SPM models. Catches and abundances are linked by an extraction rate (ϕ), which corresponds to the proportion of dolphins captured accidentally by fishing. The study aims at in particular estimating this parameter, as well as three others involved in population dynamics models: intrinsic growth (r), carrying capacity (K) and environmental stochasticity (σ). A simulation model was first developed, allowing to generate abundance trajectories which vary according to the four parameters mentioned above. This model enables to evaluate extinction probabilities and to understand the influence of the parameters on these probabilities. A second part of the work is dedicated to the estimation of the parameters ϕ , r , K and σ , performed in a Bayesian framework. In particular, the estimation of ϕ can improve by-catch management, by proposing adapted removal limits for common dolphins.	
Mots-clés : prises accidentelles, cétacés, modèles SPM, bayésien, stochasticité Key Words: by-catch, cetaceans, SPM models, bayesian, stochasticity	

* Élément qui permet d'enregistrer les notices auteurs dans le catalogue des bibliothèques universitaires