Population dynamics of elusive species : The case of the common dolphin in the North-East Atlantic Ocean

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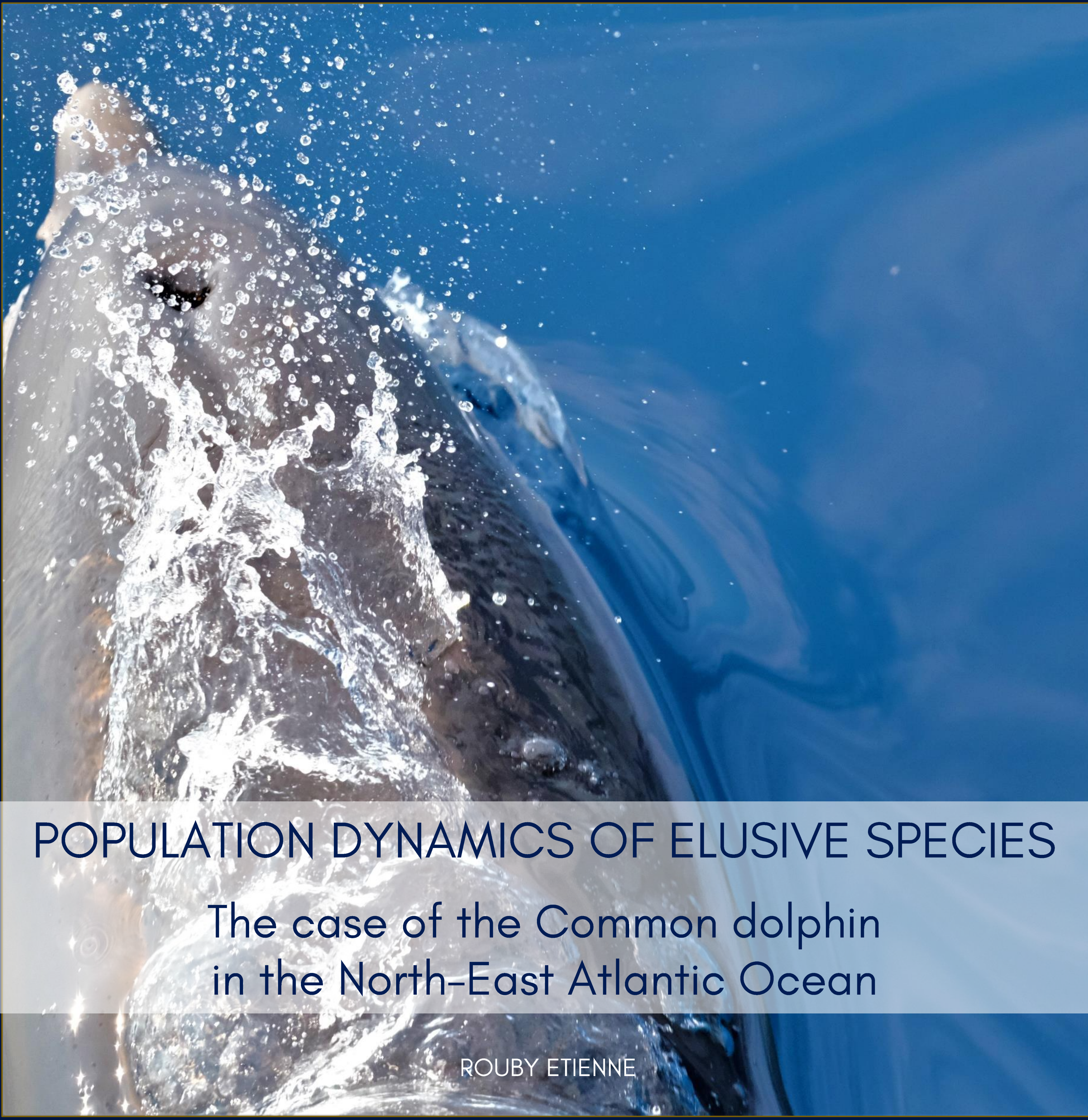

POPULATION DYNAMICS OF ELUSIVE SPECIES

The case of the Common dolphin in the North-East Atlantic Ocean

ROUBY ETIENNE

Under the supervision of Vincent Ridoux and Matthieu Authier
La Rochelle Université 2022

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Population dynamics of elusive species: The case of the common dolphin in the North-East Atlantic Ocean

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Abbreviations

ASCOBANS - Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas

CFP - Common Fishery Policy

CITES - Convention on International Trade in Endangered Species of Wild Fauna and Flora

CMR - Capture-Mark-Recapture

CO - Conservation Objective

DCF - Data collection framework

DPMA - *Direction des pêches maritimes et de l'aquaculture*

EC - European Commission

EU - European Union

GLG - Growth Layer Group

GNS - Gillnetters

GTR - Gill trammel netters

ICES - International Council for the Exploration of the Sea

Ifremer - *Institut Français de Recherche pour l'Exploitation de la Mer*

IUCN - International Union for Conservation of Nature

mPBR - modified Potential Biological Removal

MMPA - Marine Mammal Protection Act

MSFD - Marine Strategy Framework Directive

NAO - North Atlantic Oscillation

NEA - North East Atlantic

NGO - Non Governmental Organisation

ObsMer - *Observation des captures en Mer*

OMMEG - OSPAR Marine Mammal Expert Group

OSPAR - Oslo-Paris Commission

PBR - Potential Biological Removal

PTM - Pair trawlers

PTB - Bottom pair trawlers

RLA - Removal Limit Algorithm

RNE - *Réseau National Échouage*

Shom - *Service Hydrographique de la Marine Nationale*

UK - United Kingdom

USA - United States of America

VAST - Vector-Autoregressive-Spatio-Temporal

WGBYC - ICES Working Group on Bycatch of Protected Species

WGMME - Working Group on Marine Mammal Ecology

WKEMBYC - ICES Workshop on fisheries Emergency Measures to minimize BYCatch of short-beaked common dolphins in the Bay of Biscay and harbor porpoise in the Baltic Sea

WKMOMA - Workshop on estimation of MOrtality of Marine MAmmals due to Bycatch

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1.1 Demography and management of marine megafauna

Marine Megafauna: essential and impacted

The term megafauna comes from the combination of the Greek word "*megalos*", which means large, and the Latin word "*fauna*", which means the total number of animals living in a certain area at a certain time. The term megafauna is broad and ambiguous. It can refer to large animals, large vertebrates, large mammals or even giant mammals. In the scientific literature, the term can also lead to confusion. Moleón et al. (2020) recently proposed a critique of the use of the term megafauna through a literature review and proposed a goal-oriented framework for megafauna research. Megafauna can be defined in several ways. The most common definition is based on the size of organisms: mass for vertebrates and length for invertebrates. Another possibility is to define megafauna according to its functional role in the ecosystem and in particular in the food chain. The megafauna can be described as "apex megafauna" in the case of top predators or "keystone megafauna" in the case of keystone species.

The marine megafauna is a compartment of the ecosystem that includes long-lived marine species such as reptiles, birds, sharks, turtles and mammals. The species diversity of the marine megafauna is marked by the presence of top predators within it. These top predators are so called because they are at the top of the food web. They directly regulate the abundance and biomass of their prey, which may themselves be predators of other species. Within an ecosystem, each species is structured into populations. A population of marine megafauna can thus be defined as all the individuals of the same megafauna species living together in the same environment at the same time. The predatory action of top predators causes a trophic cascade of regulatory effects on the other populations that compose the ecosystems. This regulatory action of lower trophic levels in terms of abundance and biomass is theorised as top-down control (Hairston, F. E. Smith, and Slobodkin 1960; Paine 1969). The presence of top predator populations is therefore essential to maintain the balance of energy flows within the ecosystem. These populations therefore structure the entire ecosystem despite their proportionally lower abundance than other populations. Their presence contributes to structuring the communities (set of populations) that make up the biotic part of the ecosystem (Odum and Barrett 1971). Populations of top predators can sometimes be considered as keystone species, a concept developed from the observation of the ecological importance of the purple starfish (*Pisaster ochraceus*, Brandt 1835; Paine 1969; L. S. Mills, Soulé, and Doak 1993; Paine 1995).

Definition of the term "population" used in this project

I will use here the following definition of a population, provided by Berryman (Berryman 2002): "*A group of individuals of the same species that live together in an area of sufficient size to permit normal dispersal and/or migration behaviour and which numerical changes are largely determined by birth and death processes.*"

The presence of certain species is essential for maintaining the diversity of ecosystems. Some species are considered keystone species, a concept that includes, but is not limited to, predatory species and species associated with megafauna (Figure 1.2). For example, elephant populations (genus *Loxodonta*, Anonymous 1827) control the tree population in the savannah and allow other herbivores access to the plains for grazing (Western 1989; Ishida et al. 2018). But top predator species are often key species for the ecosystem. For example, the grey wolf (*Canis lupus*, Linnaeus 1758) was an important top predator in Yellowstone National Park, preying mainly on the abundant elk (*Cervus canadensis*, Erxleben 1777) and bison (*Bison bison*, Linnaeus 1758) herds. The disappearance of the grey wolf from Yellowstone Park around 1920 led to a proliferation of elk that consumed primary producers in large numbers. Other populations dependent on primary producers were affected and the biodiversity of the ecosystem was greatly reduced (Ripple and Larsen 2000). The reintroduction of wolves in the 1990s helped to regulate the elk population and promote greater biological diversity (Ripple and Beschta 2012). The concept of keystone species should not be confused with the concept of umbrella species. Confusion is possible because both terms refer to a species on which other populations depend. One of the main differences is that umbrella species cover a wide geographical area and are linked to a wide variety of habitats and ecosystems. This difference is important from a conservation point of view. The umbrella species concept is linked to ecosystem conservation. It is recognised that the conservation of umbrella species is a means to preserve one or more ecosystems and their associated communities. An example of an top predator umbrella species is the Amur tiger (*Panthera tigris altaica*, Temminck 1844; Miquelle et al. 1999). Populations of

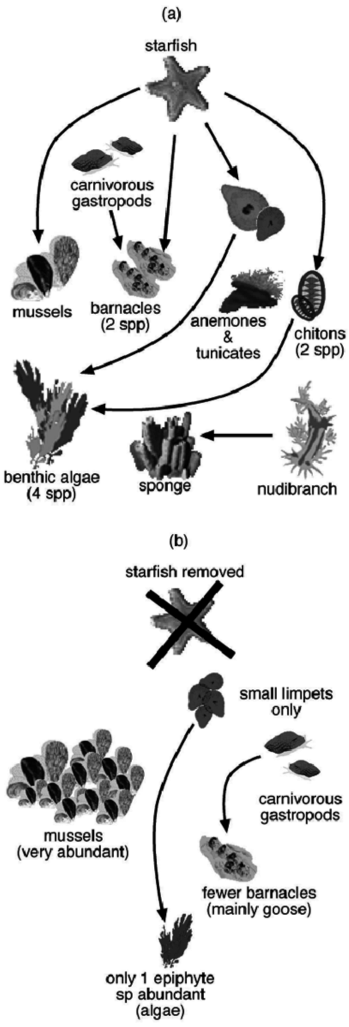

Figure 1.1: Schematic representation of the keystone role of predatory starfish *Pisaster ochraceus* in an intertidal ecosystem in Washington. (a) *Pisaster ochraceus* predation maintains a diverse community. **(b)** removal of *Pisaster ochraceus* allows mussels to dominate, and reduces species diversity.
Based on (Paine 1969).

this predator extend over a vast area covering part of Southeast Asia. They are at the top of the food chain in many ecosystems with different environments (Carroll and Miquelle 2006). The conservation of keystone and umbrella species is an interesting conservation approach, as it helps to maintain the diversity and balance of one or more ecosystems. From a marine ecosystem management (and conservation) perspective, it can be effective to focus on populations of top predatory marine species (Roberge and Angelstam 2004).

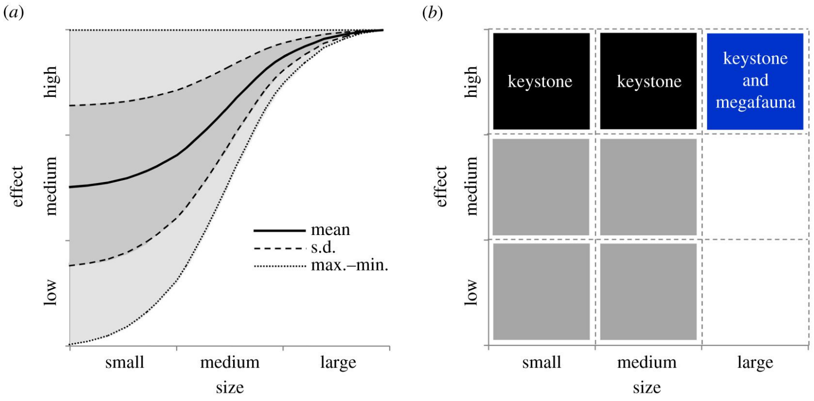

Figure 1.2: Conceptual definition of megafauna based on size and importance for the ecosystem.
a. Large animals have an high impact on local ecosystems whereas the impact of smaller ones is more variable. There is a challenge to correctly define the size-effect relationship.
b. Two-dimensional qualitative disruption of animal species. The two-dimensional space is defined by body size and ecosystem effect. Keystone species have an high effect on ecosystems and only the largest keystone species are defined as megafauna. Figure from Moleón et al. 2020.

Humans are currently impacting marine megafauna in a variety of ways. These impacts can be described as indirect if the human action affects an intermediate factor that has an impact on the population (*e.g.* human-induced climate variations). Conversely, they can be defined as direct if the human action directly affects the population (*e.g.* hunting or accidental capture in fishing gear). Recently, Authier et al. (2017) has proposed a new classification of impacts using the example of marine megafauna populations, these impacts are classified into three categories. Each is associated with a pressure that generates a different response within the population (Figure 1.3). The pressure is classified as tertiary if it generates a response in the behaviour of individuals in the population. Pressure is classified as secondary if it generates a response in the health of individuals in the population. Pressure is classified as primary if it generates a response in the demographic rates of the population or individuals within the population. In my opinion, this classification is relevant because it allows for more nuance. For example, it has been shown that pile driving during the construction of offshore wind farms can impact marine mammals such as the harbour porpoise (*Phocoena phocoena*, Linnaeus 1758) by causing displacement of individuals (Nabe-Nielsen et al. 2014; Pirotta et al. 2014; Graham et al. 2019). This displacement can generate an energy cost which is then passed on to other levels of response (Authier et al. 2017). These impacts constitute tertiary pressures in the proposed new form of classification, which allows for better mapping of their effects on population status. Demography is considered to be the response level with the most direct effect on population status, although populations are rarely exposed to only one type of pressure, particularly marine megafauna (Authier et al. 2017). It is mainly this level of response that interests us here and in particular the primary pressure associated with it, especially for marine mammal species.

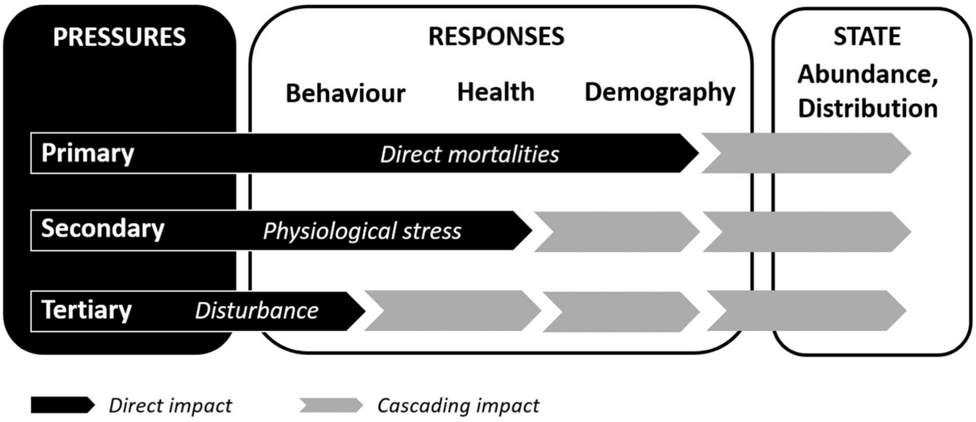

Figure 1.3: Typology of pressures based on their effects on marine megafauna. Figure from Authier et al. 2017.

Marine mammal demography

The life histories of marine mammal species are typical of long-lived species. The life history of an organism is its survival and reproductive pattern, as well as characteristics that directly affect survival and the timing or amount of reproduction. As long-lived species, marine mammals have low reproductive rates, high survival rates and a focus on caring for young individuals. They are iteroparous with several reproductive episodes during their lifetime (Cole 1954). They can also be described as *K* species, according to the definition of MacArthur and Wilson (2016), as they exhibit stable strategies with low growth rate values, high care for young survival and low fecundity in stable environments. If we take into account the continuous reference framework proposed by Pianka (1970) and Stearns (1976) which described the strategies as a continuum, they would tend towards the extreme of the slow strategy. The slow strategy is characterised by a long life expectancy with low reproductivity (*i.e.* high investment in survival and growth over reproduction). The life history of marine mammals is characterised by a trade-off between survival and reproductive vital rates that appears to favour survival over reproduction. Although life histories within a species, or even a population, may appear to be uniform, they may in fact differ between individuals.

Vital rates definition

Vital rates are refereed as demographic parameters such as age-specific survival and fecundity distributions (Reilly and Barlow 1986).

Differences in life history between individuals in the same population can be explained by observable factors (*e.g.* age or sex) but some inter-individual variability is not accounted for by these factors (Camus and Lima 2002). This variability is defined as individual heterogeneity or frailty (Cam, Aubry, and Authier 2016). Heterogeneity can be defined as time-invariant if we consider the differences between individuals acquired at birth and inherent to the individual's phenotype (Van Noordwijk and de Jong 1986). Time-invariant differences between individuals are considered as the basis of the quality of individuals (Camus and Lima 2002; Vaupel, Manton, and Stallard 1979; Coulson and C. Thomas 1985). The quality of an individual can be seen as the latent probability of surviving and reproducing in a time interval. High quality individuals are therefore more likely to survive and reproduce than lower quality individuals who will tend to die younger. These differences between individuals due to time-invariant effects, acquired at birth, can lead to a selection process. The best phenotypes are thus selected by mortality selection within the birth cohorts (Curio 1983; Endler 1986). Lower quality individuals may not contribute to population renewal to the same extent as higher quality individuals, which would lead to an age-related decrease in the proportion of lower quality individuals in cohorts and this would lead to an increase in population-level survival (C. S. Thomas and Coulson 1988; Vaupel and Yashin 1985). The proportion of individuals with a low probability of survival, tends to decrease over time while the probability of survival of the remaining (*i.e.* better quality) individuals should increase (Camus and Lima 2002). Thus, the apparent probability of survival of the population would appear to increase while in reality the probability of survival of individuals would not change. This could be the source of surprising correlations between the probability of survival of an individual and its age, since this probability of survival would be linked to the population (Camus and Lima 2002). The probability of survival and viability of a population is also influenced by human activities. For marine mammals, one of the activities that has the greatest impact on them is fishing. This is particularly the case for odontocetes.

Some concepts

Fitness: Ability of an individual of a given genotype to reproduce. Also called selective value or reproductive success.
Cohort: A group of individuals who have experienced the same event during the same period. The term cohort is usually used to refer to birth cohorts which refers to all individuals born in the same year.
Phenotype: The set of apparent characteristics of an individual conferred by its genotype, its development and its environment.

The link between Frailty Hazard and Survival

In demography, frailty can be referred to as susceptibility to disease or death (Kannisto 1991). Individuals in a population do not have the same life histories, particularly with regard to hazard and survival. Differences between these components of the life history of individuals that are not explained by observable factors are called heterogeneity or frailty (Aalen 1994). Susceptibility to death or disease can vary from one individual to another but this variation cannot be explained directly (*i.e.* by observing the phenotype of individuals). It is impossible to take these variations into account as covariates in survival analyses because they are hidden. However, it is possible to statistically account for this inter-individual frailty in order to model its effect on the survival and hazard of a population. These models are called frailty models (R. Henderson and Oman 1999). Frailty models include the notion of individual frailty in demographic models (Kannisto 1991). Individual frailty is then taken into account statistically as a random effect having a multiplicative action on hazard (Hougaard 1995). This random effect can be individual or common to several individuals. In case of individual random effect, modelling is called univariate and frailty describes heterogeneity. In this thesis project, we have developed a new approach to survival analysis, based on taking into account the effect of individual frailty on hazard (Reed 2011).

The case of odontocetes, especially delphinids

Among the marine megafauna, odontocetes are particularly threatened because they are often subject to bycatch pressure. Of the human activities that can have an impact on odontocete populations, fishing has the greatest impact on populations worldwide (A. J. Read, Drinker, and Northridge 2006). Odontocetes are cetaceans with teeth, as opposed to mysticetes, which are baleen whales. Because of their top predator position, odontocetes compete with humans for food resources (*i.e.* fish). These interactions can sometimes be positive for odontocete populations by favouring their survival. One example is the phenomenon of depredation, which is defined for marine mammals as the removal of fish caught on commercial fishing gear. Recently, it has been shown that among the orcas of the Crozet Island population (*Orcinus orca*, Linnaeus 1758), individuals with depredation behaviour have a better survival than those that do not engage in depredation (Margin-Figure 1.4). From a more general point of view, these interactions are deleterious to odontocetes as they can reduce the survival of pop-

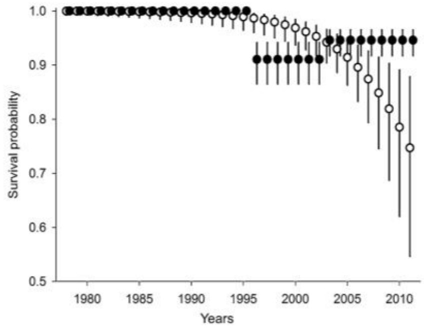

Figure 1.4: Survival probability of killer whales along time. Non-depredating killer whales are represented with empty circles whereas depredating killer-whales are represented with black circles. Error bars are the 95% CI.
From Tixier et al. (2017).

ulations (and by extension their growth and viability). One of the most worrying phenomena associated with competition for food resources is the phenomenon of bycatch. It is defined as the accidental capture of a non-commercial or even protected species (M. A. Hall 1996). Populations, even species, of odontocetes have already disappeared or are on the brink of extinction because of this additional mortality pressure, which they cannot withstand. This is the case of a Chinese river dolphin named Baiji (*Lipotes vexillifer*, Miller 1918). This species is now considered extinct. Intensive human activity in the Yangtze River, including shipping traffic, water pollution and bycatch, is suspected to have caused its extinction (Dudgeon 2005; D. Wang et al. 2006). Another example is the vaquita (*Phocoena sinus*, Norris and McFarland 1958), whose population is now almost extinct. The vaquita is in fact the most critically endangered marine mammal, with very few individuals remaining in the wild. This species is endemic to the shallow, turbid and highly productive habitat of the upper Gulf of California, between Baja California and mainland Mexico (Rojas-Bracho, Reeves, and Jaramillo-Legorreta 2006). The Vaquita population has been subject to increasing bycatch pressures associated with fisheries that target totoaba (*Totoaba macdonaldi*, Charles Henry Gilbert 1980) and has been severely depleted. This fish, which is about the same size as the vaquita, is targeted for the black market trade in its swim bladders in China (Rojas-Bracho et al. 2019). The implementation of management measures is one way to prevent a population from becoming too depleted. It is based in part on determining the viability of delphinid populations. This viability can be determined from population dynamics models (Wade 1998; Mannocci et al. 2012).

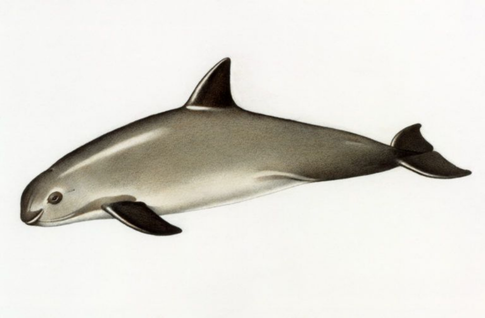

Figure 1.5: Vaquita (*Phocoena sinus*, Norris and McFarland 1958). Picture from `https://cseweb.ucsd.edu/~awilby/Brink-of-Extinction_NGS.html`

1.2 Describe, quantify and predict population dynamics

Contribution to the management

Management of wildlife populations can be considered as "management of wildlife populations in the context of the ecosystem" or could be considered in a broader sense by integrating several socio-economic aspects (Fryxell, Sinclair, and Caughley 2014). Managing a population can be done in four ways: increasing the population, decreasing the population, harvesting the population for a continuous yield, leaving the population alone and monitoring it (Fryxell, Sinclair, and Caughley 2014). The management of each living resource therefore involves a trade-off between promoting the continued existence of the resource (*i.e.* conservation aspect) and obtaining an economic benefit from it (*i.e.* exploitation aspect; Harwood 2010). The concept behind managing exploited animal populations is intrinsically linked to growth rate. A population that is reduced from its maximum level of abundance given the environmental conditions (*i.e.* carrying capacity) will have a positive growth rate. It is on this positive growth rate that the removal of the population is carried out (Harwood 2010). More specifically, it is assumed that density-dependence influences population recruitment in a stock-recruitment relationship that is at the heart of population harvesting (Sale 1990). This foundation is inherited from fish stock management studies (Beverton and Holt 1957, 2012). The use of population growth models is therefore particularly interesting in the context of the management of exploited populations and in the event of accidental catches, the bycaught population can theoretically be considered as an exploited population (Barbraud et al. 2008; Lebreton 2005). Theoretical bases related to the science of fisheries management can therefore be applied to implement bycatch management measures. The basic premise changes. We no longer seek to exploit the population for a continuous yield, but we want to reduce bycatch to a sustainable level that is relative to the dynamics of the population concerned. To do this, we use models that take into account either abundance (Wade 1998) or abundance and vital rates by age (Hammond, Paradinas, and Smout 2019; Genu et al. 2021) within or outside of a Management Strategy Evaluation procedure (Punt et al. 2016). European waters are fishing grounds where many different gears are used at different times of the year, with complex and structured ecosystems, including marine megafauna (Peltier et al. 2021; Corrales et al. 2022). Among the 17 cetacean species frequently observed in these waters (and in particular in the Bay of Biscay), the common dolphin (*Delphinus delphis*, Linnaeus 1758) currently presents strong conservation challenges and is possibly a Keystone species (Peltier et al. 2021; Corrales et al. 2022; Murphy et al. 2021).

Population growth models

Population dynamics is the scientific field of ecology concerned with the changes in abundance that populations experience over time and the factors that influence these changes (Gotelli 2008). The main objective of the study of the dynamics of a population is to carry out an evaluation of the population which can be considered as the evaluation of both the status of the population and its vitality (or viability, Skalski, Ryding, and Millspaugh 2010). The population status corresponds to the current state of the population with regard to certain characteristics such as age and sex structure or abundance in relation to a certain reference. Status using abundance can be assessed through time series of abundance estimates,

Here, the margin notes will include the mathematical expressions of what is said in the text. This is done so as not to interfere with the reading, but to provide a more mathematical background and insight.

but it is also possible to study the underlying mechanisms that shape these changes in abundance (J. D. Baker, A. Westgate, and Eguchi 2010). To do this, it is possible to assess the viability of the population through the evaluation of its demographic health and its capacity to maintain itself from one year to the next. Several models (*i.e.* representation of reality. In our case, representation of the dynamics of a population from a mathematical point of view) have been developed in order to represent the annual dynamics of populations.

Geometric population growth models

Basic dynamic changes within a population are due to the losses of individuals through processes of death/emigration and additions through processes of births/immigration (J. D. Baker, A. Westgate, and Eguchi 2010). Considering a closed population (without immigration and emigration) it is possible to imagine its growth dynamic geometrically (*i.e.* in way that each abundance value is determined by the multiplication of its previous value by a constant factor) according to a continuous or a discrete time stamp (depending on population dynamic to be modelled). Considering a continuous time model (*i.e.* birth and deaths occurs continuously) associated with a continuous population growth, the rate of change in population size through a continuous time period could be explained as the difference between births and deaths. They depends on the total abundance, instantaneous births and death rates. In other words, the rate of change in population size through a continuous time period is equal to the intrinsic rate of increase r effect on population abundance (Gotelli 2008). The rate of increase value is determinant to understand the viability of the population and define if it is stationary ($r = 0$), decreasing ($r < 0$) or increasing ($r > 0$). It can also be used to model the abundance of the population at any time given the initial abundance estimate. Depending on the value of the rate of increase, the population can grow exponentially. One example of exponential growth on large mammal was demonstrated (Scheffer 1951) with the reindeer (*Rangifer tarandus*, Linné 1758). The intrinsic rate of increase of the population can also be expressed when no resource is limiting and can be referred as r_{max} compared to the observed intrinsic rate of increase which can be defined as r_{real} and the intrinsic rate of increase under a stable age distribution r_{stable} (Skalski, Ryding, and Millspaugh 2010; Caughley and Birch 1971).

The abundance at time $t + 1$ (N_{t+1}) is obtained from the previous abundance at time t (N_t), additions through births and immigrants ($B + I$) and losses through deaths and emigrants ($D + E$):

$$N_{t+1} = N_t + (B + I) - (D + E)$$

The rate of change in population size through time $\frac{dN_t}{dt}$ is expressed given instantaneous birth rate b, instantaneous death rate d and intrinsic rate of increase r:

$$\begin{aligned}\frac{dN_t}{dt} &= B - D\\ &= (b - d)N_t\\ &= rN_t\end{aligned}$$

The abundance at any time t (N_t) is obtained from the initial abundance (N_0), time t, the intrinsic rate of increase r and the exponential function e:

$$N_t = N_0e^{rt}$$

From the expression of the geometrical continuous time populations model, which admitted that birth and deaths occurs continuously, it is possible to represent the dynamic of populations for which births and deaths are not continuous. This is the case

λ is the finite rate of increase expressing the proportional changes in abundance from on year to the next ($\frac{N_{t+1}}{Nt}$). To project the population size at any time t the initial abundance N_0 is also used:

$$\begin{aligned}\lambda &= \frac{N_{t+1}}{Nt}\\ N_{t+1} &= Nt\lambda\\ N_t &= \lambda^tN_0\end{aligned}$$

for numerous animal species which present a breeding season and unequal mortality levels through the year. Such models are refereed as geometrical discrete time populations models. The use of r as instantaneous rate of increase is replaced by the use of λ as finite rate of increase. This rate expresses the proportional changes in abundance as a multiplicative factor by which abundance changes from one year to the next (Skalski, Ryding, and Millspaugh 2010). As a proportional change, the rate λ expresses the viability of the population relatively to 1, reference value for a stationary population ($\lambda = 1$), growing population ($\lambda > 1$) and declining population ($\lambda < 1$). The way time is considered in the choice of representation of population dynamics regarding geometric growth determines the relationship between growth rates as r is the intrinsic per capita growth rate, R is the net discrete per capita growth rate and λ is the discrete per capita growth rate (J. D. Baker, A. Westgate, and Eguchi 2010).

Relationships between growth rates:

$$\lambda = R + 1$$
$$\lambda = e^{r}$$

Logistic population growth models

The previously seen models admit that the population can grow forever which is not the case in natural population due to several factors such as predation, hunting, starvation or overcrowding (Leopold 1933). Natural populations can also be limited in growth due to a lack of resources and some environmental effects leading the growth in logistic population growth (Krebs 1994). The access to resources may be limited among organisms through population density. This factor can be defined as a density-dependent factor. Density-independent factors, on the other hand, have an effect on population growth rates independently of the population size or density. Density-dependent processes are important to take into account, as they directly influence the maximum sustainable yield value regarding fisheries and harvested species. The maximum sustainable yield (MSY) is the highest theoretical equilibrium yield that can be continuously taken from a stock under the average environmental conditions (Schaefer 1954). The highest catch value allows the population to sustain through somatic growth, spawning and recruitment (Tsikliras and Froese 2019). We will see that this concept may be adapted to set up management plans for accidentally harvested species. Density-dependence is an important factor shaping the growth of animal populations, in particular considering large mammals (Fowler 1981). The basis of the concept is the relationship between instantaneous birth rate, instantaneous death rate and abundance at a given time. When the population size tends to increase, the instantaneous death rate increases too. Assuming that resource are limited, the instantaneous birth rate tends to decrease as abundance increases. The equilibrium between both rates is obtained when the population attains the carrying

Logistic models forms:

$$\frac{dN_t}{dt} = r_{max} \times N_t \times \left(1 - \frac{N_t}{K}\right)$$
$$N_{t+1} = N_t + N_t \times (\lambda_{max} - 1)\left(1 - \frac{N_t}{K}\right)$$
$$N_{t+1} = N_t + N_t \times (\lambda_{max} - 1)\left(1 - \left(\frac{N_t}{K}\right)^{\theta}\right)$$

capacity (K) level which can be viewed as the maximum population size that a population can reach given its environment its resource limits and associated pressures.

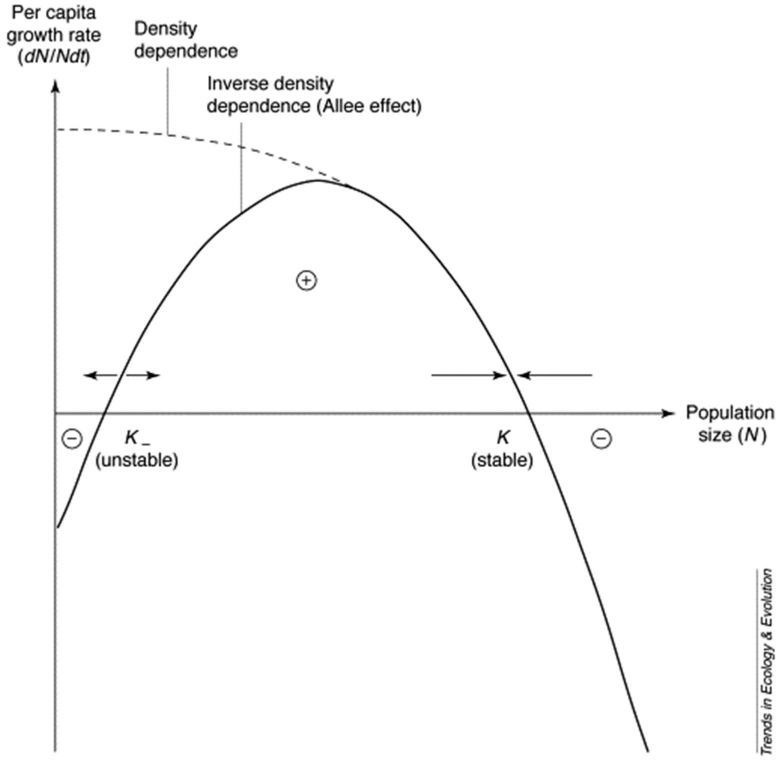

Figure 1.6: Relation between per capita growth rate, abundance and carrying capacity. When abundance (N) is low, the per capita growth rate is high enough to allow the population to produce individuals and increase abundance to the carrying capacity which is the stable equilibrium point. In the case of a population subject to the Allee effect, a too low abundance below a critical threshold is associated with a decline in growth rate. It is no longer high enough to support mortality and the population disappears.

From the link between those parameters, (Verhulst 1838) created the familiar logistic population growth model assuming a continuous time. From this model the discrete one was obtained and allows to represent the dynamic of a population given density-dependence with a discrete time stamp (Pearl 1925). Then, the generalized logistic model was introduced taking into account the rate (θ) at which the population reaches its carrying capacity (J. D. Baker, A. Westgate, and Eguchi 2010). Depending on the value of this rate, the population can grow at a rate equal to that of a standard logistic growth ($\theta = 1$), can growth more rapidly in an exponential way close to the carrying capacity ($\theta > 1$), can fluctuates about the carrying capacity ($\theta \geq 10$) and can grow at a rate lower than that of the standard logistic due to an anticipated effect of density dependency on growth ($\theta < 1$) (Pella and Tomlinson 1969).

While density dependence is commonly seen as a limiting factor for population growth, Warder Clyde Allee proposed in 1931 another view, that can have strong consequences for modelling population dynamics, which he developed in his book: Allee et al. 1949. Its premise is that some populations are affected by a positive relationship between population growth rate and density when they reach low levels of abundance which can lead to their

Baseline Allee Effect model with K^* as the Allee threshold (Courchamp, Clutton-Brock, and Grenfell 1999):

$$N_{t+1} = N_t \times \left(1 + R_{max}\left(1 - \frac{N_t}{K}\right) \times \left(\frac{N_t}{K^*} - 1\right)\right)$$

extinction if the density of individuals is too low (Courchamp, Clutton-Brock, and Grenfell 1999). If abundance is not high enough, the reproduction or survival of the population may be impacted in a negative way which leads to a decrease in the per capita growth rate that can reaches negative values as it is depicted in Figure 1.6. The Allee effect can also be refereed as the depensation, positive density dependence (W. F. Morris et al. 2002) or Allee's principle (Odum and Barrett 1971). Factors that may lead to this inverse density dependence at low density can be classified into three types according to (Courchamp, Clutton-Brock, and Grenfell 1999) which has led to the recent emphasis on the importance of this idea in modelling population dynamics (Skalski, Ryding, and Millspaugh 2010). The first type of factor is genetic (*i.e.* genetic inbreeding). It is characterized by a loss of heterozygoty that lead to a decrease in fitness. The second type of factor is demographic (*i.e.* demographic stochasticity). It is characterized for example by sex-ratio fluctuations that lead to a low reproductive output (*e.g.* Kakapo *Strigops habroptilus*, Gray 1845). The third type of factor is interactive (*i.e.* facilitation or behavioural). It is characterized by less interactions that are important for the survival of the population '(*e.g.* bluefin tunas *Thunnus thynnus*, Linné 1758) or the shortage of receptive mates (*e.g.* Kakapo) and cooperative breeders (*e.g.* African wild dogs *Lycaon pictus*, Temminck 1820) (Courchamp, Clutton-Brock, and Grenfell 1999). As it is illustrated in Figure 1.6 Allee effect produces unstable equilibrium at low densities and increases the probability of extinction. A strong Allee effect is characterized when there is population density below which the per capita growth rate. It is therefore dangerous to harvest a population that may be sensitive to the Allee effect. It is also possible that population growth models that do not consider Allee effects underestimate the risk of extinction (Skalski, Ryding, and Millspaugh 2010).

Age-Structured population growth models

These population models are limited to study the influence of specific age-specific demographic rates on growth rates and it could be of interest to represent the dynamic of a population given particular age or stage classification (Leslie 1945; Lefkovitch 1965). The use of matrix population models allows to project the population state given initial abundance or in terms of percentages which is particularly useful for studying viability. Here only the Leslie matrix will be discussed as this concept is part of two aspects of the project. This matrix model reflects the dynamics of a unisex population (usually females) independently of the density dependency processes discussed earlier (Skalski, Ryding, and Millspaugh 2010;

Matrix notations and models for the Leslie 1945 matrix modelling approach:

$$\underline{\mathbf{n}}_{t+1} = \mathbf{L}\underline{\mathbf{n}}_t$$

$$\begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ N_3 \end{bmatrix}_{t+1} = \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ N_3 \end{bmatrix}_t \times \begin{bmatrix} F_0 & F_1 & F_2 & F_3 \\ S_0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 \\ 0 & 0 & S_2 & 0 \end{bmatrix} \tag{1.1}$$

$$N_{0t+1} = N_{0t}F_0 + N_{1t}F_1 + N_{2t}F_2 + N_{3t}F_3$$
$$N_{1t+1} = N_{0t}S_0$$
$$N_{2t+1} = N_{1t}S_1$$
$$N_{3t+1} = N_{2t}S_2$$

Leslie 1945). The conceptual model of this population dynamics matrix model can be represented as follows:

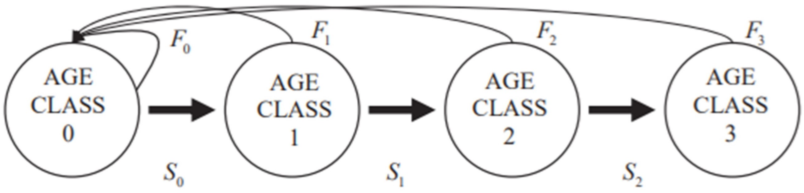

Figure 1.7: Conceptual model a age-based-matrix model. Individuals can reach the maximum age of 3. Each age class contributes to the renewal of the population with its associated fecundity rate F. Each individual advances in age in the population with a probability equal to the age-specific survival rate.

This population model involves two components to project the number of females of a population through time that are the number of females within each age-class and the probability for female each age-class to both survive and produce a new female in the population. These matrices are associated with eigenvectors and eigenvalues which will not be discussed in detail as it is not the purpose of this chapter but for more mathematical information see Caswell 2000. They are key properties of populations that can be represented by the matrix populations models. The asymptotic population growth rate λ corresponds to the dominant eigenvalue and the stable age distribution is represented by the eigenvector. Another interesting component of matrix population models are obtained through perturbation analyses. Caswell 2000 explains that the "results of perturbation analyses are sometimes more interesting, more robust and more useful than the parameter estimates themselves". The two common perturbation analyses are the elasticity and the sensitivity analyses. They provide both the proportional response of the growth rate to a proportional perturbation in the vital rates and the magnitude of changes in the growth rate with respect to each element of the matrix (J. D. Baker, A. Westgate, and Eguchi 2010). These information are particularly valuable in case of population management when it is necessary to have information about the age-classes the most important to manage in terms of the value of the growth rate.

Table 1.1 summarise important information about the models introduced here. Only those most relevant to the project are presented. These models are of importance to assess the viability of a population and have also been developed in the context of exploitation of some populations (*e.g.* population of fishes or whales). They therefore serve as a reference for the implementation of management strategies. Both for populations that are exploited voluntarily and for populations that are accidentally exploited.

Population matrix models that have an age-dependent structure need to be filled with vital rates. To obtain these age-dependent vital rates (survival and fecundity), it is necessary to monitor mammal populations. Two categories of monitoring exist and only one is applicable to elusive populations.

Table 1.1: Examples of population dynamic models. Other exists but these are the main used in the project.

Model	Equation	Reference	Chapter
Exponential	$N_{t+1} = N_t \lambda_{max}$	Malthus, Winch, and P. James 1992	Chapter 4 in 4.9
Logistic	$N_{t+1} = N_t + N_t \times (\lambda_{max} - 1)\left(1 - \frac{N_t}{K}\right)$	Hutchinson 1978	-
Generalized logistic	$N_{t+1} = N_t + N_t \times (\lambda_{max} - 1)\left(1 - \left(\frac{N_t}{K}\right)^{\theta}\right)$	Pella and Tomlinson 1969	Chapter 6 in 6.2

Why "elusive" species ?

The term elusive comes from the Latin *elus*, and is an adjective meaning "difficult to find, define or achieve" (Oxford Dictionary). The term is used in this manuscript to refer to species that may have one or more of the following characteristics: difficult to track individually, sparsely distributed, for wich it is difficult to estimate anthropogenic mortality and for which it is difficult to implement management policies.

1.3 Estimation of life-history traits

Longitudinal monitoring to estimate vital rates

Quantifying the life history traits of a population is nowadays mainly carried out using longitudinal monitoring and capture-recapture protocols (CMR; B. K. Williams, Nichols, and Conroy 2002). The study of life history traits (which can be described as life history parameters) has become important since the end of the 20th century (Lebreton et al. 1992). This importance has materialised in the desire and need to detect differences in life history traits between populations in order to study their regulation, structure and viability (Stearns 1980; Noble and Slatyer 1980; Crawley and May 1987). These differences are thought to be the source of changes in life history, through a modification of fitness in relation to survival and fecundity (Manly 2013). While it is easier to estimate fecundity in wild populations, survival remains a major component of life history that is difficult to quantify (J. Clobert, Lebreton, and Allaine 1987). The importance of being able to follow each individual over the long term in order to deduce the value of vital rates in relation to survival seems to be an essential condition for achieving these objectives (Lebreton et al. 1992). The history of survival analysis modelling will not be detailed here. This will be done in the introduction to Chapter 3, which is a chapter specifically dedicated to survival analysis.

Long-term individual monitoring can use different forms of natural or artificial recognition methods. Longitudinal tracking protocols involve both the recognition of living individuals (Lebreton et al. 1992; Sandercock 2006) and dead individuals (Brownie 1985). For example, it is possible to follow individuals on the basis of physical marks that distinguish them from one another in the population (Castro and Rosa 2005; Wirsiig and Jefferson 1990). This is the case for giraffes, which can be recognised individually on the basis of their coat patterns (Berry and Bercovitch 2012). Where individuals cannot be observed directly, camera traps can be used to record the passage of individuals at points of interest (O'Connell, Nichols, and Karanth 2011). These camera traps are used to identify individuals of cryptic feline species such as the snow leopard, lynx or Siberian tiger (Jackson et al. 2006; Can and Togan 2009; T. M. Wang et al. 2014). Individual recognition can also be performed in marine mammals. The recognition of individuals is based on the shape of the tail fin and its patterns (*e.g.* humpback whale and sperm whale), the shape of the dorsal fin (*e.g.* bottlenose dolphin and killer whale) or by the recognition of specific callus patterns (Right whales; Pace, Corkeron, and Kraus 2017). These identifications of individuals in marine mammal populations are made possible by longitudinal tracking protocols called "photo identification". Sometimes it is not possible to identify a species on the basis of its natural markings, but it is possible to easily access individuals in a population and place artificial markings on them. These artificial markings can be rings, collars, ear tags, radio transmitters or bands. Ringing is widely used in population dynamics studies of birds that may sometimes be accessible in colonies (Busse and Meissner 2015). Tagging is also deployed in pinniped species that are accessible in breeding colonies (Costa et al. 2010; A. Henderson et al. 2020). Collars are preferred for small mammals or certain ungulates. For the latter, the use of earmarks is common (Swenson et al. 1999). Collars can also be designed as radio transmitters that are used to study both dispersal and survival (Millspaugh and Marzluff 2001; G. C. White and Garrott 2012). Finally, tags can also be used to collect demographic data when individuals are dead. This is particularly the case for rings used in monitoring programmes for hunted populations. These are known as ringing recovery protocols: (Brownie 1985).

Longitudinal monitoring

Longitudinal monitoring involves repeated observations of individuals through a period of time. It can be perform using Capture-Mark-Recapture, band recovery and tagging protocols. For cetaceans, the most common longitudinal monitoring protocol is photo-identification (Wirsiig and Jefferson 1990). This monitoring allows the vital rates of the population to be obtained (Lebreton et al. 1992) along with variations in vital rates and individual-heterogeneity quantification (Camus and Lima 2002; Gimenez, Cam, and Gaillard 2018).

This monitoring makes it possible to determine multiple demographic parameters of the population (*i.e.* vital rates or life-history traits) such as survival (Lebreton et al. 1992), dispersal rates (Brownie et al. 1993), recruitment rate of new breeders (Clobert 1995), breeding frequency and transitions between breeding states (Cam et al. 1998). The expansion of the use of CMR monitoring has made a considerable contribution to the quantification of many life history traits (Lebreton et al. 1992). However, it is not possible to use this monitoring on all species. For elusive species, it is necessary to use the old approach, combined with difficult assumptions, less sophisticated analysis methods and basic estimators of population life-history traits.

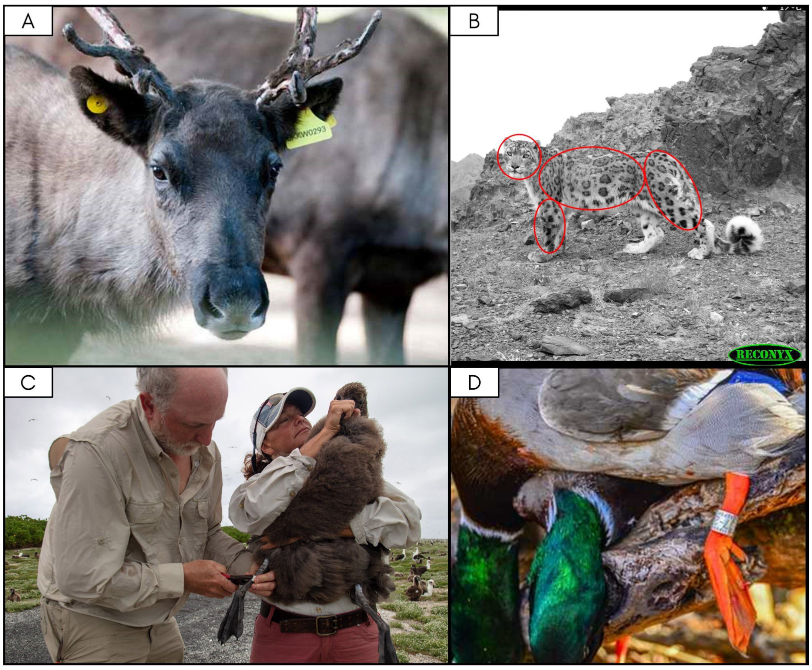

Figure 1.8: Exemples of possible individual-based long term monitorings.
A. Ear-tags.
B. Natural marks of rare animals observed thanks to camera traps.
C. Bird ringing.
D. Recovery of bands.

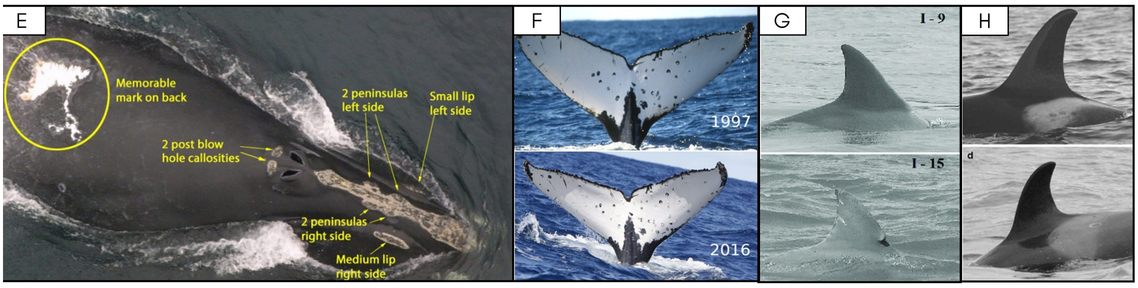

Figure 1.9: Exemples of possible individual-based long term monitorings for cetaceans.
E. Callosities on Right-Whales.
F. Caudal fin markings on Humpback whales.
G. Dorsal fin shape on bottlenose dolphins.
H. Dorsal fin shape and natural markings on killer whales.

Cross-sectional monitoring to estimate vital rates

Basically, cross-sectional monitoring has been used to describe the age distribution from which life tables can be constructed to estimate age-specific survival and mortality rates (Skalski, Ryding, and Millspaugh 2010; Gompertz 1825). The use of this type of monitoring is common in fisheries studies as it allows the age-frequency distribution to be described. The age distribution of a fish population is an essential piece of data that can provide information on changes over time, how a stock responds to exploitation and how it may recover from external disturbance (Jennings, Reynolds, and S. C. Mills 1998; Greenstreet, Spence, and McMillan 1999). The age composition of a fish population can be determined from otoliths, backbone and fin radii (Quist, Pegg, and DeVries 2012; Goldman et al. 2012; Carbonara and Follesa 2019), but also from allometric age-length relationships (Westrheim and Ricker 1978; Ailloud and Hoenig 2019) using the age-length key which may be subject to bias (Kimura 1977). The use of this cross-sectional tracking scheme, especially from otolith ageing, is still common in fisheries studies to obtain age composition and demographic parameters (Durant et al. 2013).

Cross-sectional monitoring has historically been widely used to monitor fish stocks. It is still used today to monitor fish populations and exploited stocks.

In the case of tetrapod populations, age composition (or age distribution) is obtained by analysis of morphometric features or even samples of biological material (Caughley et al. 1977). The determination of the age of amphibians is generally done using osteological techniques (Peabody 1961) whereas sauropsids are generally aged according to their size (*i.e.* allometric relationship) (Caughley et al. 1977). For some bird species (Fulmar, Shag, Redshank and Great Skua), it is possible to count the endosteal layers of the tibia to determine the age of individuals (Klomp and Furness 1992). For turtles, age can be determined by the annuli method on the carapace (Sexton 1959; Gibbons and Semlitsch 1982). For mammals, the methods of age determination are varied. The eruption of the teeth can be an indicator, particularly for bovine species such as mouflons or equids (Garel et al. 2007), but also for sea otters (Nicholson et al. 2020). Body size and size frequency classes could also be an indicator of age (Klomp and Furness 1992). The most widely used and effective method for obtaining a population age distribution and creating the associated life table is the use of biological material taken from dead animals (Caughley et al. 1977). The biological material used consists of teeth (Laws 1953; Benjaminsen 1973), claws (R. B. Thomas et al. 1997) and horns (Geist 1966). The method (*e.g.* odontochronology) consists of counting the number of growth rings (or groups of growth layers) that make up the biological tissue. The age data obtained by this method is called age-at-death data and the age distribution can be called the age-at-death distribution. Classically, these data were obtained by harvesting and recovering dead carcasses (Caughley 1966).

Cross-sectional monitoring

In contrast to long-term monitoring of individuals, a population can be monitored by means of snapshots over a given period. This type of monitoring is called cross-sectional or transversal. For example, the characteristics of a few individuals in a population will be collected at a given time. From the data collected, an extrapolation will be made to the whole population. It is from this type of monitoring that the life tables are constructed (Caughley 1966).

The process of obtaining vital rates associated with survival and mortality from these data therefore constitutes a cross-sectional monitoring of wild animal populations (Caughley 1966). Since Deevey Jr (1947), this type of monitoring has been used to estimate vital rate parameters and construct associated life tables. From these life tables, it is possible to provide age-specific vital rates to inform population dynamics matrix models such as Leslie's matrix model (Leslie 1945). It is also possible to explore the covariation of age-specific life-history traits to test certain life history theories (Purvis and Harvey 1995).

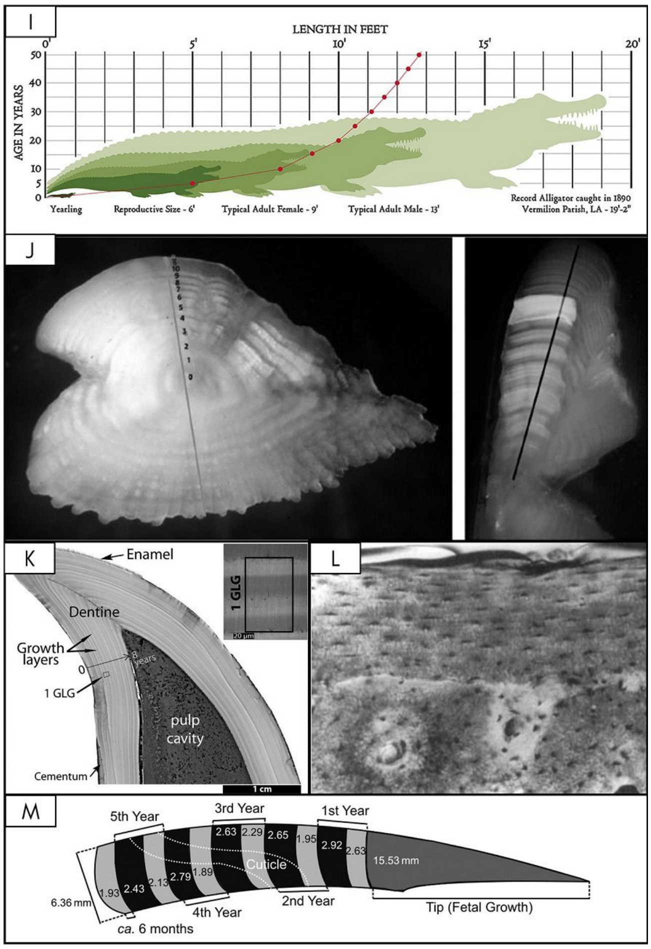

Figure 1.10: Exemples of possible cross-sectional monitorings.
I. Length-age relation for reptiles from `https://www.mcgeesswamptours.com/`.
J. Otholits for fishes from Knopp et al. (2012).
K. Growth layer groups in tooth from Martin et al. (2011).
L. Endosteal layers in tibia for birds from Klomp and Furness (1992).
M. Claws growth layer groups from E. O. Ferreira, Loseto, and Ferguson (2011).

However, the derivation of these rates is based on cross-sectional monitoring, which itself is based on basic assumptions that can be problematic (Caughley 1966). The most important assumption to take into account in this type of monitoring is that the age-at-death distribution obtained from the age-at-death data is representative of the stationary age distribution of the population (Caughley 1966). In other words, the sampled population must be in a stationary state (*i.e.* neither increasing nor decreasing) and there must be no selection bias of individuals at the time the data set is constructed (Caughley 1966). One problem is that mammal populations are rarely stationary in nature as they are in a con-

Preference for longitudinal monitoring

Longitudinal monitoring is preferred for species that offer adequate opportunities for longitudinal studies.

stant state of flux influenced by biotic and abiotic factors, which are themselves in a state of flux (Szuwalski and Hollowed 2016). Furthermore, when population dynamics studies are conducted, it is precisely to determine whether the population is viable because there is reason to believe that it is not (*i.e.* it is not stationary). The impetus for conducting a population dynamics study is often at odds with the basic assumption that must be made to conduct the study. Cross-sectional monitoring is associated with strong assumptions, unrepresentative data and the difficulty of trusting life history trait estimates. It is mainly for these reasons that cross-sectional monitoring has been abandoned in favour of longitudinal monitoring in species that offer adequate opportunities for longitudinal studies. Although cross-sectional monitoring is less expensive in terms of data collection (Seber 1965). In order to provide the best possible information on the demographic rates of these populations, it is necessary to carry out methodological developments associated with their monitoring. In particular, statistical developments through models integrating essential demographic parameters (*e.g.* frailty). This work would allow more accurate assessments of the viability of elusive mammal populations, taking into account various covariates and random effects.

Stationary and Stable age distributions

The concepts of stationary and stable age distribution are both related and different. If the population growth rate is constant over time, as are its fertility and survival rates, its age distribution will eventually take a stable form. Age frequencies will remain constant over time. When a population is stationary, the population growth rate is equal to 1. Therefore, the stationary age distribution is the stable age distribution for which the population remains constant over time. A stationary population necessarily has a stationary and stable age distribution, but a population with a stable age distribution does not necessarily have a stationary age distribution. The stationary age distribution is a special case of the stable age distribution. (Caughley 1966).

Table 1.2: Pros and cons of both monitoring schemes.

Monitoring	Strengths	Weaknesses	Key reference
Longitudinal	▶ Underlying processes are highlighted ▶ Individual differences to be highlighted ▶ Population growth rate are estimated directly	▶ Costly monitoring scheme ▶ May involve small samples	▶ Lebreton et al. 1992 ▶ Sandercock 2006
Cross-Sectional	▶ Include large parts of the population ▶ Allows to apply simple growth models ▶ Not very costly compared to longitudinal	▶ Does not highlight the changes an individual undergoes over the course of its life ▶ Low representativeness of the data if the time series is short ▶ Assumes the population to be at stationary age distribution	▶ Caughley 1966 ▶ Deevey Jr 1947

1.4 The case of the common dolphin population in the North-East Atlantic ocean

The common dolphin is the most abundant and widespread odontocete cetacean species in the North-East Atlantic Ocean and is associated with significant management issues (Peltier et al. 2021; Perrin 2018). It is a top predatory species in the North-East Atlantic ecosystems, with a possible (*i.e.* no formal recognition) keystone role in the Bay of Biscay (Corrales et al. 2022; Lassalle et al. 2011). The Bay of Biscay (Margin-Figure 1.11) is a biologically productive area of the North-East Atlantic associated with high fishing activity, involving for example pair trawlers and larger scale driftnets (between the Azores and Ireland) since 1986 (Peltier et al. 2021). The history of fisheries management in this area is closely linked to the common dolphin. Several legislative initiatives related to common dolphin mortality events in the area took place between 1985 and 2020 (Figure 1.12). As with other odontocete populations worldwide, the main threat to the common dolphin population in the waters of the North-East Atlantic, and in particular in the Bay of Biscay, is bycatch (M. A. Hall 1996; Peltier et al. 2016; ICES 2019).

Figure 1.11: Diagram of Bay of Biscay location.
Picture from `https://es.m.wikipedia.org/wiki/Archivo:Bay_of_Biscay_map.png`

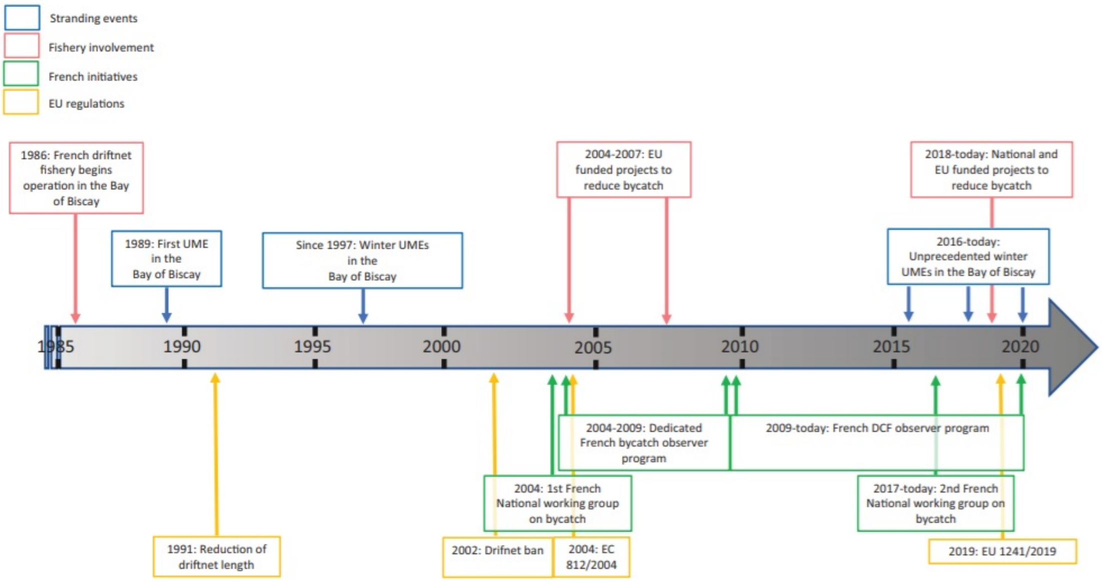

Figure 1.12: Main historical events in common dolphin bycatch management in the Bay of Biscay. DCF, Data Collection Framework; EC, European Commission; UME, unusual mortality event.
From Peltier et al. 2021.

Issues of the thesis project

It is necessary to assess the viability of the common dolphin population and to quantify the main human pressures (*i.e.* bycatch) on it in order to propose appropriate management objectives with regard to the conservation objectives of European waters. The common dolphin is defined here as an elusive species for which it is almost impossible to track individuals longitudinally through CMR or radiotagging protocols. Furthermore, despite the programmes for observing incidental catches at sea, it is difficult to quantify the actual number of common dolphins bycaughts in the Bay of Biscay. It is therefore difficult to know whether the number of dolphins removed is sustainable for the population, given its demographic viability. A study should be designed to make the best use of the cross-sectional analysis protocol to obtain the population's vital rates. This study should also make it possible to use data from at-sea observers to quantify bycatch. Finally, it should also allow the proposal of sustainable removal thresholds that do not threaten the viability of the population.

1.5 Project outlines

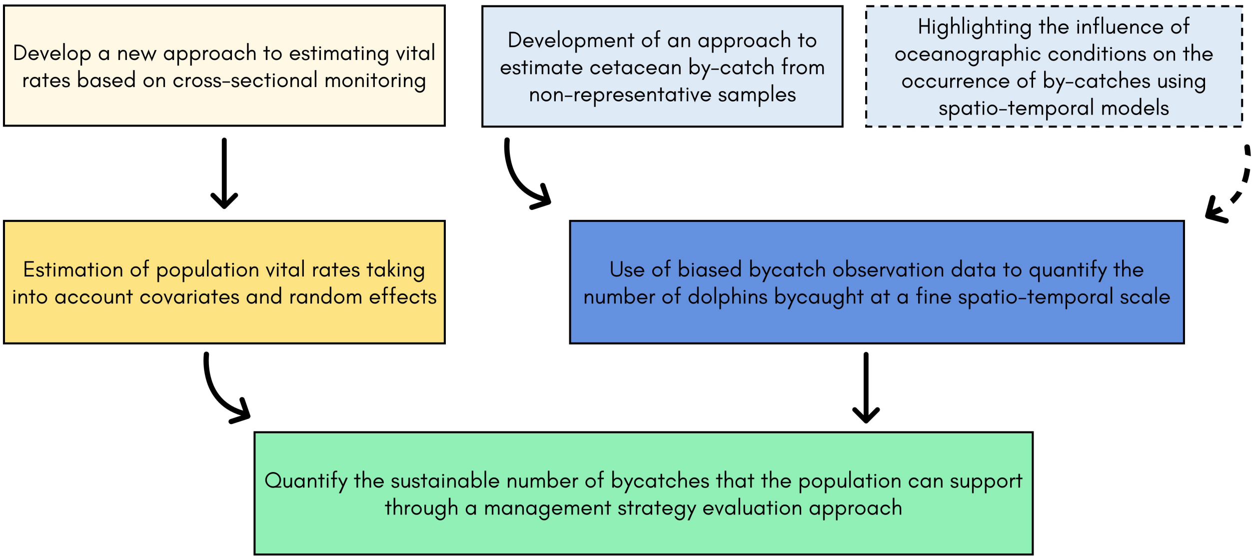

Figure 1.13: Flowchart of the thesis project.

The challenges of this thesis project are multiple and fall into two main categories. From an applied research point of view, it is now necessary to produce demographic indicators for small cetaceans in the North-East Atlantic and in particular for the common dolphin. These demographic rates are of interest from the point of view of the management of this population as they will provide information on its status in the context of the OSPAR Convention and the Marine Strategy Framework Directive. Some life history traits have been partially estimated and biological characteristics are already known but the need is still there. Secondly, given the apparent impact of fishing on the population in terms of additional mortality, it is essential to quantify this pressure. Finally, given the management issues related to the population, it is necessary to determine the maximum number of removal that the population can sustain in the current state of knowledge and by applying a precautionary principle. This limit constitutes a support point for public policies, in close collaboration with the European Commission. This work is therefore closely linked to the production of the ICES scientific expert groups' opinions and is sometimes cited in the reports of the working groups focused on the case of the North-East Atlantic common dolphin population. This thesis project therefore has a very applied basis.
In my opinion, it is important to place this applied basis in a more fundamental context. This recontextualisation is part of a desire to place the present work in the scientific history of the study of population dynamics. I believe that this work has its place as a reflection on the problem of studying the dynamics of elusive animal populations. It was therefore necessary to identify a methodological gap in terms of cross-sectional analyses and to partially fill it. A new approach to sample collection and vital rate modelling is proposed. A general discussion linking the work is also proposed.
The present manuscript summarises this three-year work in seven parts. The first part was the general introduction.

Chapter 2 is a description of the important aspects related to the common dolphin. This chapter is not intended for publication. It was written to provide an overview of the current state of knowledge on common dolphin demography and associated monitoring and conservation programmes.

Chapter 3 includes a description of survival analysis and a history of associated methodological developments. I then discuss the main problem identified and how we responded to it by developing a new method for estimating survival that takes into account covariates and random effects. This part was carried out during the first year of the project and was published: Rouby, Ridoux, and Authier (2021). I presented this work at the poster session of the World Marine Mammal Conference 2019[*].

Chapter 4 is the central part of the manuscript, from the point of view of writing and organisation of the project. It includes the acquisition of demographic data (age-at-death, reproductive-status-at-death) after the definition of a sampling plan respecting carefully chosen criteria. It also includes the analysis of these data using methods commonly accepted in the literature as well as those developed in the framework of the project. The highlight of this work is the estimation of the influence of several factors on the demographic rates of the North-East Atlantic common dolphin population. I will present this work orally at the Society for Marine Mammal Conference 2021[†]. This part was carried out during the 3 years of the project and is currently being prepared for publication.

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[*] `https://www.wmmconference.org/`

[†] `https://www.smmconference.org/`

Chapter 5 corresponds to the quantification of the human impact on the dolphin population through bycatch and to the explanation of bycatch by studying oceanography. The first part required a methodological development but my greatest contribution was the use of this method with an applied case. The strength of this approach is that it allows an estimate from biased bycatch observation data. This work led to the publication of the development of the method: Authier2021a and my contribution was essentially related to part of the writing of this manuscript. Concerning the application, I was able to use this method on the dolphin case study. This work is published: Rouby et al. (n.d.). This work was carried out in close collaboration with Ifremer (*Institut Français de Recherche pour l'Exploitation de la Mer*), which provided the data and participated in the writing of the article. This work was carried out during the second and third years of the project. I presented it in the ICES working groups WGBYC and WGMME. I also presented it at the ICES workshop WKMOMA.
The second part of the development of this chapter, concerning the influence of oceanography on bycatch, is for me the most collaborative part. It was carried out as part of a Master 2 internship that I co-supervised with the support of Matthieu Authier and Emilie Tew-Kaí from the Shom (*Service Hydrographique de la Marine Nationale*) in Brest. The Shom provided us with oceanographic model outputs allowing us to link the occurrence of mesoscale oceanographic structures to dolphin mortality at sea. This work has been published as: Gilbert et al. (2021). I have chosen not to include this section in its entirety as I was not at the heart of the data analysis. This part will serve as a basis for introduction in Chapter 5. This work was carried out during the second year of the project.

Chapter 6, deals with the management and conservation aspects of the common dolphin population. It includes the practical and conceptual use of the preliminary draft (including demographic rates and numbers of dolphins caught) to produce tolerable bycatch thresholds on a European scale. This part still needs to be refined in the analysis but is in preparation to be proposed for publication. This work was carried out during the last 5 months of the thesis project. It is not currently planned to valorise this work in the form of a conference.

THE PROJECT

The common dolphin in the North East Atlantic

2

2.1 Distribution and biology 28
2.2 Conservation and monitoring 33

The common dolphin is a long-lived delphinid species that presents important conservation challenges in European waters. Individuals of this species appear to live on average up to 25 years and produce between 3 and 8 pups per female during their lifetime (Perrin 2018). In European waters, there is a resident population that appears to number around 700,000 individuals (Hammond et al. 2017). Vital rates are already available for this population, including sexual maturity profiles and survival rates (Mannocci et al. 2012; Murphy et al. 2009). These rates appear to show that the population is not viable and will become extinct within 100 years. Since 1990, the number of dolphins found stranded on European shores has increased significantly (Murphy, Pinn, and Jepson 2013). In 2020, eighty percent of stranded dolphins showed signs of bycatch (Dars et al. 2020) and it is estimated that between 3,000 and 5,000 dolphins are bycaught each year(Peltier et al. 2016). The state of this population is worrying with regard to the conservation objectives set by the Habitats Directive and the MSFD (Peltier et al. 2021; Murphy et al. 2021). The common dolphin population is monitored both by aerial surveys and by collecting biological data on stranded individuals. This chapter presents the current state of knowledge on the North-East Atlantic common dolphin population. It also provides a description of each entity or instrument involved in the conservation of this population. Finally, it presents the different monitoring schemes carried out on the population.

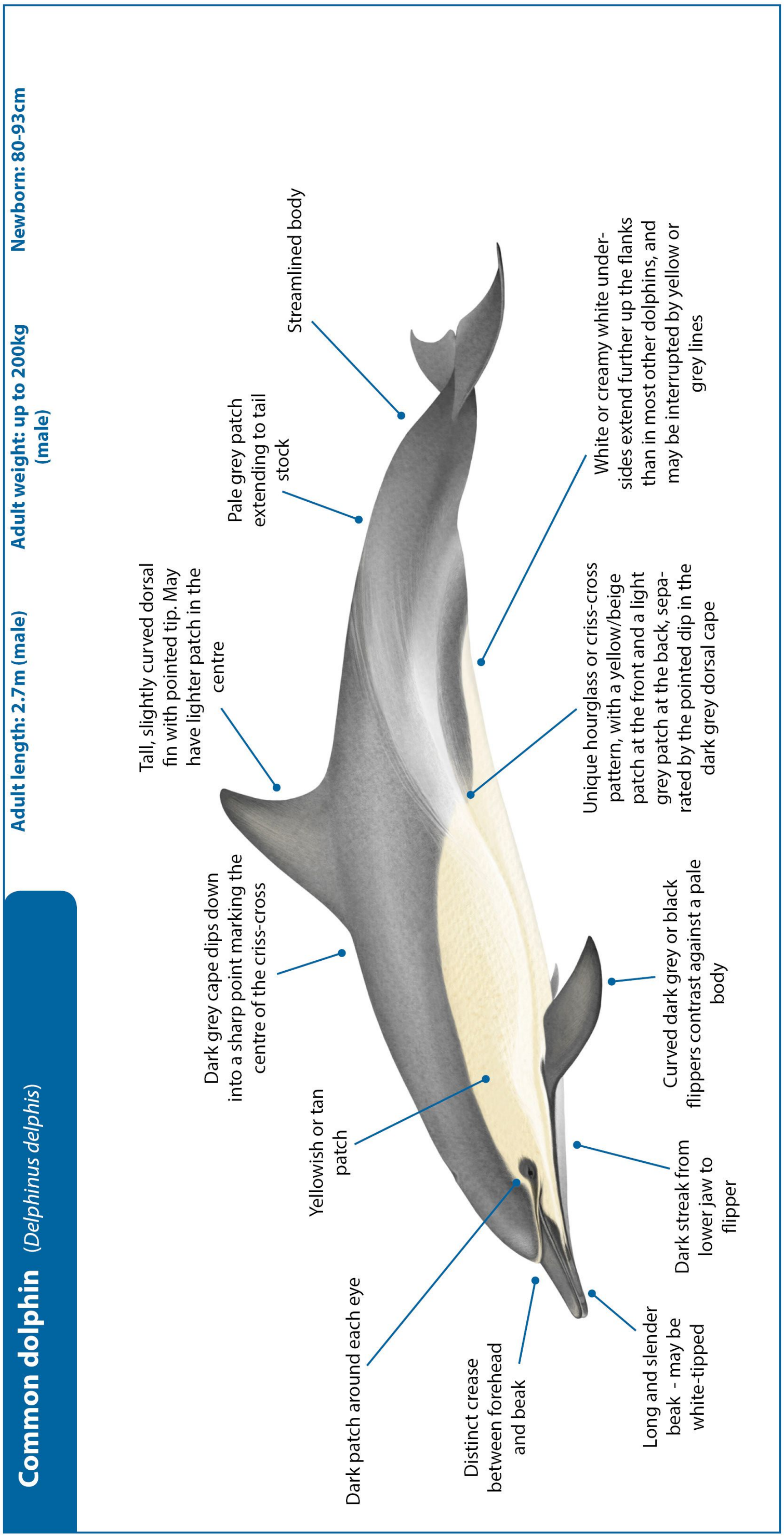

Figure 2.1: Common dolphin morphological recognition traits and morphological parameters. Figure from the International Whaling Commission handbook `https://wwhandbook.iwc.int/en/species/common-dolphin`

The common dolphin has undergone a recent change in phylogenetic classification. Within the odontocetes, it belongs to the family *Delphinidae* and the subfamily *Delphininae*. It belongs to the genus *Delphinus* which is closely related to the genera *Stenella*, *Lagenorhynchus*, *Sousa*, and *Tursiops* (Perrin 2018). Initially, two species of common dolphins were considered. The short-beaked common dolphin (*Delphinus delphis*) and the long-beaked common dolphin (*Delphinus capensis*). Recent genetic studies have modified the phylogeny of these species. Now, only one species of common dolphin is recognised (Committee on Taxonomy 2017). Within this species, there are 4 subspecies: the common dolphin (*Delphinus delphis delphis*), Eastern-North-Pacific long-beaked common dolphin (*Delphinus delphis bairdii*), Black Sea common dolphin (*Delphinus delphis ponticus*) and Indo-Pacific common dolphin (*Delphinus delphis tropicalis*) (Cunha et al. 2015; Margin-Figure 2.2).

The subspecies studied here

Throughout the manuscript and subsequent chapters, when the term "common dolphin" is used, it will refer to the current subspecies of common dolphin *Delphinus delphis delphis* and to the former species considered in the classification as the short-beaked common dolphin *Delphinus delphis*. The name common dolphin (and its Latin name *Delphinus delphis* in figures) will be used to designate this subspecies only and it will be the only one studied in this project.

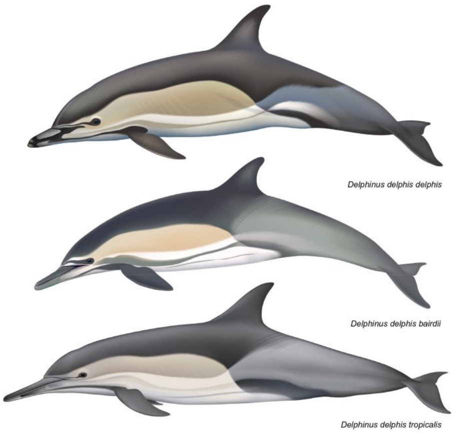

Figure 2.2: Common dolphin oceanic subspecies.
Figure from Perrin (2018), illustration by Uko Gorter.

2.1 Distribution and biology

On a global scale

The common dolphin is a widely distributed odontocete cetacean species with a known life cycle. Its distribution ranges from tropical to temperate waters across the globe (Perrin 2018; Figure 2.3). This species occupies both oceanic and continental shelf habitats. It appears to exhibit seasonal distributional movements, sometimes linked to changes in water temperature (Perrin 2018; E. E. Henderson et al. 2014). Individuals may form groups ranging in size from a few hundred to a thousand.

The common dolphin is a long-lived species, with a maximum recorded lifespan of 30 years (Perrin 2018). It is an iteroparous species with a calving interval of approximately 2-4 years. The gestation period is estimated to be 10-12 months. Maximum length is about 270cm for males, which are slightly longer than females. Calves at birth measure 80-90cm. The life history traits of the species have common characteristics but are population dependent. In Table 2.1, characteristics (including age at sexual maturity) are presented for several common dolphin populations.

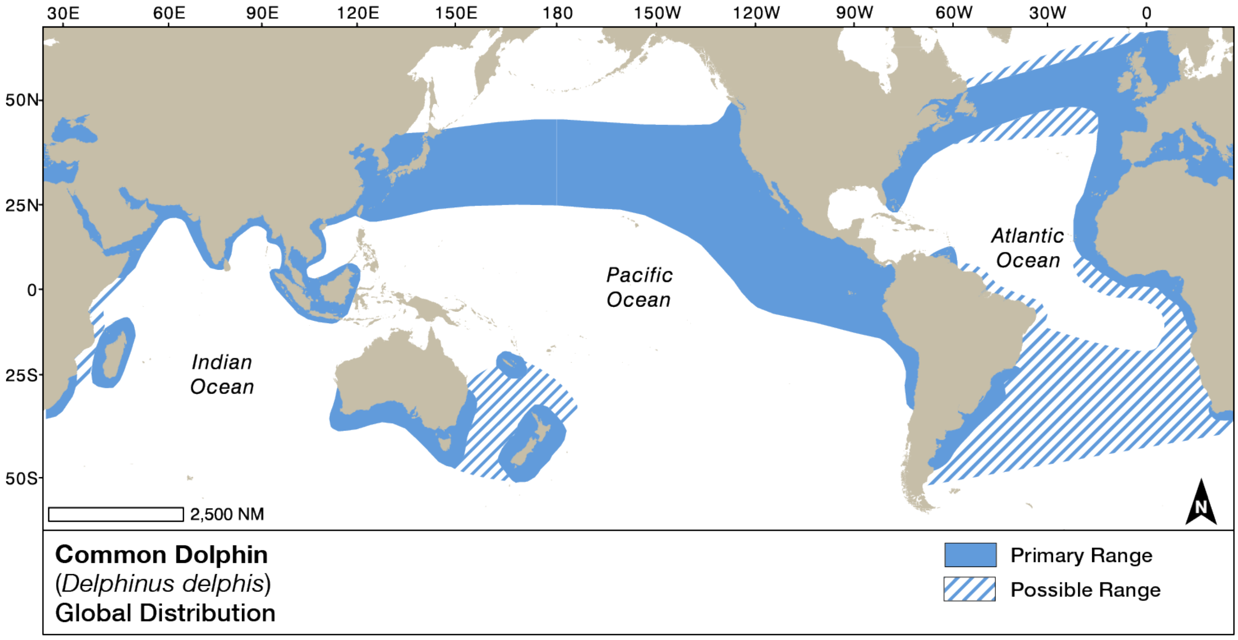

Figure 2.3: Global distribution of the common dolphin. The species is distributed in temperate and tropical waters. It is distributed in several populations.

Table 2.1: World common dolphin populations features. This table summarises some important current knowledge about the global populations of common dolphins.
Table from Murphy et al. (2021).

Area	**Climate**	**Sample period**	**Mating period**	**Age at sexual maturity**	**Dataset**
North-East Atlantic	Temperate	1990-2006	May-September (spring-summer)	8.22 years	Murphy et al. (2009)
North-West Atlantic	Temperate	1989-1998	July-August (summer)	8.33 years	A. J. Westgate and A. J. Read (2007)
Tropical-East Pacific	Tropical	1979-1993	Calve all year round	7.8 years	Danil and Chivers (2007)
North Pacific	Temperate	1990-1991	May-June (spring)	8 years	Ferrero and Walker (1995)
New Zealand	Temperate	1992-2012	Primarily austral summer	NA	Institute of Zoology (2015)
South Africa	Temperate	1969-1988	Austral summer	8-9 years	Mendolia (1990)

In the North East Atlantic and European waters

In European waters, the population appears to be abundant and absent from some areas. The common dolphin population appears to be distributed in both oceanic and continental shelf waters. However, common dolphins are rarely recorded in the Eastern Channel and North Sea. The highest densities and abundances of animals are found on the continental shelf (Hammond et al. 2017, 2013; Laran et al. 2017). The population in European waters is currently estimated at 634,286 individuals (352,227 - 1,142,213) while 493,591 (342,094 - 718,593) individuals are estimated in the Bay of Biscay (Hammond et al. 2017; high density area: Figure 2.4). The history of abundance estimates is provided in the Supplementary-Table 1.

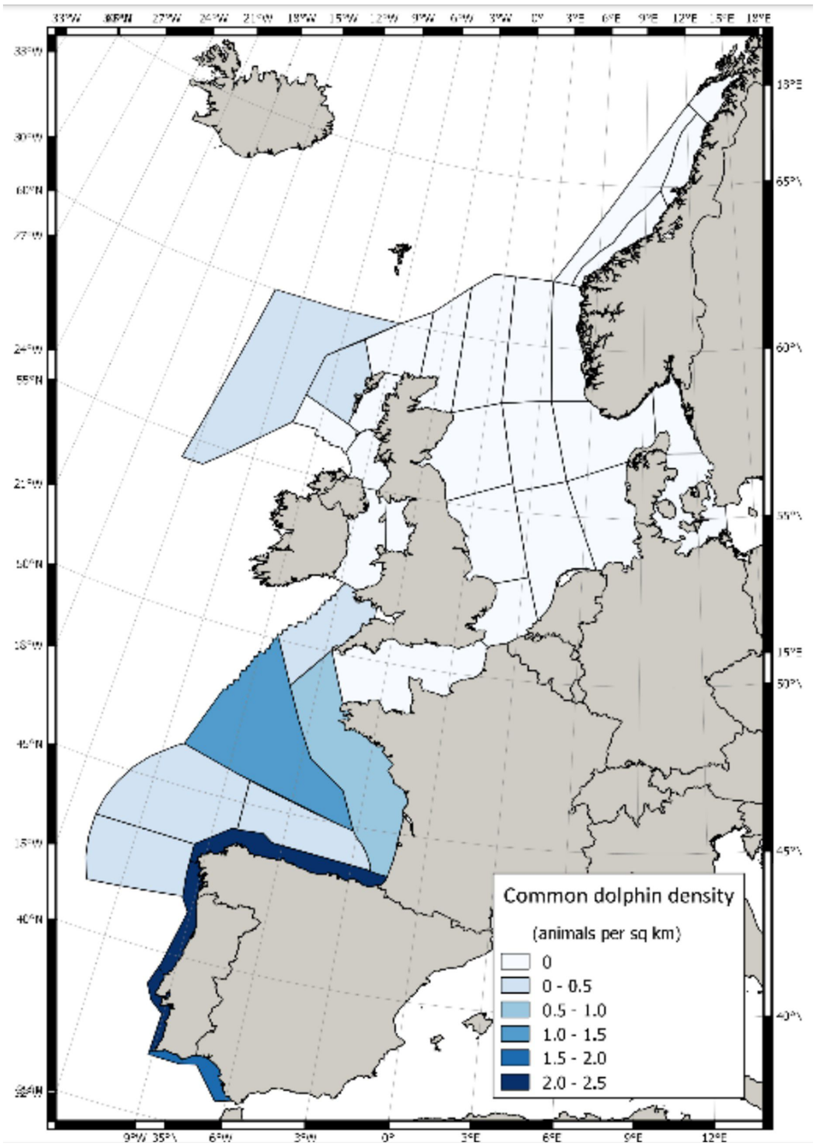

Figure 2.4: Common dolphin density within the North-East Atlantic. The density of common dolphins is expressed as animals/km^2. The highest densities are recorded for the continental shelf areas associated with the Bay of Biscay. The Celtic Seas and the oceanic part of the Bay of Biscay also have high densities, as well as the Spanish-Portuguese and Galician coasts. The English Channel and the North Sea, on the other hand, have low densities. These estimates are made in the framework of the SCANS III monitoring programme. Figure from Hammond et al. (2017).

Some life history traits and demographic parameters are known for this population. The studies highlight important demographic parameters such as the age distribution of the population, the proportion of mature females at each age and even the survival profile of females. It is only possible to monitor the population cross-sectionally. Published examples of biological data are provided in Figure 2.6 but there are unpublished datasets such as the one shown in the Margin-Figure 2.5. The maximum age recorded in the population is 29-30 years and longevity appears to be around 20-25 years. The age at sexual maturity of females varies slightly between studies but appears to average over 8 years (Mannocci et al. 2012; Murphy et al. 2009).

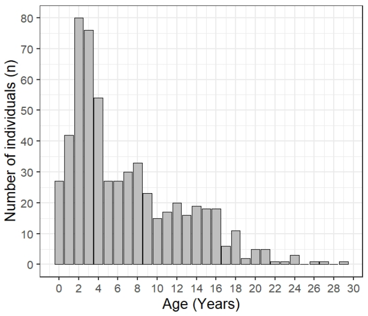

Figure 2.5: Common dolphin age-at-death data. These age-at-death were obtained on stranded dolphins. Data are from Saavedra (2018). Data are not published and do not have associated survival estimates. However, it is possible to estimate the survival, mortality and viability of the population based on the protocol detailed in the study.

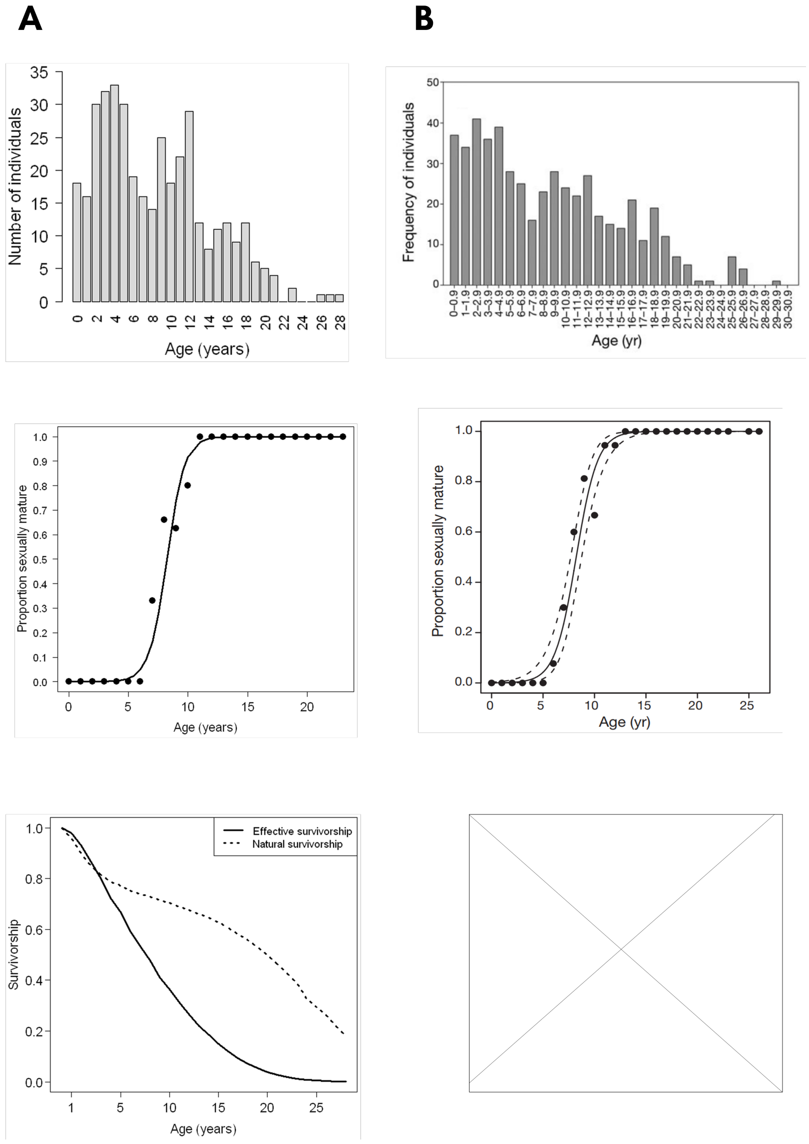

Figure 2.6: Age at death and vital rates data available for the population. Three types of biodemographic parameters are presented. The first line is age-at-death. The second is sexual maturity profiles of females. The third is the estimated survivorship of the population which is only available for study A.
Column **A** corresponds to the study Mannocci et al. (2012).
Column **B** corresponds to the study Murphy et al. (2009).
Figures are extracted from these studies.

Since the 1990s, an increasing number of common dolphins have been found stranded on European seashores. Among the European countries, France is the country with the highest number of stranded common dolphins on its beaches (Figure 2.8). In France, the number of individuals found is increasing almost constantly, with a stranding record of 1298 individuals for the year 2020 (Margin-Figure 2.7; data provided by *Observatoire Pelagis*). This phenomenon is notably characterised by Unusual Mortality Events (UME) that are seasonal (Peltier et al. 2021). The majority of dolphins stranded during the year are stranded in winter, from January to April (Dars et al. 2020). A significant proportion of stranded dolphins show evidence of capture in fishing gear. From 1990 to 2019, the number of stranded dolphins with evidence of incidental capture was approximately 205 ± 177 whereas from 2016 to 2019 this number increases to 520 ± 172 (Peltier et al. 2021; Dars et al. 2020). Examples of evidence of bycatch on stranded common dolphins are provided in Figure 2.19 at the end of this chapter.

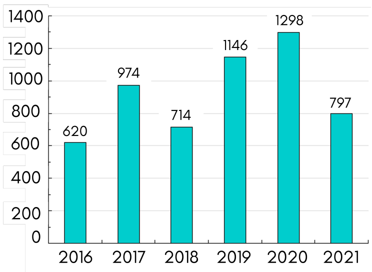

Figure 2.7: Common dolphin strandings in France from 2016 to 2021. Data from Observatoire Pelagis.

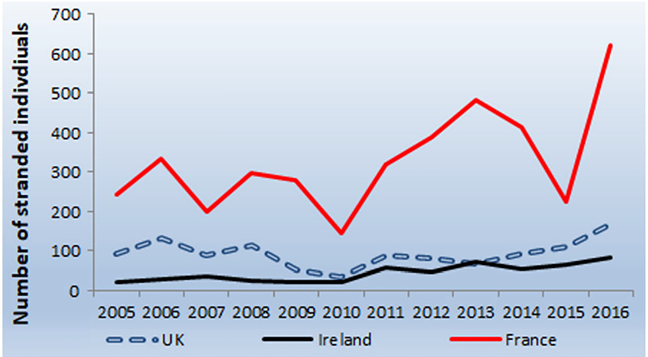

Figure 2.8: Common dolphin stranding records in Europe from 2005 to 2016. Only three countries are represented as these are the ones with the most strandings of common dolphins in Europe. France is the country with the most. It can be seen that the trend has been upwards since the early 2000s for all three countries, particularly France.
Figure from Murphy et al. (2021).

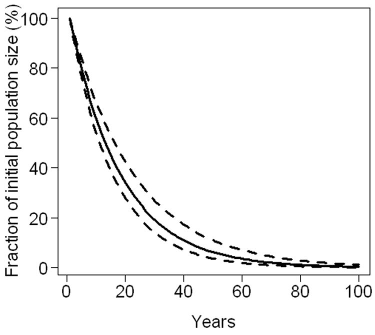

Figure 2.9: Projected population trend. From the vital rates obtained in their study, Mannocci et al. (2012) projected the evolution of the population from the growth rate estimated by Leslie's matrix model. It appears that the population will become extinct within the next 100 years.
Figure from Mannocci et al. (2012).

It is estimated that around 4,000 dolphins are incidentally caught in fishing gear each year in the Bay of Biscay (Peltier et al. 2016), which could pose a major threat to the viability of the population. Bycatch pressure appears to have increased since the late 1990s and is now a recurring pressure on the population (Peltier et al. 2021). From 2016 to 2018, the number of incidental captures of common dolphins has been estimated at between 5,000 and 10,000 (Peltier et al. 2020). This recurrent incidental capture pressure is a point of concern for the viability of the population. The mortality suffered by the population is in the order of 0.9% to 5.7% of its total abundance each year[1] (Peltier et al. 2016). Mannocci et al. (2012) projected its abundance over the next 100 years (after 2006) using the vital rates depicted in Figure 2.6 panel A. It appears that the population would not be viable. Data collected for population projections, and to quantify the number of incidental catches in absolute terms and relative to the total population abundance, are obtained from population monitoring programmes. The main types of monitoring associated with the common dolphin, as well as the main legislations and its current conservation status, are

[1] 1: whole NE Atlantic population.

presented in the following section.

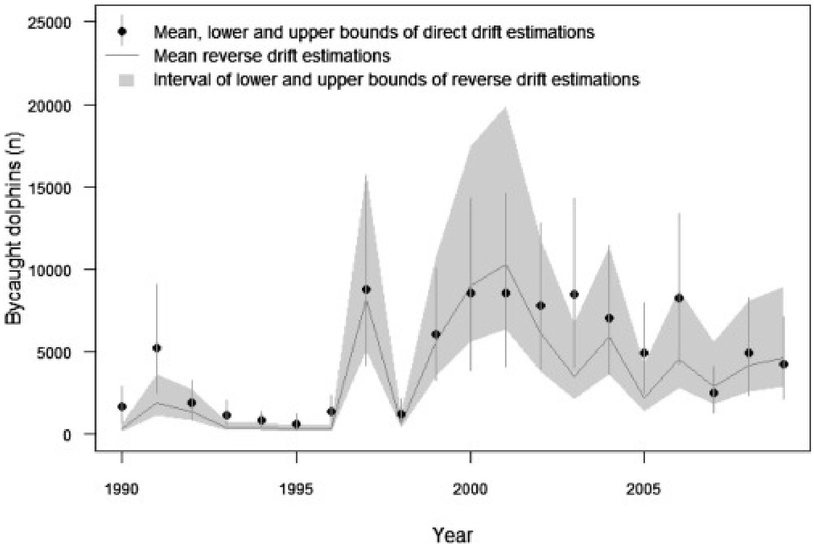

Figure 2.10: Common dolphin bycatch estimates from strandings. Estimation was done was made to cover the time series from 1990 to 2016. It was done using direct drift modelling (black points, associated with the confidence interval in grey bars), and using reverse drift modelling (grey polygon). These estimates use the dolphin's drift trajectory corrected by the probability of being buoyant (24%), stranded (depending on drift conditions) and discovered (95%). Drift conditions are weather dependent and are modelled by the meteo France drift model MOTHY. For more information on the method see Peltier et al. (2016) from which the figure is taken.

2.2 Conservation and monitoring

In the North East Atlantic and European waters

The conservation status of the common dolphin differs according to the instrument or regulation used. At the international level and independently of populations, the species is currently classified as being of least concern on the IUCN[2] Red List of Threatened Species (Perrin 2018). Its international conservation status is that of a protected species under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which has listed it in Appendix II (Perrin 2018; CITES 2021). On a global scale, the species is therefore not listed as threatened but as a protected species.

The conservation status of the population in European waters is less favourable and conservation objectives associated with monitoring programmes have been set up on a European scale. The Habitat Directive[3] (European Directive on the conservation of natural habitats and of wild fauna and flora, 92/43/EEC) is an instrument of European environmental legislation. The objective of this instrument is to achieve a favourable conservation status for listed species and habitats, including the common dolphin (listed as a species in need of strict protection under Annex IV). In 2007, the conservation status of the common dolphin population was assessed as "Unknown". Since 2013, it is now assessed as "Unfavourable-Inadequate" in European Atlantic waters and "Unfavourable-Bad" within French waters (Murphy et al. 2021).

[2] Common dolphin as a species is considered Least Concern on the IUCN list and is included in Appendix II of CITES.

[3] The Habitat Directive classifies the North-East Atlantic population as Unfavorable-inadequate.

In order to promote the conservation status of the common dolphin in European waters, the European Commission adopted in 2004 the Bycatch regulation[4] (Regulation no. 812/2004) which encompasses requirements for bycatch monitoring schemes with on-board observers schemes to be set up for vessels ≥15m (length), and the implementation of pilot studies for vessels less than this size. It also provides for the application of bycatch mitigation measures using acoustic deterrent devices in areas and fisheries that are either known or foreseen to have high levels of bycatch (vessels ≥12m). This regulation is no longer in use and has been replaced by the new bycatch regulation (Regulation no. 2019/1241). It is within this framework of regulating catches and estimating their value that the Observer programmes, such as "Obsmer"[5] , have been set up. However, they are not dedicated to bycatch and are carried out under the Direction Framework of the Common Fishery Policy[6] . More details on this dataset and its use will be provided in Chapter 5.

Data acquisition to achieve conservation objectives is also part of the Marine Strategy Framework Directive(EU MSFD[7] ; Directive 2008/56/EC). It establishes a framework within which Member States shall take the necessary measures to achieve or maintain "Good Environmental Status" (GES) of marine environment. This European directive defines descriptors of good environmental status of ecosystems. Within these descriptors, criteria are also defined to enable the achievement of this good environmental status. Among these criteria, we find, for example, the need for biological indicators linked to the demography of the common dolphin. All the descriptors and criteria important for the common dolphin in terms of demography are detailed in Chapter 4.

In support of established conservation policies and conservation objectives, international expert groups or agreements can operate. The International Council for the Exploration of the Sea (ICES[8]) is an Intergovernmental marine science organization which aims to synthesise and coordinate scientific work to achieve the legislative objectives set by the European Commission and provides science advice to environmental ministries and international agencies (such as OSPAR). ICES defines ecoregions (based on ecosystems) and statistical areas (based on important fishing areas) (Figure 2.11). With regard to the common dolphin population, ICES works on its status mainly in two working groups. The first is the Working Group on Marine Mammal Ecology (WGMME). The second is the Working Group on Bycatch of Protected Species (WGBYC).

[4] Bycatch regulation (Regulation no. 812/2004), now replaced by the bycatch regulation (Regulation no. 2019/1241) defined monitoring and bycatch mitigation schemes.

[5] `https://sih.ifremer.fr/Ressources/ObsMer`

[6] `https://www.instituteforgovernment.org.uk/explainers/common-fisheries-policy`

[7] The MSFD sets the goal of good environmental status for European waters. This status is described by descriptors whose state is informed by criteria. Criteria of relevance to the population will be detailed in Chapter 4

[8] The ICES Scientific Expert Group advises governments on how to achieve the conservation objectives of the Habitats Directive and the MSFD.

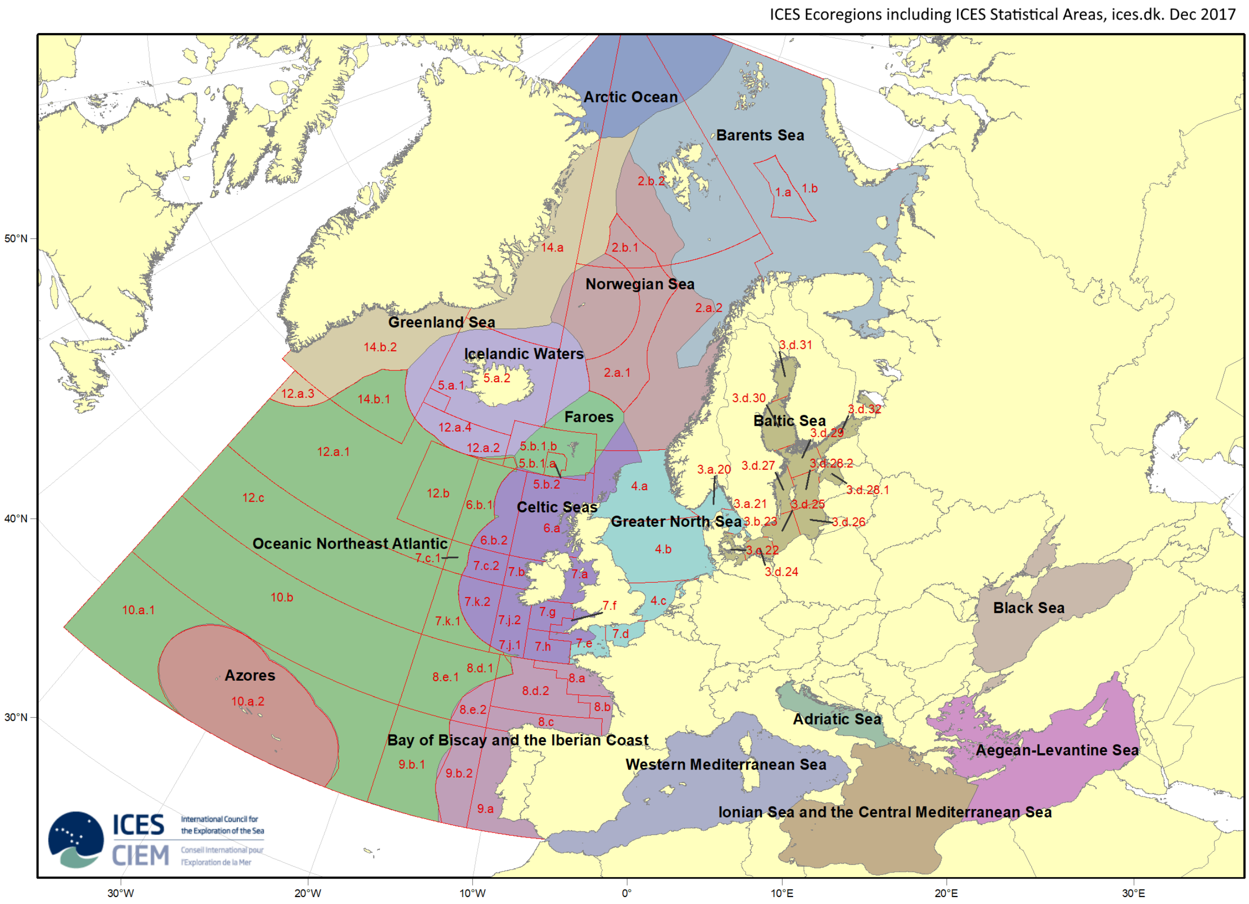

Figure 2.11: Ecoregions and statistical areas defined by ICES within the OSPAR area of the North-East Atlantic. The OSPAR area is divided by ICES into several ecoregions defined on the basis of biogeographic and oceanographic features and existing political, social, economic, and management divisions. Another division is made by taking into account statistical areas. These area are linked to ICES fishing areas are developed from historical links between an area and the collection of fisheries statistics.
Figure from `https://www.ices.dk/Pages/default.aspx`.

The Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas (ASCOBANS[9]) aims to promote the achievement of European conservation objectives, in particular with regard to cetaceans, under the auspices of the United Nations. It focuses on the achievement of cetacean-related conservation objectives and provides Member States with recommendations for achieving these objectives. The agreement takes place within a defined area in European waters (Figure 2.12). It is within the framework of this agreement that the limit of 1.7% for total anthropogenic removal has been defined, using the harbour porpoise (*Phocoena phocoena*, Linnaeus 1758) as a case study[10] . On 30 August 2019, ASCOBANS proposed the Species Action Plan (SAP) for the North-East Atlantic population of common dolphins. This action plan sets targets to address the threats facing the population. It includes a series of research, mitigation and monitoring actions to improve the conservation status of the population. The SAP seeks to involve a variety of stakeholders, including national agencies,

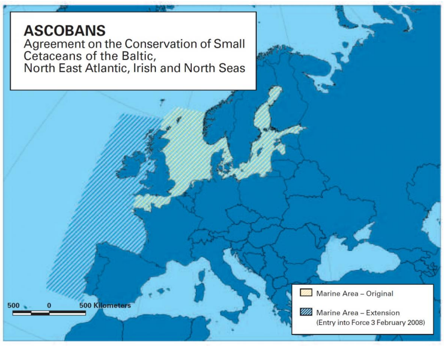

Figure 2.12: ASCOBANS Marine area. Originally, the area was restricted to English Channel, North Sea and Baltic Sea. From the 3 February of 2008, the area now takes into account Bay of Biscay, Celtic seas and offshore Portugal waters.
Figure from `https://www.ascobans.org/en/legalinstrument/ascobans`.

intergovernmental organisations, non-governmental organisations and regional bodies.

The Convention for the Protection of the Marine Environment of the North-East Atlantic[11] (OSPAR Convention) aims to periodically assess the state of the marine environment, partly in European waters. This convention originated in 1972 with the Oslo convention.It has been ratified by 15 governments and the European Union. The Convention entered into force on 25 March 1998. The OSPAR Commission provides a forum through which the 16 contracting parties coordinate international cooperation on the protection of the marine environment of the North-East Atlantic. It shares common regulation and management of human activities (except fisheries). It facilitates the coordinated implementation of the MSFD, with the aim of achieving "Good Environmental Status" in European waters. It sets out recommendations for achieving the objectives of the Habitats Directive and the MSFD. In 2017, OSPAR implemented the "OSPAR Intermediate Assessment 2017"[12] . This assessment aims at developing OSPAR's knowledg of the marine environment of the North-East Atlantic and its current status. It provides an update of the 2010 assessment and introduces some new indicators and assessment methodology. Within this framework, five regions have been defined within a maritime area (Margin-Figure 2.13).

In order to inform on the conservation status of small cetaceans and to assess their status in the light of the objectives of the Habitat Directive and the MSFD, a series of abundance surveys have been carried out. These abundance surveys are referred to as "Small Cetaceans in European Atlantic waters and the North Sea", (SCANS surveys and CODA which is a complement to SCANS II). These programmes take into account both aerial and ship-based monitoring. The first one was carried out in 1994 under the name SCANS (Hammond et al. 2002). Sampling was carried out mainly by ship from 26 June to 3 August (summer) and did not involve the Bay of Biscay. The next one was SCANS II in 2005 (Hammond et al. 2013). Sampling included the Bay of Biscay continental shelf and more extensive aerial monitoring from 27 June to 4 August (Summer). In addition to SCANS II, the CODA programme was carried out in 2007 to cover the non-continental part of European waters. The latest monitoring programme is SCANS III, conducted in 2016 (Hammond et al. 2017). This time, the continental shelf was sampled almost exclusively by aircraft, while the oceanic part was sampled by boat. Sightings of common dolphins within the framework of this programme are presented in Margin-Figure 2.14 and are the data allowing to estimate their abundance and density as presented in Figure 2.4 above. Sampling took place between 27 June and 4 August 2016 (Figure 2.15).

[9] ASCOBANS is an intergovernmental agreement focused on pressure mitigation and monitoring of small cetacean populations in European waters.

[10] `https://www.ascobans.org/en/species/threats/bycatch`

Figure 2.13: OSPAR Maritime Area. This area is divided into five Regions for assessment purposes: Arctic Waters (I), Greater North Sea (II), Celtic Seas (III), Bay of Biscay and Iberian Coast (IV) and Wider Atlantic (V). Figure from `www.ospar.org`

[11] The OSPAR Convention has led to the creation of the OSPAR Commission, which is involved in monitoring, advising and setting legislative constraints on the actions of EU Member States to achieve the conservation objectives of the EU waters.

[12] `https://oap.ospar.org/en/ospar-assessments/intermediate-assessment-2017/`

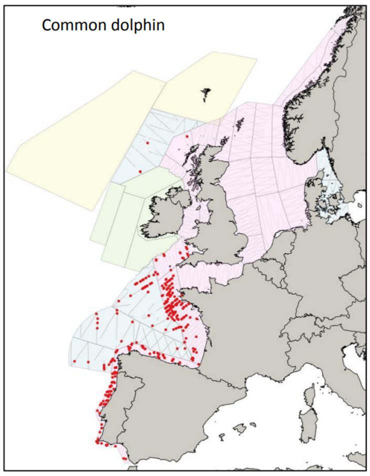

Figure 2.14: Common dolphin sightings from SCANS III surveys. Figure from Hammond et al. (2017).

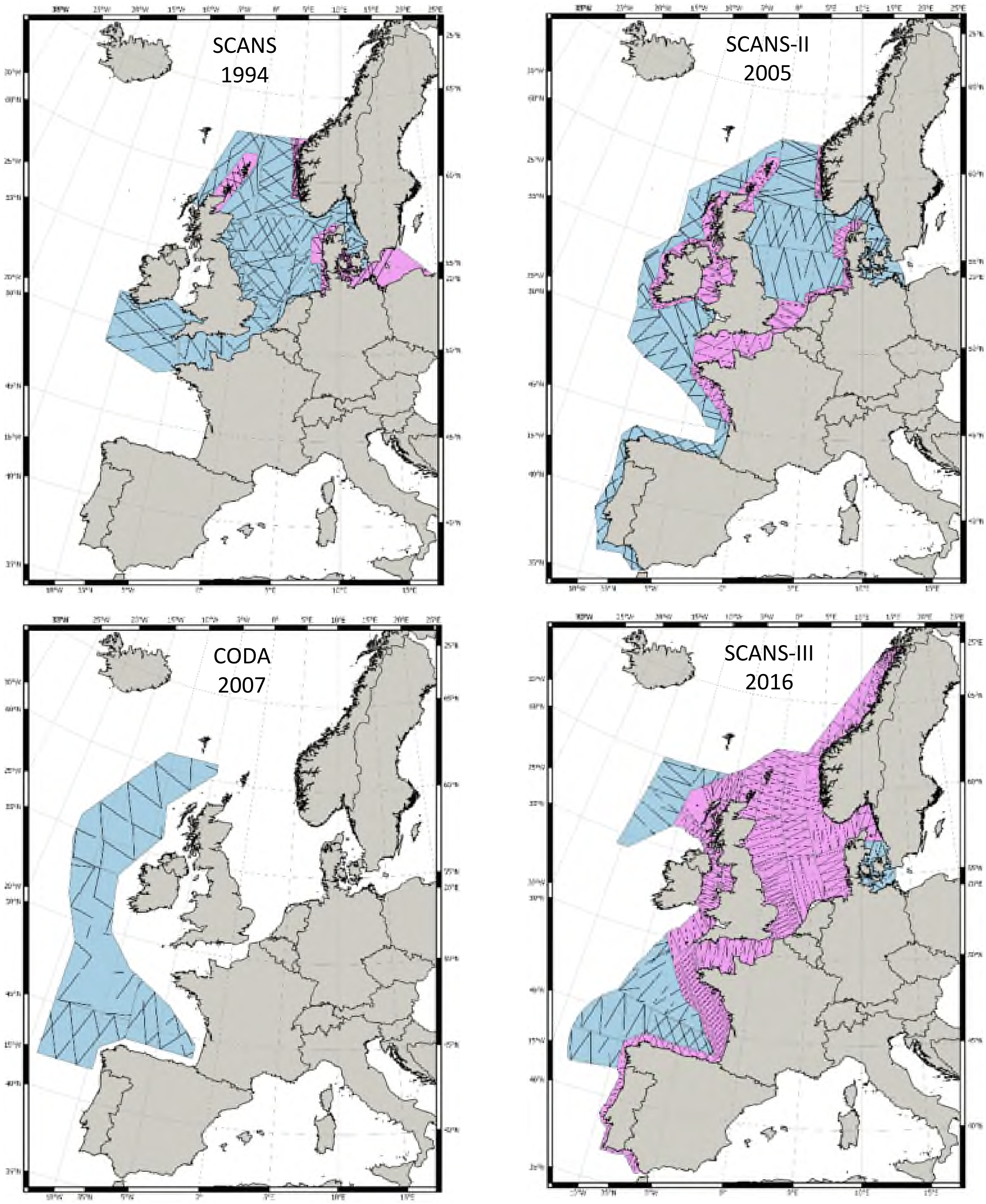

Figure 2.15: Sampling plans of the SCANS and CODA surveys. Transect solid lines are the covered effort. Blue areas were surveyed by boat and pink areas were surveyed by planes. Campaigns made were conducted for SCANS in 1994 (topleft), SCANS-II in 2005 (topright), CODA in 2007 (bottom left) and SCANS-III in 2016 (bottom right).
Figure from Hammond et al. (2017).

Table 2.2: Summary of tools, legislative instruments and organisations relevant to the conservation status of the North-East Atlantic common dolphin population.

Instrument/Tool/Organization	Type	Year	Application scale
IUCN - International Union for Conservation of Nature Red List of Threatened Species	Non Gouvernemental Organization	1964	Worldwide
ICES - The International Council for the Exploration of the Sea	Intergovernmental marine science organization	1964	North-Atlantic
CITES - Convention on International Trade in Endangered Species of Wild Fauna and Flora	International agreement	1979	Worldwide
ASCOBANS - Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas	International agreement	1991	European waters
HD - Habitats Directive	European Directive	1992	European waters
OSPAR - Convention for the Protection of the Marine Environment of the North-East (Oslo-Paris)	International legislative instrument	1998	European waters
Bycatch Regulation no. 812/2004[a]	European regulation	2004	European waters
MSFD - Marine Strategy Framework Directive	European Directive	2008	European waters
CFP - Common Fisheries Policy	Fisheries policy of the European Union	2014	European waters
Bycatch Regulation no. 2019/1241	European regulation	2019	European waters

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[a] repealled in 2019

Current management unit for the common dolphin in the North-East Atlantic

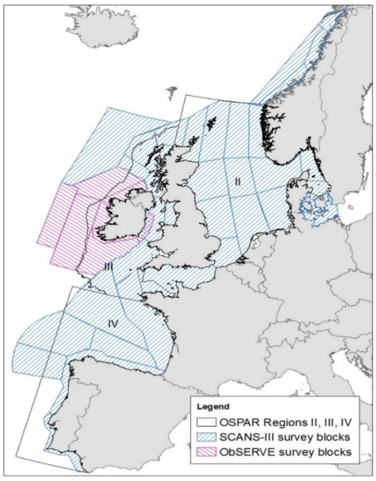

Figure 2.16: SCANS-III and ObSERVE surveys areas that approximate the North East Atlantic Assessment Unit. OSPAR Regions depict the AU proposed by ICES (2014).
Figure from ICES (2021a).

To manage the common dolphin population, several management units have been proposed in the North-East Atlantic Ocean (ICES 2021a). On the basis of ecological tracers (stable isotopes, fatty acids, metal tracers, stomach contains), two management areas should be considered for the management of the common dolphin with oceanic and neritic ecological stocks (Caurant et al. 2009; Lahaye et al. 2005). Based on the low genetic differentiation throughout the North-East Atlantic, it is commonly admitted that common dolphins can be managed as a single management area (Murphy, Pinn, and Jepson 2013). In order to support the study and conservation of the common dolphin in the area covered, ICES WGBYC and OSPAR have defined the population as a single management unit based on genetic analyses (Murphy et al. 2021; ICES 2014, 2021a). The area of the proposed management unit for North-East Atlantic common dolphins covers OSPAR Regions II (Greater North Sea), III (Celtic Sea) and IV (Bay of Biscay and Iberian coast) (Margin-Figure 2.16 regions along with SCANS III and ObSERVE surveys blocks).

In France

The monitoring of the common dolphin population in French waters is mainly carried out in two ways. The first approach is a monitoring based on abundance surveys. In addition to the SCANS campaigns presented above, the seasonal SAMM abundance campaigns (Laran et al. 2017) were conducted (only in French waters) between November 2001 and February 2012 for the winter part and between May and August 2012 for the summer part (Figure 2.18). The objective of these campaigns is to explore seasonal changes in the abundance of small cetaceans in French waters to inform the Habitat Directive and the MSFD. These campaigns have highlighted a seasonal change in abundance of common dolphins in the Bay of Biscay. In winter, their abundance (estimated jointly with the stripped dolphins) was estimated at 285,000 (95% CI: 174,000-481,000) individuals compared to 494,000 in summer (95% CI: 342,000-719,000). These surveys provide information on biological indicators of abundance for common dolphins within the MSFD.

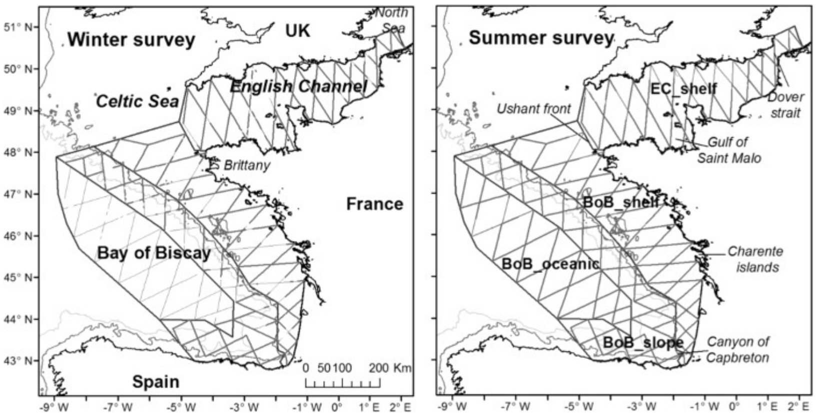

Figure 2.17: Sampling plans of the SAMM surveys. Surveys were conducted between November 2001 and February 2012 (winter part) and between May and August 2012 (summer part).
Figure from Laran et al. (2017).

The other type of monitoring carried out in France is the monitoring of marine mammals strandings. This monitoring is carried out by the french national stranding network (*"Réseau National Echouage"*) which covers the entire French coastline (metropolitan France + DOM-TOM). This network was created in 1970 by Dr. Duguy Raymond[13] and today consists of around 500 trained volunteers. The French National Stranding Network is coordinated by the Observatoire Pelagis (CNRS/La Rochelle University), mandated by the French Ministry in charge of the environment. The observatory trains volunteers to collect samples according to a strict and standardised protocol (Van Canneyt et al. 2015). When a dolphin washes up on the beach, it is reported to the Pelagis observatory (often by citizens). The observatory sends a volunteer to the site to establish an initial diagnosis on the cause of death and to take biological samples, which vary according to the animal's state of decomposition (Figure 2.20 and Figure 2.19). Stranding reporting rates handled by the RNE are considered stable since the 1990s. The observed increases in strandings are therefore not due to a difference in reporting over this period but to other factors such as increased bycatch (Authier et al. 2014). The biological samples collected in this project were collected by the RNE.

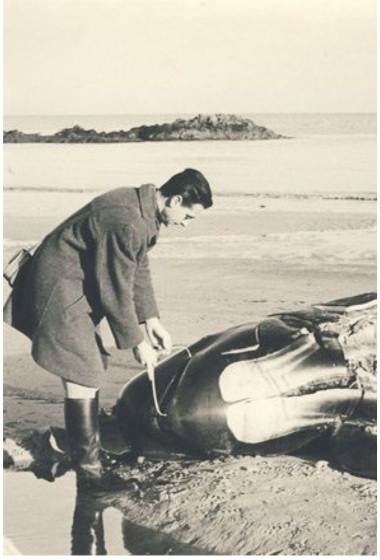

Figure 2.18: Dr. Duguy Raymond. Photo from `https://www.observatoire-pelagis.cnrs.fr/dr-raymond-duguy/`.

We have seen that the common dolphin population is subject to major conservation issues in European waters. In particular, there is a need for demographic data within the framework of the MSFD, which must complement the abundance surveys carried out. Demographic data on this population are already available, including vital rates such as survivorship. However, survivorship is obtained using survival analysis methods that are not very flexible. In the next chapter, we will see a recent methodological development, which allows us to obtain survivorship curves by taking into account the effects of covariates and inter-individual frailty.

[13] Link to a historical video on the stranding of pilot whales at "Ile d'Yeu" in 1963 `https://dai.ly/xp3zp7`. More informations on Dr. Duguy Raymond in `https://www.observatoire-pelagis.cnrs.fr/dr-raymond-duguy/`

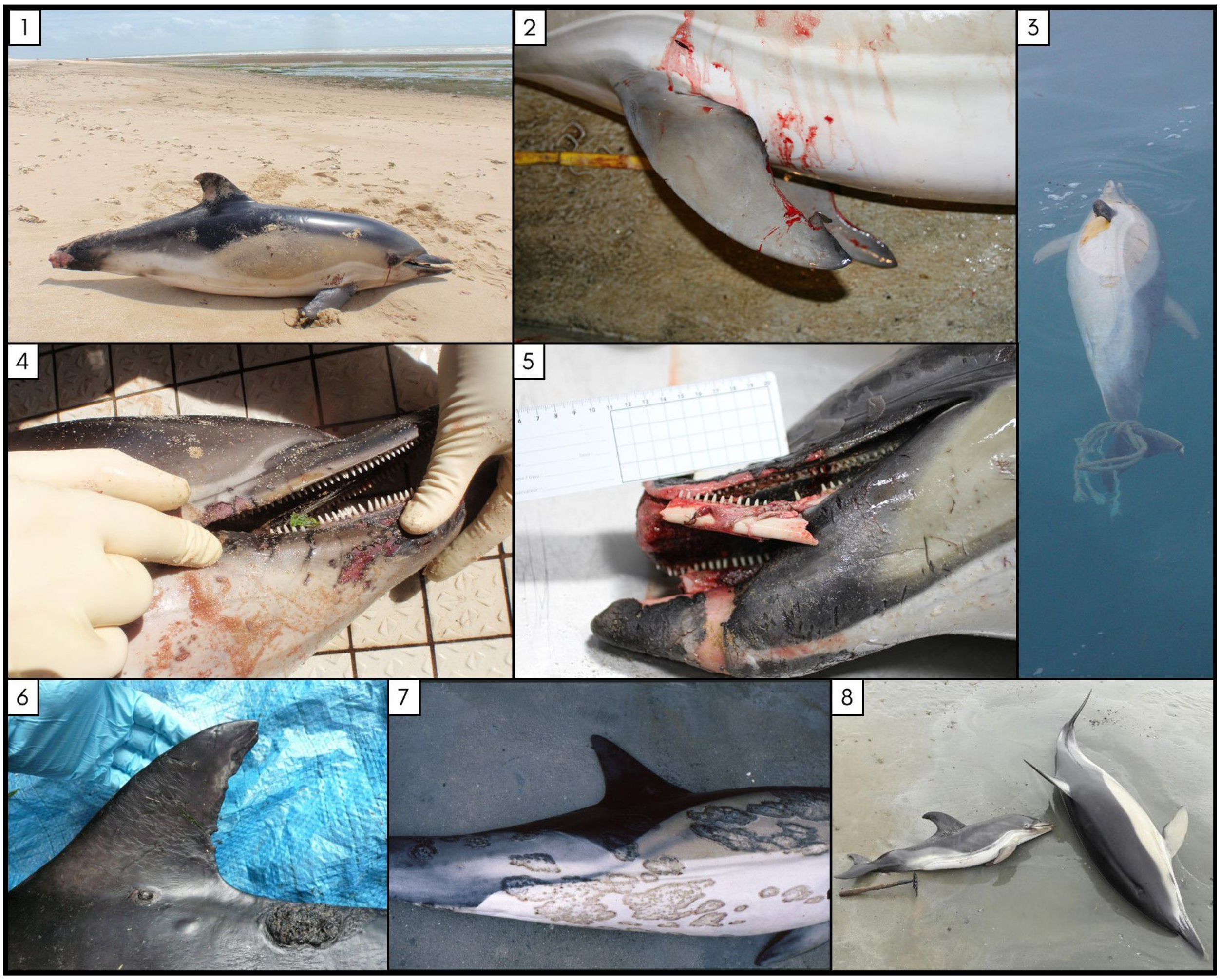

Figure 2.19: External examinations of the common dolphin. The pictures show different cases of mortality assumed by external examinations (which sometimes have to be confirmed on the basis of internal examinations or even biological analyses in the case of pathologies).
1: Amputated tail (Bycatch evidence).
2: Cut pectoral fin (Bycatch evidence).
3: Rope hanging from the tail (Bycatch evidence).
4: Trace of fishing nets (Bycatch evidence).
5: Fractured rostrum (Possible bycatch evidence).
6: Pathological necrosis (Pathology).
7: Possible bacterial infection (Pathology).
8: Unknown cause with scoliosis on calf (Unknown).
For information purposes, in 2020 80% of stranded dolphins are due to bycatch (according to external reviews). 14% are stranded without the cause being known. 3% from pathological reasons and 3% for unknown reasons. These percentages vary slightly after internal review. To see more detailed data: **rapportecouhage2020**.
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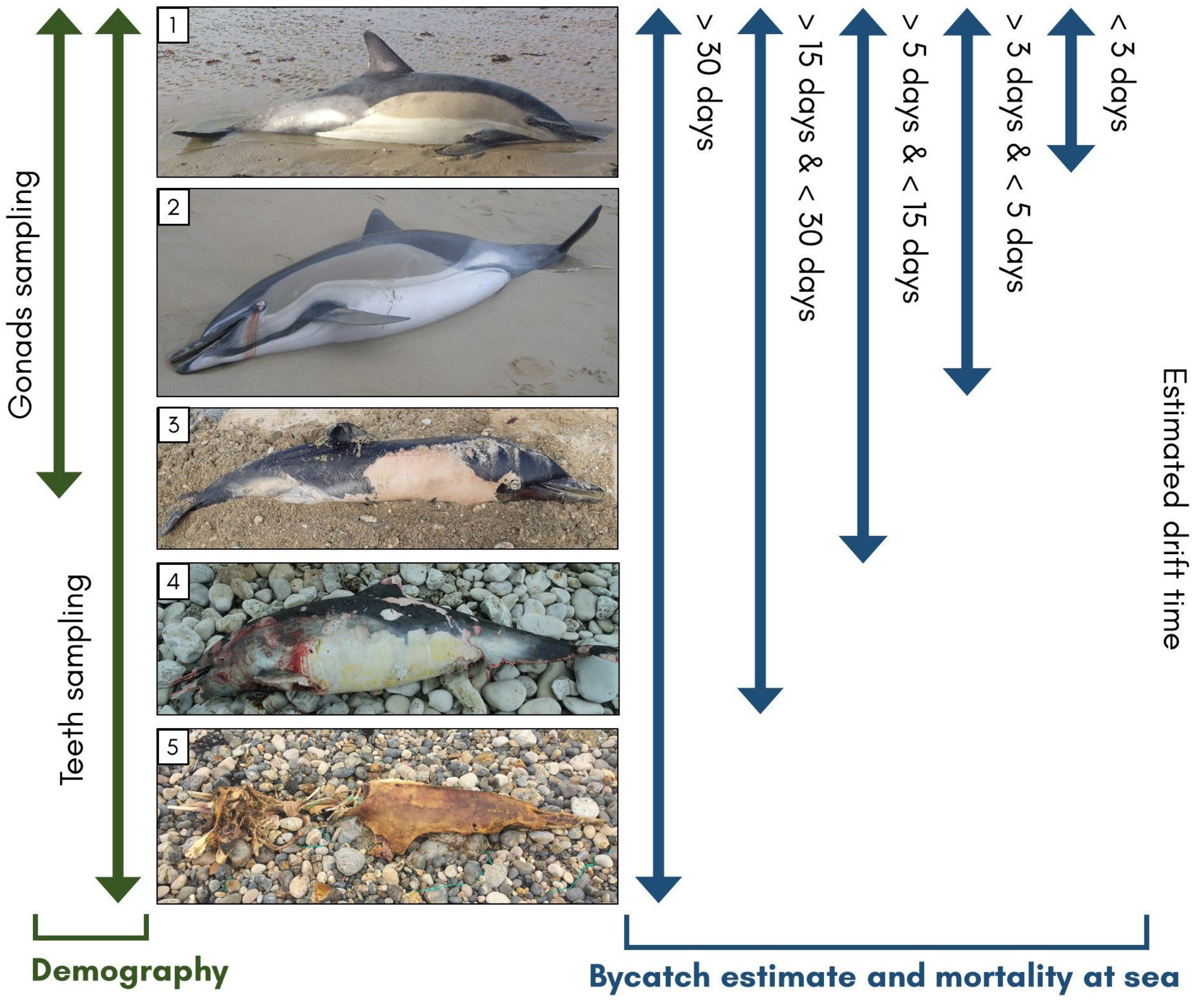

Figure 2.20: Influence of decomposition states on the demographic data collection and on bycatch estimates. The collection of teeth and gonads is carried out to obtain biological data on the population and to estimate its vital rates in the context of the MSFD (Mannocci et al. 2012). It is also possible to estimate the drift time of individuals based on their state. This drift time is then corrected by the probability of floating, the probability of running aground and finally the probability of being discovered. This correction makes it possible to estimate the number of dolphins captured by fishing gear each year (Peltier et al. 2016).
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Studying survival

3

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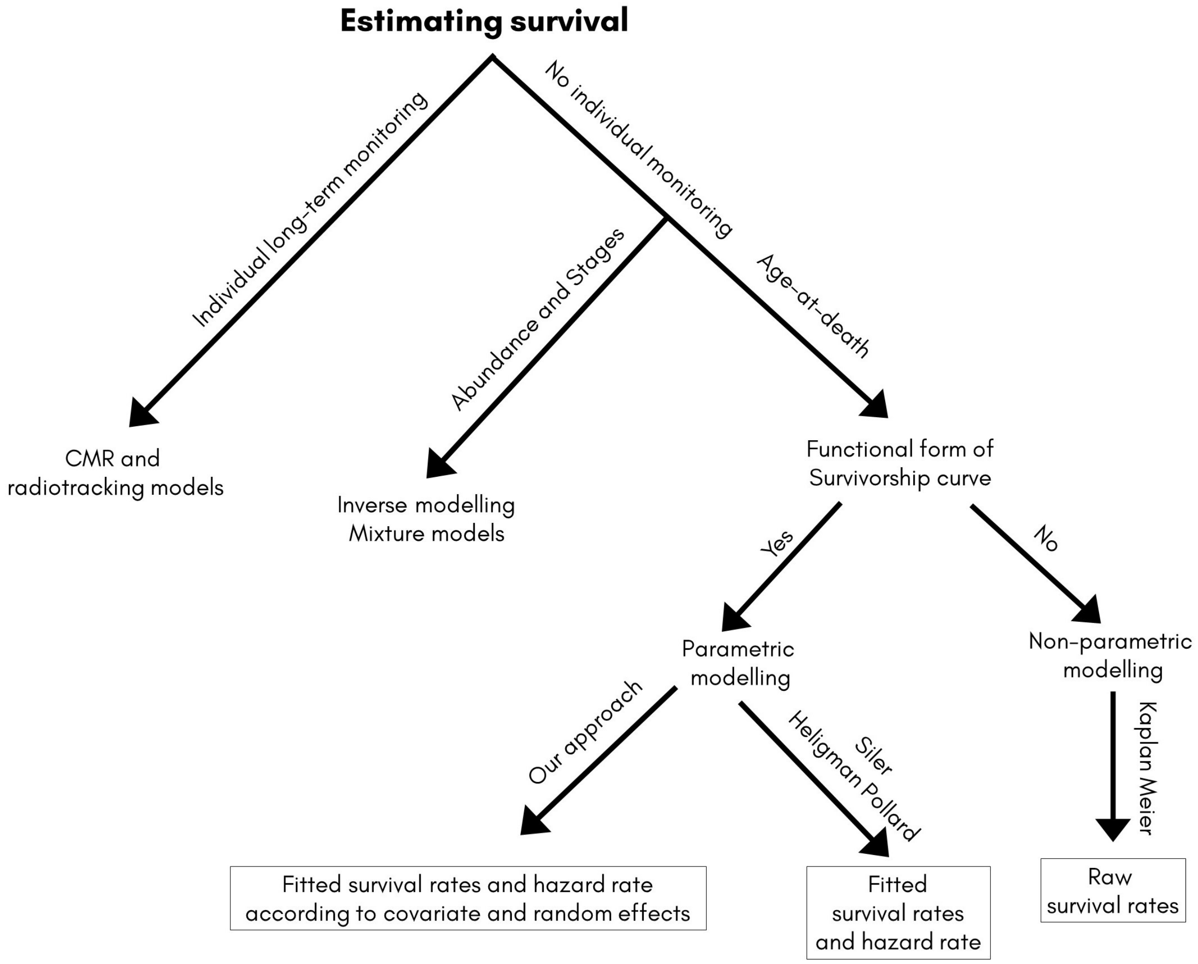
3.2 Methodology: Designs and modelling 47

3.3 Results: Simulation study 58

3.4 Discussion: Implications of this new cross-sectional parametric approach 65

Survival analyses are essential for estimating life-history parameters and producing life tables which are then used in the implementation of management strategies if required by the population status. Where longitudinal studies (*e.g.* capture-mark-recapture monitoring) are not feasible, the only data available may be cross-sectional, for example in the case of marine mammal strandings. Survival analysis deals with data on age-at-death (*i.e.* time-to-event) and allows for the estimation of survival and hazard rates assuming that the cross-sectional sample is representative. Accounting for a bathtub-shaped hazard, as expected in wild populations, has historically been difficult and has required specific models. We identified a simple linear regression model with individual frailty that can fit bathtub-shaped hazard, account for covariates, allow for goodness-of-fit assessments, and give accurate survival estimates in realistic settings. We first performed a Monte Carlo study and simulated age-at-death data to assess the precision of the estimates in relation to the sample size. We then applied the framework to a handful of case studies drawn from published studies of marine mammals, a group with many threatened and data-deficient species. We found that our framework is flexible and accurate in estimating survival with a sample size of 300. This approach holds promise for obtaining important demographic information on data-poor species.



Survival analyses decision tree diagram. The decision tree focuses on cross-sectional survival analyses.

Published work

This chapter is associated with one publication:
Rouby, E., Ridoux, V. and Authier, M. Flexible parametric modeling of survival from age-at-death data: A mixed linear regression framework. Population Ecology. 63:108–122. Doi:`10.1002/1438-390X.12069108`.

3.1 Introduction: About survival analyses

Conservation needs demography which is logistically challenging.

Minimising human impacts on wildlife is a major challenge in the Anthropocene, where human-induced pressures are both geographically and temporally far-reaching, and have an acute impact on biodiversity (Bongaarts 2019). Long-lived species are particularly sensitive to these pressures, especially from a demographic point of view. Their demographic trajectory (*e.g.* extinction) can also affect the functioning of ecosystems, especially in the case of top predators (Beschta and Ripple 2009; Ritchie et al. 2012) since they can act as keystone species for entire ecosystem (Heithaus et al. 2008). Assessing the demographic viability of long-lived species in the face of current and future pressures is necessary for their proactive conservation and is sometimes used to complement indicators of abundance status; but such an undertaking can be hampered in practice by the logistical challenges of monitoring and collecting relevant data at appropriate spatio-temporal scales.

Cross-sectional monitoring may be logistically easier than longitudinal monitoring, depending on the species.

The classical method of assessing the viability of a population consists firstly of constructing a life table in which the mortality and fertility rates of a cohort of individuals are given at each (st)age of their life cycle (Caughley 1966). Knowledge of mortality at each (st)age allows the study of associated hazards, the estimation of vital rates, such as (cumulative) survival, and the projection of the population trajectory over time using age or stage matrix models (Leslie 1945; Lefkovitch 1965; Caswell 2000). Historically, the data on age-at-death used to construct life tables were obtained by cross-sectional monitoring (*e.g.* Gompertz 1825): a sample of the population is taken at a specific time and the observed age structure is assumed to be similar to that of a cohort of individuals if we had been able to monitor them individually from birth to death. This cross-sectional monitoring allows for a quick demographic assessment (Margules and Austin 1990; Boyd, Bowen, and Iverson 2010, pp. 126–127) whose accuracy, however, relies on the assumption that the cross-sectional monitoring does approximate a longitudinal monitoring.

Some definitions

Survivorship:. Fraction of the population that is still alive at a given age.
Age-specific Survival: Fraction of the population of a given age that is still alive at the next age.
Fecundity: Physiological maximum potential reproductive output of an individual (usually female) over its lifetime.
Fertility: Current (actual) reproductive performance of an individual.
Hazard rate: age-specific mortality rate, or instantaneous probability of dying at time $t + dt$ given that an individual has survived until time t.

An essential process to observe when studying demography, regardless of the type of monitoring design, is survival. Survival is an essential component of population demography as it contributes strongly to the growth of a population and its life history, particularly for large mammals such as cetaceans (Heppell, Caswell, and Crowder 2000). Annual survival has been identified as more important than annual fecundity in shaping the fitness of species with life spans greater than one year (Crone 2001). The study of survival in a given population can be called "survival analysis". Historically, survival analysis ranged from the collection of demographic data to statistical methodologies applied to characterise the time-to-event process (*e.g.* time to death) and has been transposed into ecology from epidemiology and industry (Kleinbaum and Klein 2010). The time to events can also be considered as sequential while characterising the time between several events (Skalski, Ryding, and Millspaugh 2010). The two main frameworks for measuring survival are annual survival (*i.e.* year-to-year frame) and survivorship (*i.e.* birth-to-death frame). The latter is the most informative and can be applied as a survivorship curve, or function, to an entire cohort (Ferguson 2002). To measure survival, several modelling or estimation methodologies have been developed, depending on the monitoring design. In this chapter, I briefly review each modelling and estimation approach that has been developed to measure the survival of wildlife populations. In the case of longitudinal monitoring, developments allow the effect of various variables on vital rates to be quantified at the population and individual level. Developments associated with cross-sectional monitoring do not currently allow such flexibility. The review begins with the approaches associated with longitudinal monitoring models, as these are the preferred approaches for obtaining population vital rates because of the less stringent underlying assumptions and greater flexibility. Next, I review the estimation and modelling of survival inherent in cross-sectional monitoring, approaches that require more restrictive and sometimes unrealistic assumptions (*e.g.* a stationary age distribution of the sampled population; Caughley 1966). However, they are of interest for rapid demographic assessment, for studies of populations in crisis (*i.e.* which paradoxically may not satisfy the stationary age assumption) and are often the only applicable methodologies for studying the demography of mammalian populations.

Survival is the essential component that determines the value of the growth rate of a population. The analysis and modelling of survival is very important in demography.

Several methods of survival analysis exist. They depend mainly on the type of monitoring (longitudinal or cross-sectional). In the case of cross-sectional monitoring, they depend on the inclusion of modelling parameters (non-parametric and parametric).

The methodological developments associated with estimating mammalian population survival from age-at-death data are limited. They do not allow for easy estimation of covariates or random effects and do not allow for easy comparison of the resulting vital rate values. It would be interesting to develop a new approach to survival estimation that overcomes these limitations. There are two ways of estimating survival from age-at-death data (for the sake of clarity, I do not discuss the Cox proportional hazard model which allows the use of truncated data). The first estimation method is called non-parametric. This method is mainly limited in the case where the number of data is small. The second estimation method is called parametric and is mainly limited by its implementation and the impossibility of testing the factors and comparing the quality of the estimates. It is in this context that we have developed a new parametric flexible linear regression approach to facilitate the estimation of survival in cross-sectionally monitored populations. Our work is based on Reed's model (Reed

We have developed a parametric approach based on the Reed (2011) model which has the following advantages: inclusion of covariates, inclusion of random effects, evaluation of goodness of fit and individual heterogeneity parameter.

2011) which admits a bathtub-shaped hazard rate curve (*i.e.* representative of the long-lived mammalian mortality pattern). We believe that this approach is an important and innovative contribution to the literature of cross-sectional survival analyses, and thus to the study of associated population dynamics. Its strengths are the consideration of the effect of covariates, the facilitation of goodness-of-fit measurement, and the consideration of the effect of random variables that can highlight key temporal processes in relation to cohorts, as I will show in the Chapter 4.

3.2 Methodology: Designs and modelling

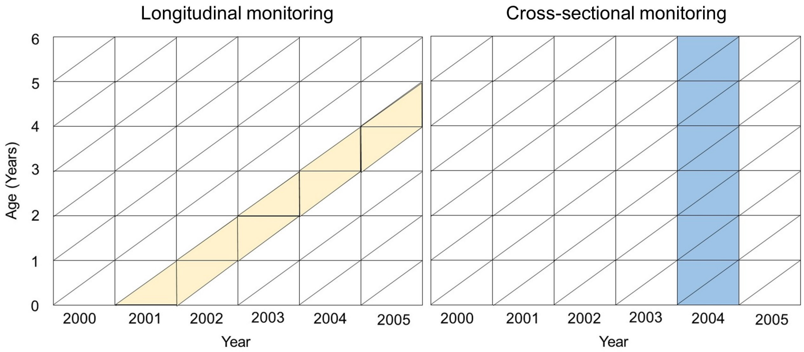


Figure 3.1: Lexis diagrams for each monitoring. With the longitudinal monitoring, an individual born in 2001 is monitored through each year as it ages. With the cross-sectional monitoring, an individual is sampled in 2004 and its age (here 6 years) is determined at the time of its death.

Survival models based on longitudinal monitoring

Longitudinal studies, in which individuals and cohorts are monitored from birth to death (Figure 3.1 for the associated lexical diagram) are, in wildlife ecology, a by-product of capture-recapture studies. The initial motivation for the latter was the accurate estimation of abundance in open populations when detectability is less than perfect (Seber 1965; Cormack 1964; Jolly 1965). Models (*e.g.* the Cormack-Jolly-Seber model) fitted to these life history data can provide accurate estimates of survival that can be fed into population matrix models (*e.g.* Fujiwara and Caswell 2001). Since the 1980s, the focus of capture-recapture studies in wildlife ecology shifted from abundance to survival estimation (Lebreton et al. 1992) and the inclusion of individual-level covariates, which has paved the way for a better understanding of life history evolution and natural selection in nature (Cam 2009). Models for estimating survival (initially abundance) use either the recovery of live animals ("live recapture") or dead animals ("band recovery"). Some models may also combine the two data sources (J. D. Baker, A. Westgate, and Eguchi 2010).

Longitudinal monitoring was essentially a means of estimating abundance. They were then used to estimate vital rates.

The objective of capture-recapture modelling is to develop probability-based models characterising the biological processes that shape the capture history data (B. K. Williams, Nichols, and Conroy 2002). The common approach to each modelling mode is to model the subsequent entries of an individual, after the initial capture, as a function of parameters associated with both sampling and actual population change (B. K. Williams, Nichols, and Conroy 2002). Survival probabilities are then estimated by focusing on the loss of individuals within the population (Lebreton et al. 1992). There are several types of models, more or less complex. Here is a brief review of them. The first type of survival model is the single-age model. It considers a population in which individuals are considered to have a single age. The model traditionally used to estimate survival in this case is the Cormack-Jolly-Seber (CJS) model (Seber 1965; Cormack 1964; Jolly 1965). With this model, the only component of survival that can be estimated is apparent survival. The multiple-age model is an extension of the single-age model that allows capture and survival probabilities to vary with time and age. The model that generalises the single-age model to multiple-age modelling was developed by Pollock (Pollock 1981). The multi-state modelling approach allows some stochasticity to be incorporated between transition states. The states can be considered for example as different locations or phenotypes. This modelling approach was developed to study transition states. It was first introduced by Arnason (Arnason 1972). The inverse time modelling approach developed by (Pollock, Hines, and Nichols 1984) allows the recruitment process to be deduced by considering the recaptures in an inverse temporal order. All these approaches use capture-recapture data from live animals. Approaches have also been developed to use capture-recapture monitoring data incorporating the recapture of dead individuals. This is the case, for example, with survival modelling based on band recoveries, which is of interest for species that are harvested (Burnham 1993). A common feature of all these modelling approaches is that they are based on the use of data obtained through longitudinal monitoring. They require individuals and cohorts to be followed throughout their lives. For species where this may be difficult, other approaches have been developed. Approaches using the same data but taking into account only certain life stages or even using only abundance data have been developed to avoid the cost of long-term monitoring.

Longitudinal survival analysis models can be distinguished in this way: single-age model, multiple-age model, multi-state model and inverse-time model.

Survival models with longitudinal monitoring and abundance data

From an applied conservation perspective, the obvious drawback of capture-recapture studies is the time and man-power required to collect the data, especially for long-lived species. E. R. White, Nagy, and Gruber (2014) recently proposed a new development that allows to avoid birth-to-death monitoring at the individual level. This is a physiologically structured model with age class as the structuring variable. Although the model is age-structured, only the juvenile population is observed. From juvenile mortality and adult fecundity, it is possible to infer adult mortality. However, this requires monitoring the juvenile part of the whole population in order to model the overall population dynamics. An alternative to long-term individual monitoring for estimating vital rates is the use of count data. This approach may involve building an N-mixed model based on knowledge of individual states. Zipkin et al. (2014) has proposed a development that allows the data to be taken into account even if the individual stage is unknown. Another way to obtain vital rates with count data, in the form of time series, is to conduct an inverse modelling approach: this method also has the advantage of considering state data at the individual level (E. J. González, Martorell, and B. 2016). Although these approaches are promising for elusive species, they remain difficult to apply to highly mobile ones. The time lag between data acquisition and the urgency of mitigation on conservation decisions can be acute, suggesting an interest in cross-sectional data which have the added advantage of being applicable to species where individual identification is difficult (B. K. Williams, Nichols, and Conroy 2002).

Survival models have been developed to relay partly on longitudinal data or to get rid of it and use abundance data.

Survival models with cross-sectional monitoring

Long-lived, mobile and elusive (weakly marked) species are difficult to monitor longitudinally. This is particularly true for species that live in a large and sometimes three-dimensional space in the case of the marine environment. Instead, data on these species can be collected through cross-sectional monitoring. One or more samples are taken during a time series (snapshots; Figure 3.1). Sampling of the study population is carried out as described in 1.3. Once age-at-death data have been collected, they can be used to calculate the survival of the population. This calculation relies heavily on modelling choices. Assuming that cross-sectional age-at-death data are available and representative, ecologists are now faced with other choices, such as non-parametric or parametric modelling.

Elusive species are impossible to monitor on an individual basis and abundance data can be very scarce. It is therefore necessary to use age-at-death data. In the case of marine mammals, these are collected from stranded individuals.

Non parametric modelling

The non-parametric modelling approach does not assume any functional form of the survival curve. This approach allows the raw observations (*i.e.* data) to dictate the shape of the survival curve. Two non-parametric approaches are commonly used in wildlife demography. The first was developed by E. L. Kaplan

Non-parametric survival modelling requires a large amount of data. It does not allow to obtain survivorship in the case of elusive species.

and Meier (1958) and is referred to as the Kaplan-Meier estimator, or product limit estimator. It consists of monitoring a cohort of individuals, whether or not they entered the study at the same time, and reporting the remaining number of individuals at each age. A fictitious cohort can be reconstructed from the ages-at-death. The first study to transpose this approach from epidemiology to wildlife demography was conducted by Pollock et al. (1989). They conclude that this estimator is flexible and useful in wildlife studies and have optimised it to allow successive entries of individuals in the survival estimate. This approach considers the maximum survival $l(t)$ at time 0 (discrete time approach): $l(0) = 1.00$. At each age-at-death interval, the survivorship decreases to 0 until the last animal of age x die: $l(x) = 0.00$. The survivorship at each time t can be estimated as follows with nlt = number of animals alive (at risk) at time t and ndt = number of animals that died in the interval between time t and $t+1$:

$$l(t) = \frac{nlt - ndt}{nlt} \tag{3.1}$$

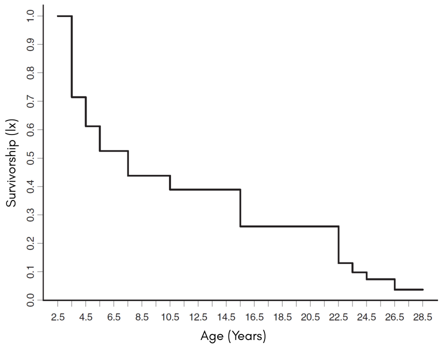


Figure 3.2: Example of Kaplan-Meier survivorship curve.

A limitation of this approach is that it performs poorly with small amounts of data because the number of points on the survival curve depends directly on the amount of data. If the number of data points is small, the curve is not smooth and has an unreliable stepwise appearance.

An alternative was developed by Nelson (1972) and Aalen (1978). This approach is known as the Nelson-Aalen estimator. The survivorship is modified based on the cumulative hazard function. The approach has better properties regarding small sample size. The cumulative hazard function is constructed as detailed here with nlx = number of animals alive (at risk) at age x and ndx = number of animals that died in the interval between age x and $x+1$:

$$h(t) = \sum_{x=0}^{t} \frac{ndx}{nlx} \tag{3.2}$$

The corresponding survivorship function at time t is:

$$l(t) = e^{-h(t)} \tag{3.3}$$

Despite its ability to accommodate smaller datasets, it is also limited for the types of datasets we are interested in studying the survival of animal populations. The use of these methods, in particular the Kaplan-Meier method, appears to be more suitable for describing "observed" survival and not estimated by modelling. The use of a parametric modelling approach is more suitable with small samples to estimate survival and characterise the mortality process of a fictitious cohort in a population over time (Skalski, Ryding, and Millspaugh 2010). It has the advantage of providing smoothing and summarising the data into a small number of parameters. Even with a small sample size, parametric modelling allows smooth survival to be estimated and parameters to be compared (Kleinbaum and Klein 2010).

Parametric modelling

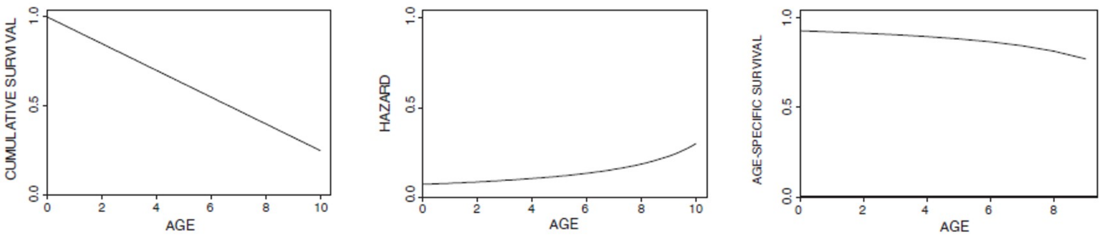
The parametric modelling approach requires the choice of a shape for the mortality curve or hazard rate. The accuracy of the approach depends primarily on the suitability of the shape of the mortality curve for the species whose survival and mortality are to be modelled. The challenge is to find a parsimonious model that takes into account the available data without fitting the analysis into a convenient but not necessarily realistic curve shape. Each parametric model is associated with a probability density function (*i.e.* pdf), a cumulative distribution function (*i.e.* cdf) and a survivorship function (*i.e.* $l(x)$) associated with a hazard rate function as follows : $h(x) = \frac{pdf(x)}{l(x)}$. Examples of survival models commonly used with associated distribution is provided in Figure 3.3.

Parametric survival modelling allows the use of small data sets. But it requires the definition of a type of mortality curve.

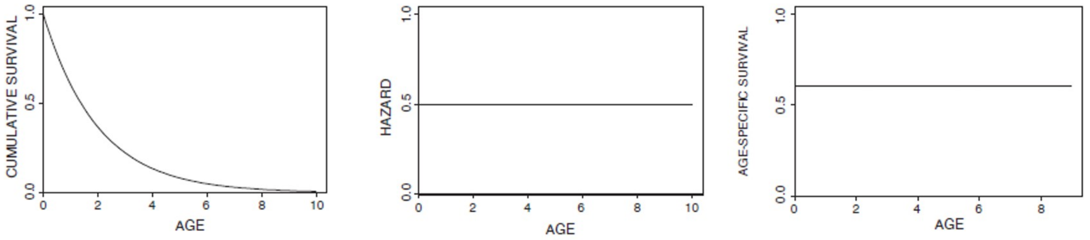
For long-lived animal species, a realistic model should provide the so-called "bathtub curve", which is characterised by high juvenile mortality, followed by lower and rather constant adult mortality and finally a late increase due to senescence (Siler 1979; Choquet et al. 2011a). The hazard should decrease as the animal adapts to its environment and becomes stronger, remain constant in mid-life when the animal is in its prime, and increase with senescence (Emlen 1970). Although there are models to accommodate this bathtub pattern (Siler 1979; Heligman and Pollard 1980), they can be difficult to fit (Saavedra 2018). Moreover, their goodness of fit is hard to measure and compare. Finally, they do not allow for testing the effect of various factors on survival and mortality.

Realistic parametric model for long-lived mammals = bathtub shape mortality or hazard rate curve.

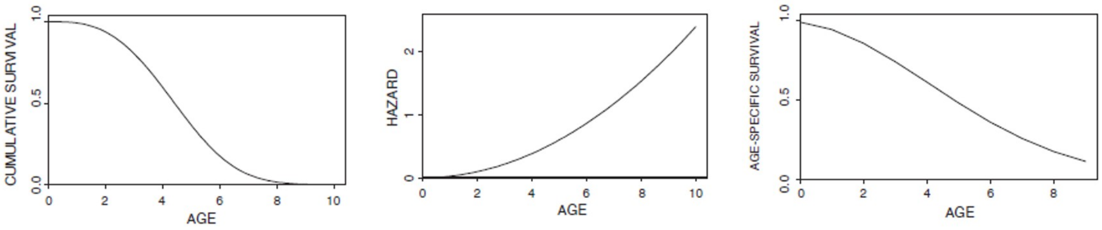
(a) Uniform Distribution



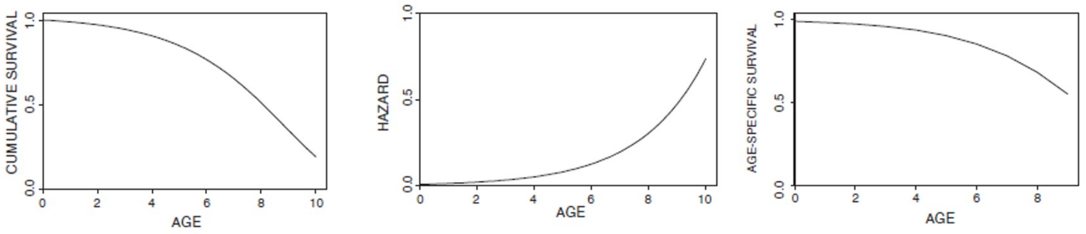
(b) Exponential Distribution



(c) Weibull Distribution



(d) Gompertz Distribution



e. Siler Distribution

Figure 3.3: Survival parametric models commonly used. For each survival model and distribution, the cumulative survival (survivorship l(x), the hazard rate curve and the age-specific survival (S(x)) are depicted.
a. Uniform distribution. Hazard mortality curve grows slowly and a little more at the end.
b. Exponential distribution. Hazard mortality curve remains constant over lifetime.
c. Weibull distribution. Hazard mortality curve increases after a short plateau at 0.
d. Gompertz distribution. Hazard mortality curve increases after a long plateau near 0.
e. Siler distribution. Hazard mortality curve is in U-shape or so called-Bathtub shape with a decrease, plateau and increase. Figure from Skalski, Ryding, and Millspaugh 2010.

Our parametric modelling approach

Reed's model can fit this hazard curve. It can do so by including a parameter for individual heterogeneity. We believe that this model can be integrated into a parametric approach.

Our aim is to develop a parametric approach for the construction of life tables in a data-poor context, with long-lived vertebrate species in mind. We will first present a simple regression modelling framework for the analysis of age-at-death data (with or without right censoring) that can accommodate mortality patterns such as constant, increasing/decreasing, unimodal or bathtub-shaped. Importantly, this framework allows for the transparent inclusion of individual-level covariates and random effects. We then perform a Monte Carlo simulation study with five biological scenarios to evaluate our framework, focusing on the accurate estimation of survivorship and mortality. Finally, we illustrate our methodology on a handful of real-life case studies, focusing on marine mammals. This group includes many elusive and long-lived species that are threatened (Avila, Kaschner, and Dormann 2018), data-deficient (Parsons 2016) and difficult to study with a longitudinal approach. The most common age-at-death data for marine mammals are obtained from strandings (*i.e.* cross-sectional monitoring). Teeth are collected from individuals found dead on the shore and are then processed to allow the reading of growth layer groups that are indicative of the age of the stranded animal (Mannocci et al. 2012). The stranding filter may introduce a selection bias of individuals between the population and the age-at-death dataset (Barlow and Hohn 1984). However, stranding samples are a source of age data from which vital rates can be obtained (J. D. Baker, A. Westgate, and Eguchi 2010). In this framework, several underlying assumptions are associated with the developed approach:

Baseline assumptions (use of this parametric approach)

- 1. Each age-at-death is known and correctly recorded
- 2. The cohort is representative of the overall population
- 3. The fate of each individual is independent
- 4. The shape of the survivorship and mortality distribution are known and well chosen to represent the life history of the species

Definitions

Survival analysis deals with the analysis of the timing of death (E. L. Kaplan and Meier 1958; Tanner and Wong 1984; T. G. Clark et al. 2003; Lesaffre and Lawson 2012). We assume data $y \geq 0$ to be time-to-event data, for example longevity, survival time or age-at-death data. Such data can be collected from strandings of animals (that is marine animals that are washed ashore), or any recovery of dead specimens (*e.g. Lepus europaeus*, Pallas 1778; *Ovis dalli*, Nelson 1884) when aging is possible (*e.g.* from growth layer groups). Let the index i denotes the i^{th} individual, and N the sample size. The equation $y_i \sim \mathcal{D}(\theta)$ reads as datum y_i follows statistical distribution $\mathcal{D}$ of parameters θ and with probability density function $f(y;\theta)$ and cumulative density function $F(y;\theta) = \Pr(y \leq t) = \int_0^t f(y;\theta)\mathrm{d}y$.

The survival function $S(t;\theta)$ gives the probability of being alive at time t, that is $\Pr(y > t) = 1 - \Pr(y \leq t) = 1 - F(y;\theta)$. At the population level, this quantity correspond to the fraction of the population that is still alive at age x, that is cumulative survival or simply survivorship. The hazard rate, or age-specific mortality rate, is the instantaneous probability of dying at time $t + \mathrm{d}t$ given that and individual i has survived until time t.

$$h(t) = \lim_{\mathrm{d}t \to 0} \frac{\Pr(t \leq y_i < t + \mathrm{d}t; y_i > t)}{\mathrm{d}t} \tag{3.4}$$

With parametric models, the hazard rate can be expressed in terms of the probability density and survivorship functions:

$$h(t;\theta) = \frac{f(t;\theta)}{S(t;\theta)}, \text{ with } S(t;\theta) > 0 \tag{3.5}$$

Data simulation scenarios

We considered five biological scenarios (*i.e.* five different life histories) corresponding to different patterns in survivorship and the underlying hazard (Margin-Figure 3.4):

1. a unimodal distribution of age-at-death corresponding to a unimodal hazard, whereby mortality risk increases in early ages, peaks and decreases in late life;
2. a mixture of two hazards corresponding to either a unimodal (a) or bimodal (b) distribution of age-at-death;
3. a bathtub-shaped hazard due to individual frailty, that is individual-specific risk of mortality; and
4. a bathtub-shaped hazard with an additional bump in early life due, for example, to an additional source of mortality.

Each scenario is associated to survivorship and hazard functions (Figure 3.4).

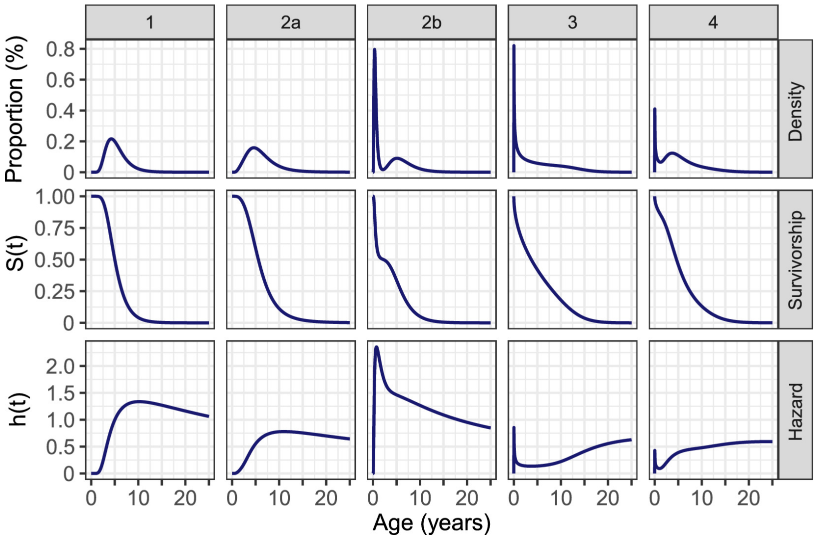


Figure 3.4: Biological scenarios considered in the Monte Carlo simulation study.
1: low juvenile mortality, a high adult mortality and no senescence.
2a: low juvenile mortality and a higher adult mortality plateau.
2b: high juvenile mortality and a lower adult mortality that decreases in a linear fashion.
3: high juvenile mortality, a lower adult mortality and senescence (bathtub shaped hazard).
4: high juvenile mortality and a high adult mortality, with a transient dip in mortality risk between these two life-stages.

Statistical Analysis of age-at-death data

We used parametric models $\mathcal{M}^{\theta}$ of age-at-death data y to estimate hazard and survivorship rates. We assumed that the exact timing of death is available, but our framework can easily accommodate censoring (that is cases when death is known to have occurred before or after measurement). Our framework consists in modelling the logarithmic transform of y_i in a regression framework (location-scale model

$$\log y_i = \mu + \sigma \times \epsilon_i - \frac{Z_i}{\beta} \tag{3.6}$$

Parameters specification of Model 3.6:
μ: location parameter.
σ: positive scale parameter.
Z_i: individual independent standard exponential deviates.
$\frac{1}{\beta}$: positive scale parameter and individual frailty (Kannisto 1991; Reed 2011) or persistent demographic heterogeneity *sensu* Cam, Aubry, and Authier 2016.

The choice of the statistical distribution for the residuals ϵ_i determines the shape of the underlying hazard rate. We considered three different choices, each corresponding to a model[1] .

- $\mathcal{M}_1$: $\epsilon_i \sim \mathcal{N}(0,1)$ and $\frac{1}{\beta} = 0$ ($\beta = +\infty$)
  This model assumes a log-normal distribution for y_i, which corresponds to a unimodal hazard curve.
- $\mathcal{M}_2$: $\epsilon_i \sim \mathcal{G}(0,1)$ and $\frac{1}{\beta} = 0$ ($\beta = +\infty$)
  This model assumes a Gumbel distribution for the residuals ϵ_i, which corresponds to a Weibull distribution for y_i. It is known as the Accelerated Failure Model. The hazard rate is monotonic: it can be constant, increasing or decreasing depending on the value of σ.
- $\mathcal{M}_3$: $\epsilon_i \sim \mathcal{N}(0,1)$ and $\frac{1}{\beta} > 0$
  This choice leads to assume a normal-Laplace distribution for $\log y_i$, which induces a flexible hazard curve depending on the value of β (Reed 2011). In particular, the hazard can be a bathtub-shaped, as expected for example for long-lived species of vertebrates in the wild (Choquet et al. 2011a).

[1] See SI Text 2 of `https://esj-journals.onlinelibrary.wiley.com/doi/10.1002/1438-390X.12069`. The next supplementary material that will be referred in margin notes will always be available at this URL. To find the supplementary material mentioned, see this URL

Our framework transcribed by the equation 3.6 3 a flexible location-scale model and boils down to a generalized linear mixed model (GLMM; Bolker et al. 2009) with a handful of parameters $\theta = (\mu, \sigma, \beta)$ to accommodate a large diversity of survivorship and hazard curves[2] . One attractive feature of this framework is the seamless incorporation of p individual-level covariates x_{ip} in equation 3.6 (Reed 2011):

$$\log y_i = \mu + \sum_{j=1}^{p} \gamma_p x_{ip} + \sigma \times \epsilon_i - \frac{Z_i}{\beta} \tag{3.7}$$

An important restriction of our approach is that only time-invariant individual-level covariates can be included. It is also impossible to take into account changes in states within the life history trajectory at the individual level. However this approach covers interesting cases such as sex-differences in survival, differences due to geography or cause of mortality (that is comparing different populations of the same species).

Monte Carlo study

Our aim is to carry a Monte Carlo study (*e.g.* T. P. Morris, I. R. White, and Crowther 2019) to investigate whether our modelling framework can provide accurate survivorship and hazard rate estimates from age-at-death data. We considered 5 biological scenarios to cover a diversity of realistic mortality patterns. For each scenario, we simulated 100 datasets of sample size 100, 200, 300, 400, 500 and 1000 to provide recommendations on the minimum sample size required for accurate estimation. Data simulation was carried out in `R` version 3.6.0 (R Core Team 2019) using base functions such as `rnorm` and `rexp`. Each simulated dataset was then analyzed with our framework that considered 3 parametric models. Crucially, we considered scenarios for which the true model was not among the set (Table 3.1). In other words, we assessed the performance of our framework under the possibility that none of the candidate models is correctly specified with respect to the data at hand. For example $\mathscr{M}_2$ is a Weibull model, which is widely used in survival analysis (Kleinbaum and Klein 2010) it is biologically unreasonable for marine megafauna and top predators as a model over their entire lifetime because it cannot accommodate the expected bathtub-shape hazard.

Model fitting was done with software Stan version 2.18 (Carpenter et al. 2017a) called from `R` via the library `rstan` (Stan Development Team 2018). Three chains were run with a warm-up of 500 iterations, followed by an additional 1000 iterations. No thinning

Model/Scenario	1	2a	2b	3	4
$\mathscr{M}_1$	+	-	-	-	-
$\mathscr{M}_2$	-	-	-	-	-
$\mathscr{M}_3$	-	-	-	+	-

Table 3.1: Design of the Monte Carlo study. Model $\mathscr{M}_2$ acts as a negative control as it was never used to simulate data. Scenarios 2a, 2b and 4 corresponds to data generated from mixture models not included in the set. They serve as tests of the performance of our framework. Scenarios 1 and 3 act as positive control as they correspond to data simulated under models $\mathscr{M}_1$ and $\mathscr{M}_3$ respectively.

[2] See SI Text 2.

was performed but the delta parameter of the NUTS algorithm was increased from 0.80 to 0.95 to avoid divergent transitions and the maximum tree depth increased to 15. Parameter convergence was assumed when its $\hat{R}$ statistics was lower than 1.10. Upon convergence, the 3 chains were pooled to obtain a sample of ≈ 1000 values from the posterior distribution.

Model fit was assessed with the Widely Applicable Information Criterion (WAIC, (2014)), computed with `R` package `loo` (Vehtari, Gelman, and Gabry 2017). Survivorship estimates from each model were computed from the posterior distribution of parameters, and visually compared to the true survivorship curve and a non-parametric (Kaplan-Meier) estimate. Because we carried out a simulation study, the true survivorship curve was known and could have been used to compute the Root Mean Squared Error (RMSE). However, in practice, this is not the case and we chose instead to compute RMSE with respect to the non-parametric Kaplan-Meier survivorship estimates. The latter were thus assumed to represent the best estimates available to researchers, and the aim was to assess whether a parametric model could provide a fit as good as that from a non-parametric approach.

$$\text{RMSE}_{\mathscr{M}} = \sqrt{\mathbb{E}\left[(\hat{S}_{KS}(t) - \hat{S}_{\mathscr{M}}(t))^2\right]} \tag{3.8}$$

Parameters specification of equation 3.8:
$\hat{S}_{KS}(t)$: Kaplan-Meier estimate of survivorship at age t.
$\hat{S}_{\mathscr{M}}(t)$: parametric model $\mathscr{M}$ over a sequence of values of t.

In order to assess model selection and model check, it is necessary to determine if the models represents well the data. (Conn et al. 2018) recently reviewed some ways to proceed. We choose to do a prior predictive check to test for adequacy between models and time to event data[3] . We also did a posterior predictive check[4] to see whereas data simulated through the fitted models are similar to that observed from the (Barlow and Hohn 1984) dataset. The comparison is done with both the true Kaplan-Meier survivorship curve and the ones from posterior simulated datasets.[5]

[3] SI text 3 and Figure S1.

[4] SI text 3 and Figure S2.

[5] SI text 3.

Our focus was on accurate estimation of survivorship, and thus we assessed goodness-of-fit by comparing the expected mean survivorship under each model to the observed Kaplan-Meier estimates. This focus was in line with downstream use of such estimates in matrix population models: here the salient statistics we want our model to reproduce (Gelman 2003) is the survivorship function.

Our study design is summarized in Table 1 and Figure 2. It consisted in a comprehensive factorial design crossing (a) sample size (100, 200, 300, 400, 500 and 1000), (b) mortality patterns (5 scenarios), (c) parametric models (3 models) and (d) individual covariate inclusion. Two covariates (x_1, x_2) were generated by sampling from a Bernoulli distribution with probability 0.5. These covariates could represent for example sex or two sub-populations in different geographic areas.

Applications

We analyzed real datasets from published case studies (Table 2) within our framework, and compared the estimated parametric survivorship curves with the non-parametric Kaplan-Meier one. All species are marine mammals except the spur-thighed tortoise (*Testudo graeca*, Mertens 1946) which was included to compare our approach with that of (Rodriguez-Caro et al. 2019) in a data-poor context for conservation. It is important to precise that data from (Rodriguez-Caro et al. 2019) were obtained from live animals, still alive at the time of measurement (Sanz-Aguilar et al. 2011; Rodrıguez-Caro et al. 2013). However, we used these data as if they were age-at-death data and ignored right-censoring.

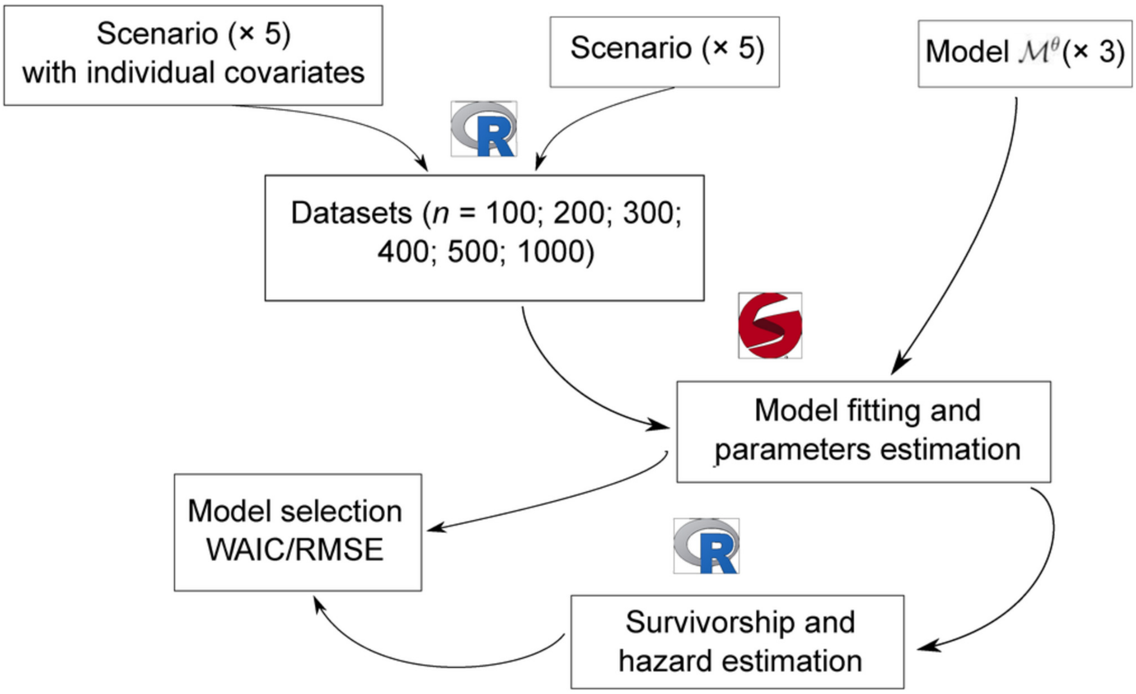


Figure 3.5: Monte Carlo study flowchart. We considered five biological scenarios, six different sample sizes for data, and three models for analysis. For each combination, we assessed model fit and the accuracy of parameter estimates. Model selection is done with Watanabe-Akaike information criterion (WAIC) and root-mean-square error (RMSE).

3.3 Results: Simulation study

Across all scenarios and sample size, parameter convergence (assessed with $\hat{R}$) was not equivalently reached depending on the model and scenario[6] . $\mathscr{M}_1$ always converged very easily. In contrast, $\mathscr{M}_2$ and $\mathscr{M}_3$ were not as good as $\mathscr{M}_1$ to converge with 1000 iterations (500 as warm up). More precisely, convergence for $\mathscr{M}_3$ was difficult

[6] Figure S3 and Figure S4 a.

for β given this configuration[7] . An increased in the number of iterations per chains (here from 1000 to 2000) solved the problem.

[7] Figure S5 to S10.

Hazard rate estimation

Estimated hazard curves are shown in Figure 3.6 for each combination of scenario, model and sample size. Models $\mathscr{M}_1$ and $\mathscr{M}_3$ were the best fitting ones in the first and third scenarios respectively (*i.e.* positive control, Table 3.1): estimates were accurate and precision increased with sample size. For scenarios 2a, 2b and 4, all estimates were biased, and precision increased with sample size. In contrast, model $\mathscr{M}_2$ never provided accurate hazard estimates (i.e negative control). The same results were obtained when covariates were included.

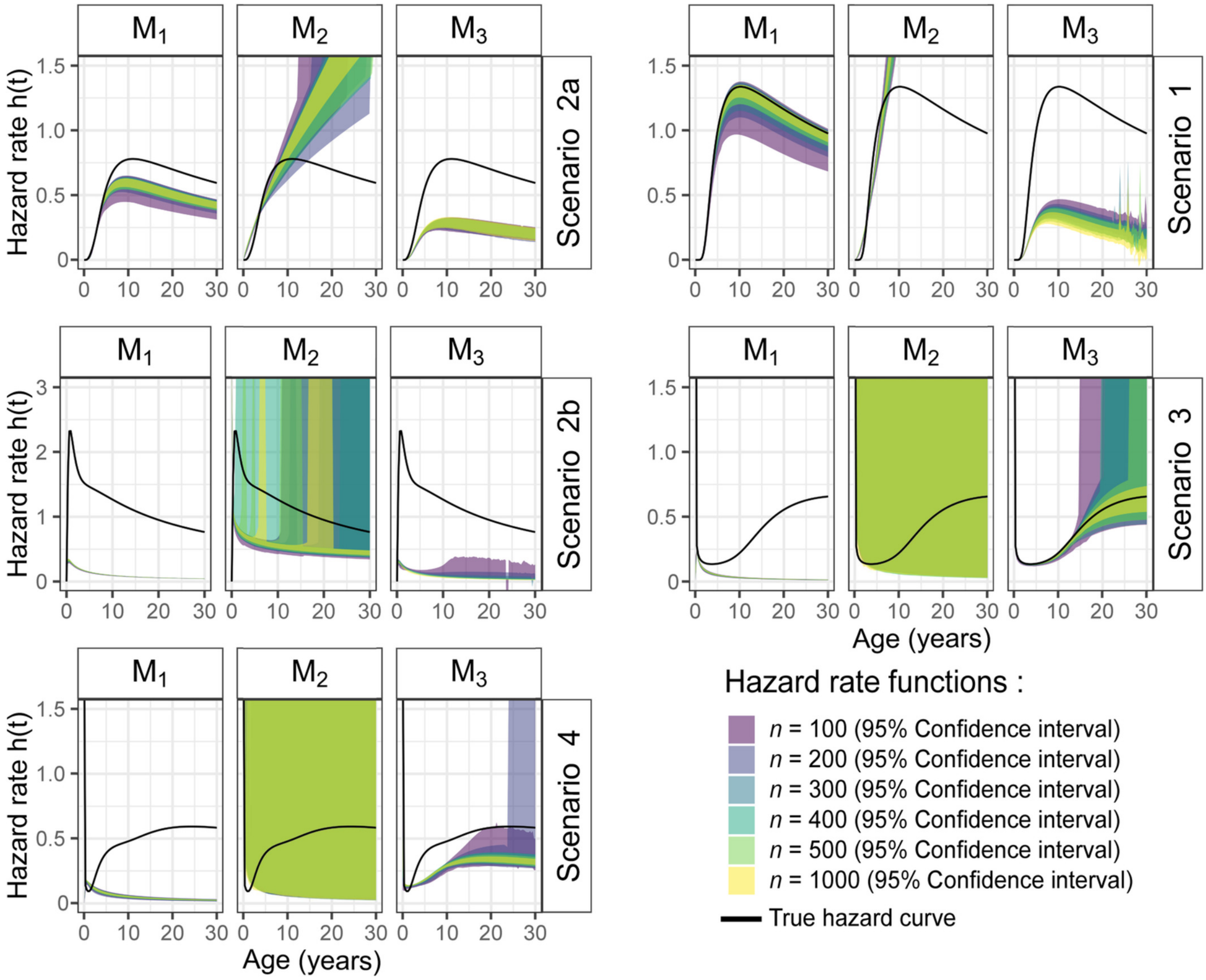


Figure 3.6: Estimated hazard curves confidence intervals for each combination of scenarios (rows), models (columns), and sample size (facets). Estimated confidence intervals are depicted in each panel and compared to the true hazard curves (in black). Even-numbered scenarios (2a, 2b and 4) are on the left, and odd-numbered ones (1 and 3) on the right.

Survivorship estimation

Estimated cumulative survival curves are shown in Figure 3.7 for each combination of scenario, model and sample size. Across all scenarios and sample sizes, estimates from model $\mathscr{M}_3$ were the most accurate[8] . Precision increased with sample size. In particular, survivorship rates estimated with $\mathscr{M}_3$ were very close to Kaplan-Meier estimates for sample size ≥ 300. This sampling size also provided a good confidence interval precision with a maximum width of 0.04 % while estimating survivorship[9] . Predictive ability, as measured with WAIC, was the greatest for model $\mathscr{M}_3$: it was consistently ranked first across each combination of scenario and sample size, even for scenario 1 where model $\mathscr{M}_1$ was the true data-generating mechanism[10] .

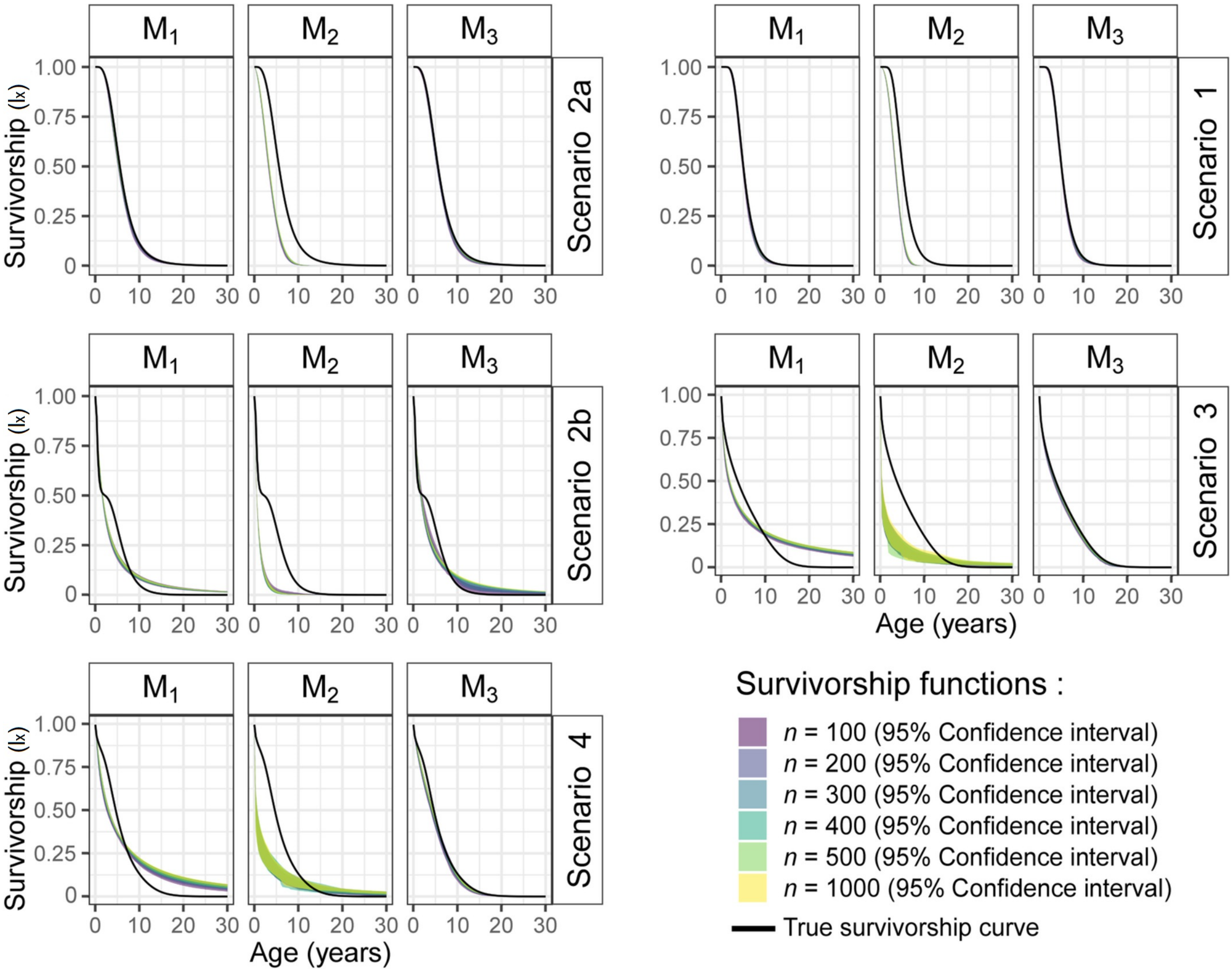


Figure 3.7: Estimated survivorship confidence intervals for each combination of scenarios (rows), models (columns) and sample size (facets). Estimated confidence intervals are depicted in each panel and compared to the truth (in black). Even-numbered scenarios (2a, 2b and 4) are on the left, and odd-numbered ones (1 and 3) on the right.

[8] Figure S5, SI Text 4 and Figure S11.

[9] Figure S12.

[10] SI Text 4 and Figure S13.

Covariate Effects

Covariate effect estimation is summarised on Figure 3.8 as a difference between survivorship rates. Model $\mathscr{M}_2$ could not estimate difference in survivorship. Model $\mathscr{M}_1$ is only effective for both scenario 1 and 2a. $\mathscr{M}_3$ could estimate accurately covariate effects when the difference is expressed as an unimodal pattern (*i.e.* scenario 1, 2a and 3). The precision of the estimated effect increased with sample size for models $\mathscr{M}_1$ and $\mathscr{M}_3$. With small sample size, sign errors on the effect of covariate was possible but disappeared with sample size ≥ 300.

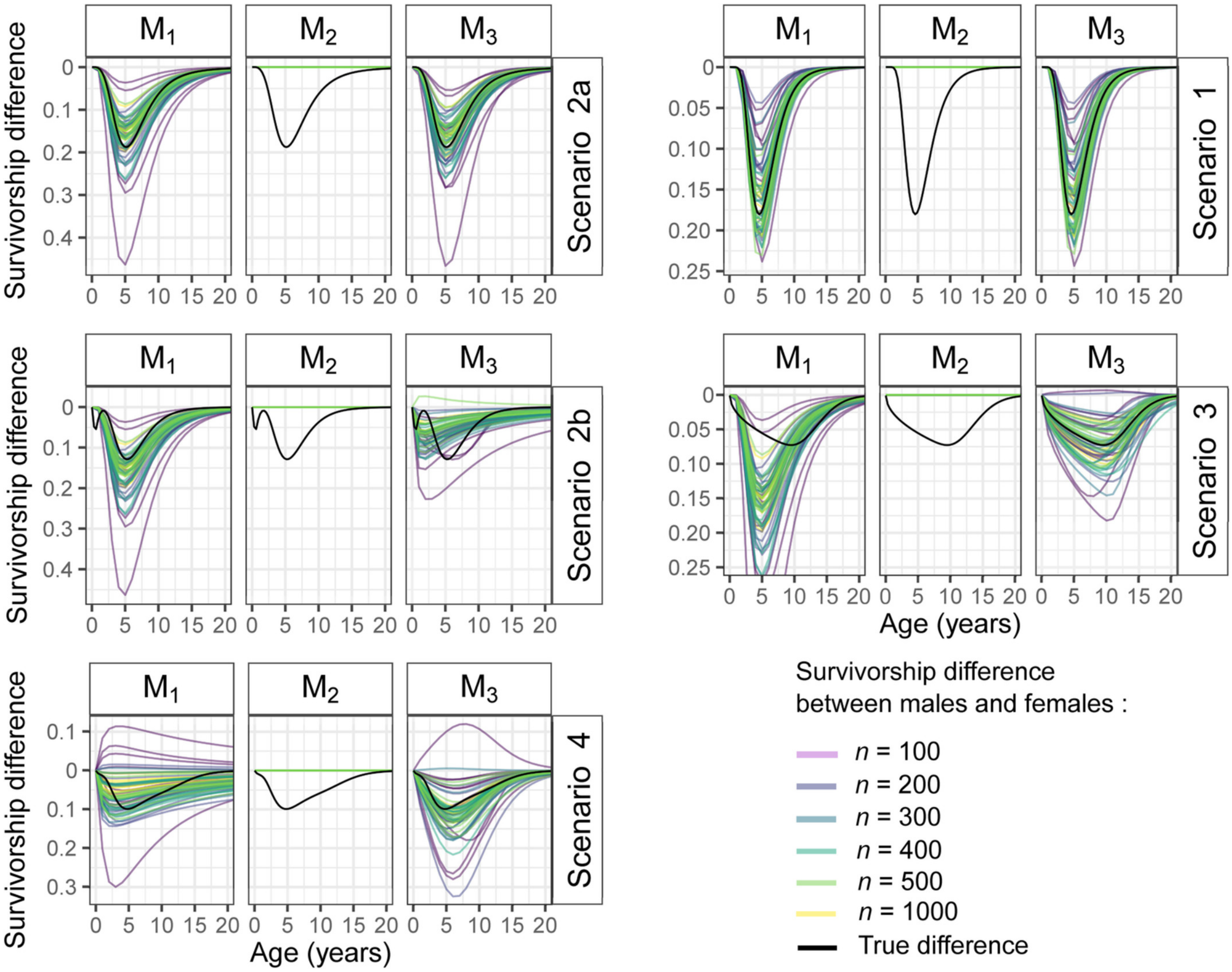


Figure 3.8: Estimated survivorship difference under each scenario. The covariate effect could correspond to that of sex (e.g., x = 1 for females and x = 0 for males). Ten estimated difference curves are depicted in each panel and compared with the truth.

Case studies

Estimated survivorship curves from published dataset are plotted against the Kaplan-Meier curves in Figure 3.9 for each model. Model $\mathscr{M}_3$ was the most flexible: it provided the most accurate estimates for each dataset. Uncertainty, as measured with 80% credible intervals were narrower with model $\mathscr{M}_3$, and overlapped most with Kaplan-Meier estimates. Model $\mathscr{M}_3$ consistently had the lowest WAIC.

In the handful of case studies where covariates were available, a similar pattern arose. Including covariate can be expected to account for more variation in the data, and a lower WAIC. For both $\mathscr{M}_1$ and $\mathscr{M}_2$, this was indeed the case. For $\mathscr{M}_3$ it was only true with the (Murphy et al. 2012) dataset[11] . The estimated covariate effect for both (Barlow and Hohn 1984) and (Kesselring et al. 2017) case studies is summarised on Figure 3.10.[12] Models $\mathscr{M}_1$ and $\mathscr{M}_3$ both estimated a survivorship difference between each covariate. As it is the case without covariates (Figure 3.9), the $\mathscr{M}_3$ curve fits the Kaplan-Meier estimate better. However, there is a discrepancy between both, for each covariate. $\mathscr{M}_3$ is able to spot a difference depending on covariate, but is not able to perfectly fit the Kaplan-Meier estimate.

[11] SI Text 4 and Table S1.

[12] SI Text 5.

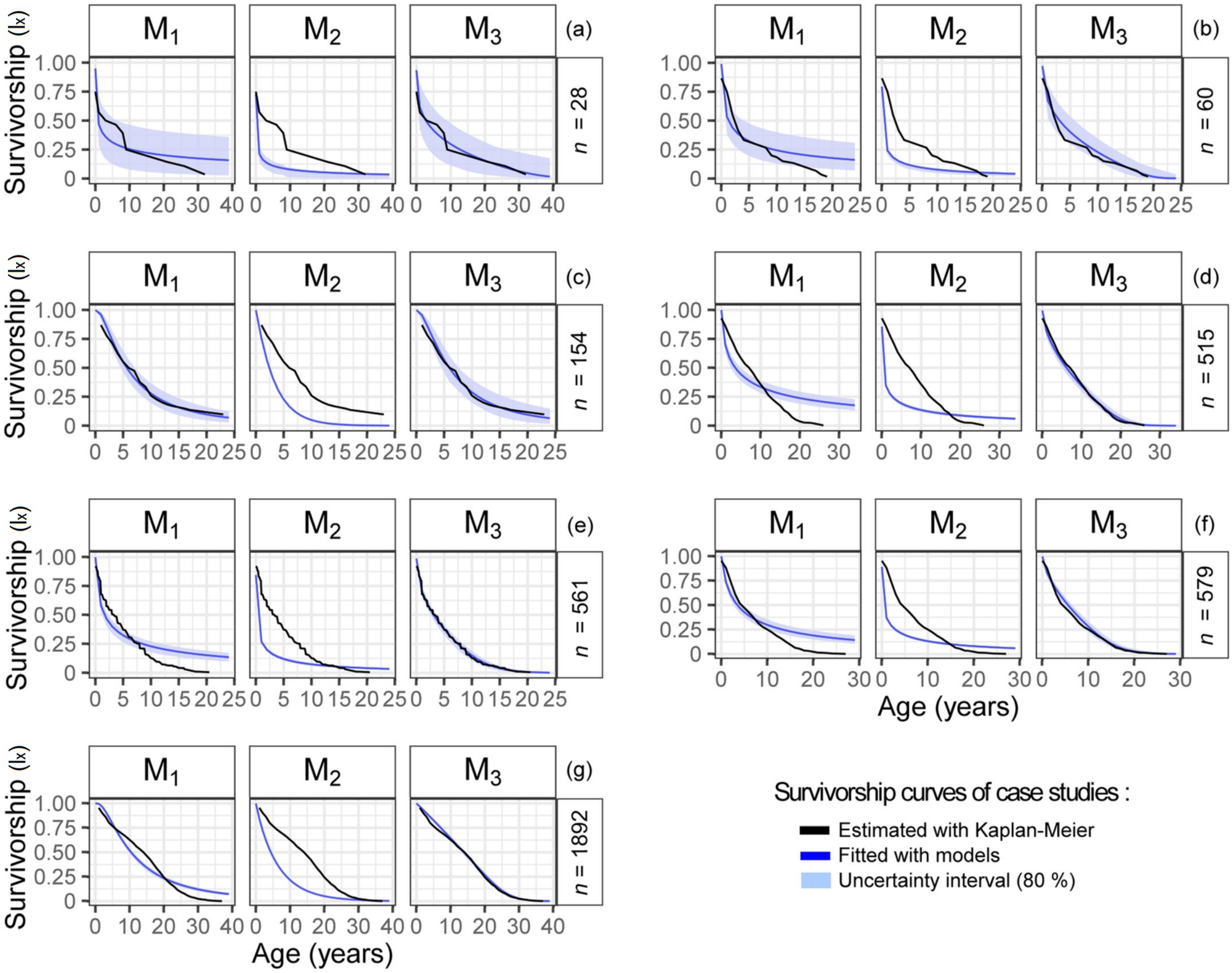


Figure 3.9: Survivorship curves estimated from published data sets. Each subpanel corresponds to a case studies in Table 2. Data set size is represented horizontally. Panels are associated to the following data sets:
a. Murphy et al. 2012
b. Slooten 1991
c. Rodriguez-Caro et al. 2019
d. Murphy et al. 2009
e. Kesselring et al. 2017
f. Saavedra 2018
g. Barlow and Hohn 1984.

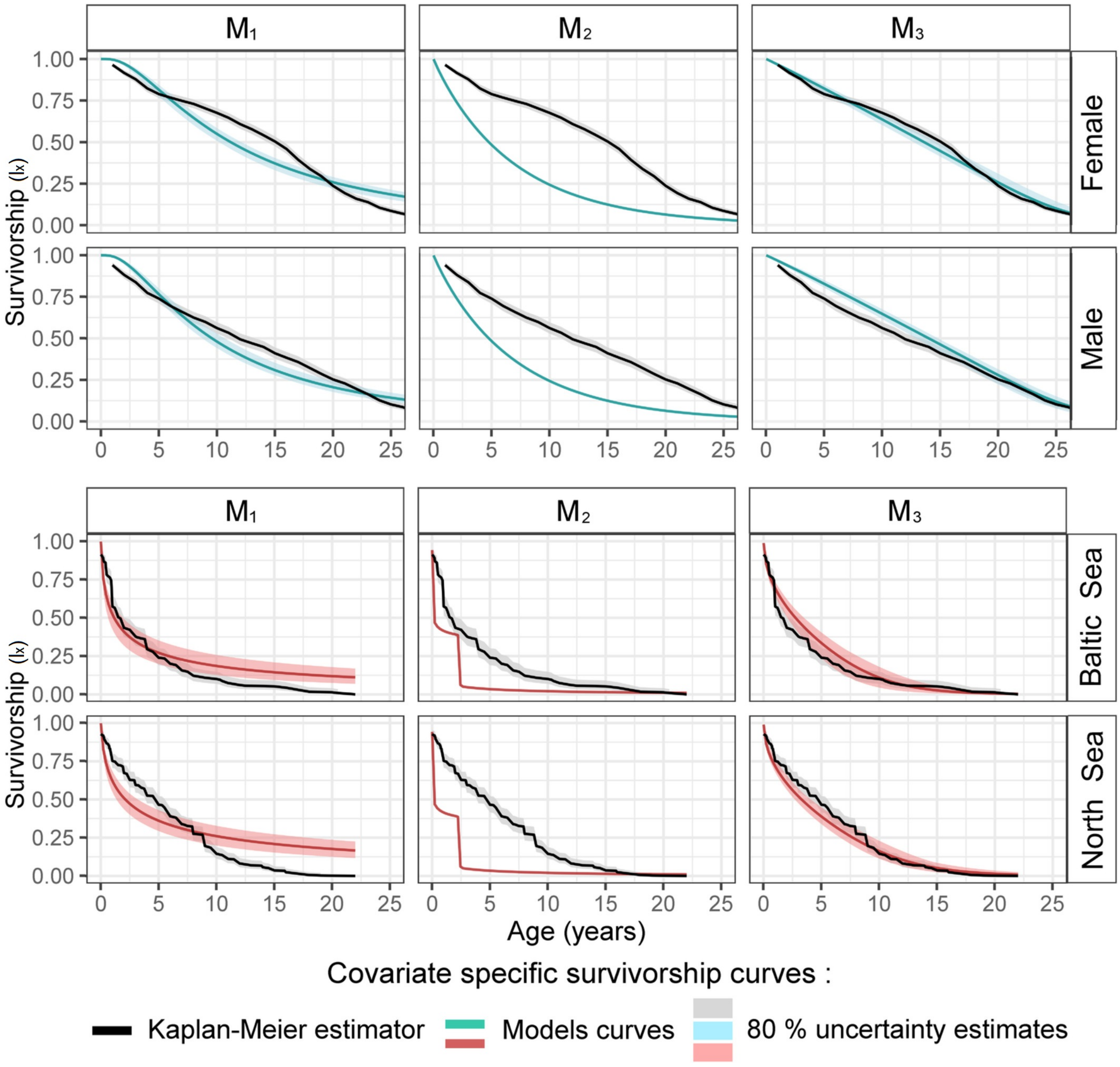


Figure 3.10: Estimated survivorship difference for both case studies.

3.4 Discussion: Implications of this new cross-sectional parametric approach

We assessed the ability of a simple linear mixed model to estimate hazard and survivorship rates with cross-sectional age-at-death data. We used Monte Carlo simulations to investigate the accuracy and precision of estimates across a variety of mortality patterns and several sample sizes. We compared the performance of three different models and found one model, the model $\mathscr{M}_3$, to be consistently better at predicting survival, even when misspecified.

Age-at-death data and sampling bias

To use age-at-death data, we assume that the population is under a stationary age distribution which is rarely the case in nature...

A crucial but implicit assumption of the cross-sectional approach to survival analysis is that the sample is representative of the population as a whole, particularly with regard to age structure (Caughley 1966). This assumption relates to the dataset, not to the modelling. The way in which the age-at-death data are collected is therefore crucial in supporting this assumption. Approximate protocols involving, for example, the recording of dead carcasses, hunting bags or population censuses must meet the representativity premise. However, it is possible that an implicit process (*e.g.* bycatch) shapes the observed age frequency (*e.g.* from stranded animals). In this case, it is necessary to explore some potential age-dependent selection bias in the population (Barlow and Hohn 1984). With stranding data, the assumption of a stationary age distribution needs to be supported by ancillary data, but ultimately it is likely to remain a working hypothesis on which any cross-sectional methods will be based. In the case of cetaceans, many species are not amenable to study with a longitudinal design, and strandings remain an important source of information (*e.g.* Murphy et al. 2009), particularly demographic information (Saavedra 2018; Ferguson, Stirling, and McLoughlin 2006). When longitudinal studies are not possible, there are very limited options to obtain demographic information. In some cases, a comparative approach may be possible where information on species with similar life histories can be leveraged (Caswell et al. 1998; Hashimoto et al. 2013). This choice is essentially based on the assumption of similarity between species. Even if comparative data are available, the ecological context may be too different to justify this approach in some instances. Strandings may be the only available source of data, and even if they are suspected to suffer from some selection bias, a pragmatic approach to conservation requires to use them (Boyd, Bowen, and Iverson 2010), keeping in

... so we should use auxiliary data to interpret results. But if age-at-death data is the only source of data available, so it should be used whenever possible.

mind the inherent limitations of these data.

Many conservation instruments specifically require the use of the "best available science" (according to the Marine Strategy Framework Directive EC 2008/56 in Europe). The operative expression "the best available science" can be broadly understood as what lies at the intersection of state-of-the-art methods, good data and accurate knowledge. In practice, there may be a hiatus between the canonical approach that should be, and the pragmatic one that can be pursued at the time conservation actions need to be decided. A conclusion of a species being data-deficient often leads to the doldrums with respect to conservation decisions (Parsons 2016). Likewise, the many uncertainties that can affect any scientific studies can easily lead to inaction regarding the implementation of conservation measures (Ascher 2004). It is because we are starkly aware of these limitations that we carried out this study to identify a pragmatic approach to estimate survivorship rates from age-at-death data. Crucially, all the models we used are conditional of the underlying sample being representative of the population it is taken from. Granting this assumption, we identified a simple model from (Reed 2011) to obtain accurate estimates.

We can inform conservation policies and management strategies with demographic parameters obtained from age-at-death data.

Prediction Accuracy and Models' Goodness of fit

Traditionally, estimating survivorship rates with cross-sectional data was done with parametric models such as the Siler or Heligman-Pollard models, and this is still the case for some marine mammals (Mannocci et al. 2012; Siler 1979; Heligman and Pollard 1980; Huang et al. 2012). These models aim at reproducing a bathtub-shaped hazard curve, but need several parameters to do so. Furthermore, they can be difficult to fit although new tools have been developed to use these models (Saavedra 2018). A remaining challenge with these models is to assess goodness of fit, to incorporate individual-level covariates and perform model selection. The simple parametric form of (Reed 2011) for analyzing the logarithm of age-at-death data provides a bathtub-shaped hazard with a linear mixed model, the current workhorse of ecologists (Bolker et al. 2009). This linear mixed modelling framework allows for a seamless incorporation of covariates, and to use standard tools for model selection and goodness-of-fit assessments. In other words, model $\mathscr{M}_3$ brings back survival analysis within the comfort zone of ecologists. We harnessed the simplicity of (Reed 2011) to conduct our Monte Carlo study, and found that the model suggested by (Reed 2011), our model $\mathscr{M}_3$, was very accurate in predicting survivorship (*i.e.* it consistently had the lowest RMSE), even in cases when it was not the true model behind the data[13] . This result

The most commonly used models for obtaining marine mammal survival from age-at-death data are the Siler and Heligman Pollard models.

These models can be used to obtain vital rates but their use is limited. Their construction is not simple and they do not allow for the estimation of vital rates as a function of various factors.

[13] SI Text 6.

is important as it suggests to start building model of increasing complexity from $\mathscr{M}_3$ (as it is done after Chapter 4) and use tools such as WAIC (Gelman, Hwang, and Vehtari 2014) to balance model complexity with prediction accuracy.

From our simulations, we can recommend a sample size of at least 300 individuals to obtain accurate and precise estimates of survivorship, from which age-specific survival estimates can be derived[14] This sample size recommendation is practical and realistic (*e.g.* Mannocci et al. 2012; Murphy et al. 2009; Kesselring et al. 2017). This recommendation is mostly to obtain precise estimates, but may be relaxed in some cases where only sparse data may be available (data-poor context hereafter). Estimates from a simple linear model with an individual frailty term, were accurate, if imprecise, with a sample size as small as 100. The possibility to use sparse data is critical as it can help conservation of elusive species, such as marine mammals, many of which being classified as data-deficient (Parsons 2016; Schipper et al. 2008). Some of the case studies presented in this paper support this statement, although, with so few data, including covariates in the model will be difficult or will require great care (see for example Cox et al. 2019). Rodriguez-Caro et al. (2019) recently provided an approach to estimate survival in data-poor settings using inverse modelling, also to obtain accurate estimates of demographic rates. With the latter, population matrix models can then be used to assess population dynamics and the fate of populations over time (Caswell 2000).

Our approach correctly estimates survivorship with 300 age-at-death data and correctly approximates hazard with 500 age-at-death data.

Hazard and Frailty

A linear mixed model can fit age-at-death data very well: this ability comes for the individual frailty term, which corresponds to an individual random effect in the mixed modelling framework. Individual frailty in statistical models translate the empirical observation that two similar individuals (with respect to observable features of their phenotypes) can nevertheless differ markedly in their longevity (Cam, Aubry, and Authier 2016; Kannisto 1991). The parametric form (*i.e.* exponential) for individual frailty gives extra flexibility to the model, and can accommodate a bathtub-shaped hazard curve (Reed 2011). However, in our simulations, we found that estimating hazard rates was more difficult than estimating survivorship rates (Figures 3.6 & 3.7). Thus, even though we identified a model ($\mathscr{M}_3$) for reliable and accurate estimation of survivorship, the same model was less reliable with respect to hazard. In other words, the individual frailty term in our model $\mathscr{M}_3$ should not be over-interpreted, and is probably best seen as a statistical device for robust estimation. Hazard estimation is a difficult statistical problem (Watson and Leadbetter 1964), for which there are better

The inter-individual frailty parameter that allows the mortality curve to have a bathtub shape should not be interpreted alone. It is not yet a biological indication in its own right.

[14] SI Figure 14.

tools available, especially non-parametric ones (see for example Hanson and Jara 2013), than the simple parametric approach we considered in this study. Non-parametric approaches to infer the shape of the hazard curve are data-hungry: Hanson and Jara (2013) use Bayesian non parametrics, which is better described as a model with a massive number of parameters (Hoff 2013). The traditional Kaplan-Meier approach is truly a non parametric approach but it does not give access to the underlying hazard, and give rough (that is, non-smooth; Figure 3.7) survivorship rates with small sample size. In data-poor settings, parametric modelling remains attractive because it has interpretable parameters (*e.g.* individual frailty) and because these parameters can smooth out noise in data, yielding more precise estimates if the model is at least approximately correct, or more pragmatically, if it is grounded in theory (*e.g.* bathtub-shaped hazard for natural populations) and cannot be rejected from a goodness-of-fit test. It is precisely in this data-poor setting that we envision our parametric modelling approach to be most useful. Because the approach boils down to linear mixed effects modelling, great flexibility in model specification of additional random effects (*e.g.* year effects, sex-specific frailties) is possible provided there are enough data to offset the increase in complexity.

Benefits and limits

Our model performs well in case of unimodal age-at-death distribution...

We believe our approach is very valuable to estimate survivorship from sparse data but may be inadequate for bimodal age-at-death data distribution. A bimodal distribution of age-at-death data may be a sign of selection in data collection (Barlow and Hohn 1984). Rather than consider the sampling as biased, our approach can accommodate the selection phenomenon through two ways. Firstly, it is possible to consider the selection bias as a covariate in the study if one such covariate is available (*e.g.* By-catch index). If no such covariate is available, it may be possible to build a mixture of two models (*e.g.* $\mathscr{M}_1$ and $\mathscr{M}_3$) in order to take into account an additional mortality on some age classes. However, such a development requires to conduct its own simulation study which is beyond the scope of this study. Since our approach is based on linear regression, it is straightforward to expand the model (*e.g.* random year effects, mixtures) while using familiar and well established methods for model selection (*e.g.* WAIC) and assessment of model fit (*e.g.* posterior predictive checks, R^2 statistics). These features are assets, and suggest that our approach is complementary to existing ones (*e.g.* Saavedra 2018; Siler 1979; Heligman and Pollard 1980) to estimate vital rates in some data-poor species. On the basis of the size and morphology of the animals, the largest can be defined as "megafauna" (Estes et al. 2016). Large animals, usually long-lived vertebrates, refereed as "megafauna" are generally elusive. When associated with the marine environment (referred as "marine megafauna") it may be more difficult to obtain data and study these animals given their living environment. This is particularly true for demographic data and studies. Given their functional importance (Pimiento et al. 2020), there is a need to inform the biology and the demography of these species. The approach presented here may be of interest to study the demography of marine megafauna, in particularly marine mamals such as the common dolphin in the North-East Atlantic. And this is what we will see in the next Chapter.

... and can allow joint estimation of fertility in a joint modelling approach.

North-East Atlantic common dolphin population viability

4

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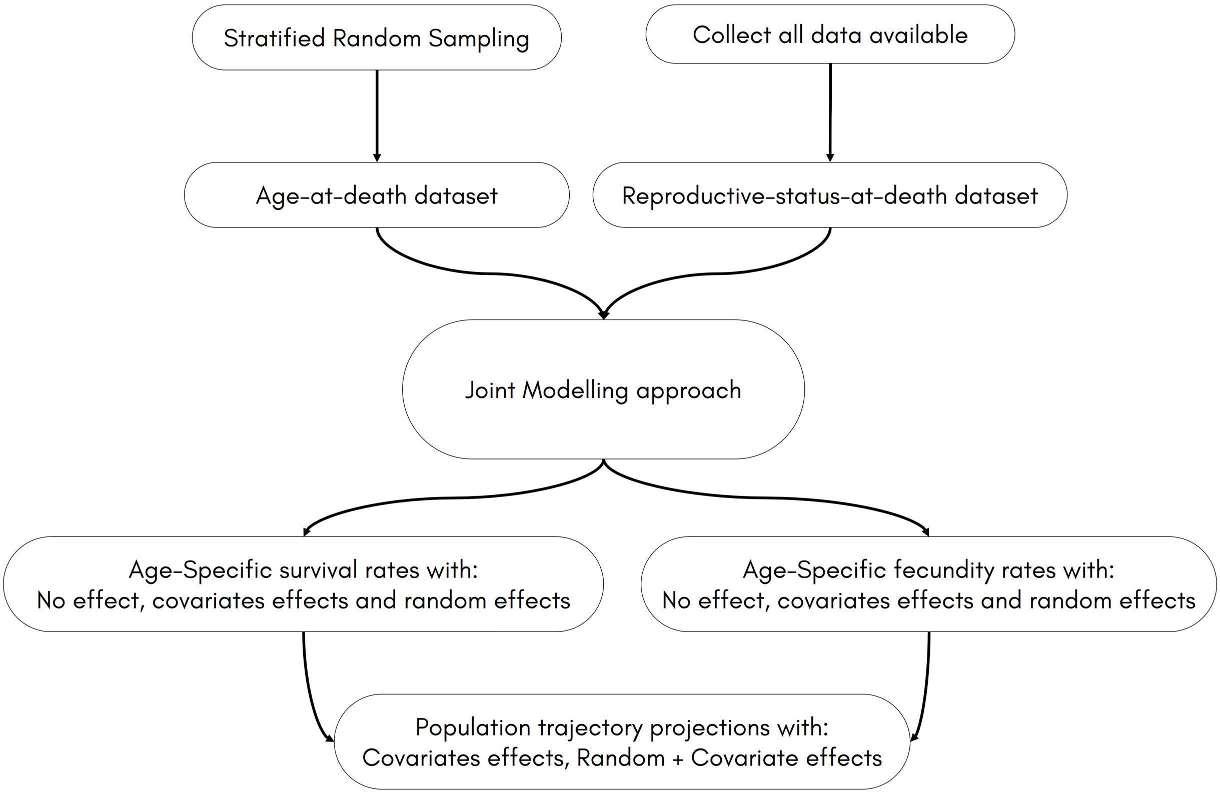
4.4 Discussion: Important aspects and implication of the study 96

The common dolphin is one of the most abundant and widespread odontocetes in the world. This species is very common in the Atlantic Ocean as it is found from the centre to the north of the Atlantic. The North-East Atlantic population, distributed from Gibraltar to Norway, is considered a management unit by the OSPAR Commission. This species is a top predator in European waters, supposedly a keystone species. The current status of this population (and its future trend) is a key issue in the MSFD for descriptors 1 and 4. Since 1997, the number of common dolphins found stranded on European coasts, notably in France, has been steadily increasing. Among these individuals, there is a high proportion of individuals showing signs of capture in fishing nets. Previous demographic studies have shown that this population is not viable. To study its viability, sampling was carried out in the conventional way (collection of all available data on age-at-death and reproductive-status-at-death). The analysis of these data was carried out using standard survival analysis methods. In the previous chapter, we saw that it is possible to use a new approach to survival analysis that allows more flexibility than conventional methods. In this chapter, we will see how it is possible to combine this new approach with a sampling procedure that has never been used before to study the demography of a marine mammal species from a cross-sectional monitoring. By combining these two methods, we will see that it is possible to quantify more precisely the vital rates of the North-East Atlantic common dolphin population. It is also possible to highlight the effect of by-catch pressure on this population from a demographic point of view. Finally, it is also possible to highlight the presence of a cohort effect showing a modification of the value of the vital rates during the temporal period considered. The population does not seem to be viable and its condition seems to have deteriorated over the time period considered. Anthropogenic mortality pressure from bycatch appears to have a negative effect on the survival of the population. As the individuals used in this study are specific to the Bay of Biscay, it is difficult to generalise the results to the OSPAR management unit. However, the vital rates produced can inform the MSFD descriptors.



Flowchart of the study presented in this chapter.

Publication in prep.

This chapter is associated with one publication which is under preparation:
Rouby, E., Authier, M., Mauchamp, A., Mendez-Fernandez, P., Dabin, W., Thobois, J. and Ridoux, V. North-East Atlantic common dolphin population viability and vital rates variations. In prep.

4.1 Introduction: A need for demographic knowledge

The common dolphin is one of the marine mammal species assessed under the MSFD, in particular under descriptors 1 and 4 which include marine mammals (Table 4.1 for details of the descriptors and their relevance to marine mammals; M. B. Santos and Pierce 2015). This marine mammal species is found in all temperate and tropical parts of the oceans (Perrin 2018). Individuals are organised into distinct populations, or stocks, which may be associated with different management issues (Natoli et al. 2006; Amaral et al. 2012). The North-East Atlantic population is a population with high conservation stakes today, particularly with regard to the MSFD (European Parliament 2008), since it is the most abundant cetacean species in European waters (Hammond et al. 2017). It is important to conserve this population for the purposes of the MSFD, but it is currently subject to high levels of extrinsic mortality through bycatch (Murphy et al. 2021; Peltier et al. 2016) which can impact on its viability (Mannocci et al. 2012).

Table 4.1: Summary of the MSFD descriptors and how they relate to the project. Each descriptor is summarised. For each, its relevance to marine mammals is addressed. As well as the associated demographic need. For a more precise description of the descriptors see M. B. Santos and Pierce (2015) or European Parliament (2008).

Descriptor	Relevance for marine mammals	Need for marine mammals demographic information
1. Maintain biological diversity	Marine mammals is an important functional group as marine megafauna and sometimes keystone species	**Yes**
2. Non-indigenous species	Not addressed	No
3. Populations of commercial fish/shellfish biologically safe	Not addressed	No
4. Elements of marine food webs occur at normal abundance	All marine mammals in european waters are top predators	**Yes**
5. Human-induced eutrophication is minimised	Not addressed	No
6. Sea-floor integrity maintained	Not addressed	No
7. Hydrographical conditions not unfavourable	Not addressed	No
8. Concentrations of contaminants	Due to their trophic position, marine mammals bioaccumulate pollutants	No
9. Contaminants in fish and other seafood	Not addressed	No
10. Properties and quantities of marine litter do not cause harm	Ingestion of plastics and entanglement in debris	No
11. Introduction of energy, including underwater noise, non-disruptive	Underwater noise can have a range of effects on marine mammals	No

The MSFD descriptors are used to assess the status of the population and are based on sets of criteria. Under the MSFD, descriptor 1 requires the production of indicators of demographic status to assess the viability of the common dolphin population in the face of bycatch pressure (Benjamins et al. 2014). The aevaluation of the achievement of the objectives set by the descriptors is carried out on the basis of a set of criteria which constitute a descriptor[1] . Within descriptor 1 in particular, the demography of marine mammals (and therefore the common dolphin) occupies an important place (European Parliament 2008). The only biological indicators recognised to define the status of the population in the North-East Atlantic (*i.e.* increasing, stabilising or decreasing) are the abundance estimates obtained from aerial and boat surveys[2] (Hammond et al. 2017, 2013). Seasonal abundance estimates have been collected on a smaller scale (Laran et al. 2017; Authier et al. 2018) but their purpose is rather to provide information on the abundance of the common dolphin population on a seasonal basis. Such abundance estimates are not sufficient to provide information on the status and viability of the population, and the impact of bycatch on its viability (Murphy et al. 2021; M. B. Santos and Pierce 2015). There is a need to produce demographic indicators (vital rates) to better inform the management policy of the MSFD and describe the status of the population (Murphy et al. 2021).

Demography is a more refined indicator than abundance for determining the status of a population and an essential complement in terms of management. The use of abundance data to indicate the viability of a population is mainly based on observed trends and the determination of depletion levels (B. L. Taylor et al. 2007). In the context of bycatch pressures, demography can be a supplementary indicator to abundance surveys to study the anthropogenic demographic impact on the common dolphin population (see A. J. Read, Drinker, and Northridge (2006) for a broader discussion regarding marine mammals). Before detecting a change in abundance, it is possible that the values of the life history traits will change because their evolution depends on the extrinsic pressures (*e.g.* bycatch) that the population is undergoing (Stearns 2000). In the case of the common dolphin, the primary pressure on the population seems to be strong, given the number of individuals found stranded on the French seashore (Dars et al. 2020). Obtaining demographic data on this population appears both essential from an applied point of view and interesting from a more fundamental point of view in order to highlight possible variations in the values of important vital rates associated with survival and reproduction. The vital rates of the common dolphin population have already been estimated, as well as the life tables, and the population has been considered non-viable under current bycatch pressures (Mannocci et al. 2012) but it is necessary to complete these analyses.

Obtaining vital rates can be improved by using a more representative sampling method and more flexible statistical methods. Previous demographic work has provided age-at-death data using all available biological material, as is usually done to study the demography of odontocetes (Barlow and Hohn 1984). From these

[1] See Table 4.2 for a schematic presentation of each criteria within the descriptors relevant to marine mammals and their need for demography

[2] See Appendix Table 1 to find out about surveys by campaign and by season.

Table 4.2: Summary of descriptor criteria within which the production of demographic state indicators is required. See European Parliament (2008) for a less schematic description and the detailed elements. The primary and secondary aspects are not shown here for the sake of clarity. But the demographic issues appear as secondary.

Descriptor	Criteria	Need for demography
1. Maintain biological diversity	**D1C1** The mortality rate per species due to bycatch is below the level that would pose a threat to the species, so the long-term viability of the species is assured	**Yes** through the use of population growth models taking into account removals and quantification of the byctach effect on vital rates
	D1C2 Anthropogenic pressures do not adversely affect the abundance of populations of the species concerned, so that the long-term viability of these populations is guaranteed	No
	D1C3 The demographic characteristics (*e.g.* size or age structure, sex distribution, fertility rates, survival rates) of the species' populations indicate a healthy population, unaffected by anthropogenic pressures	**Yes** through the production of life-tables and vital rates using new cross-sectional methodologies
	D1C4 The range of the species and, where appropriate, their pattern of distribution within that range, is consistent with prevailing physiographic, geographic and climatic conditions	No
	D1C5 The habitat for the species has the necessary extent and condition to support the different stages in the life history of the species	No
4. Elements of marine food webs occur at normal abundance	**D4C1 – Primary** Diversity (species composition and relative abundance) of the trophic guild is not affected by anthropogenic pressures	No
	D4C2 – Primary: The balance of total abundance between trophic guilds is not affected by anthropogenic pressures	No
	D4C3 – Secondary The size distribution of individuals within a trophic guild is not affected by anthropogenic pressures	No
	D4C4 – Secondary The productivity of the trophic guild is not affected by anthropogenic pressures	**Yes** through the use of population growth models taking into account anthropogenic pressures

data, vital rates were estimated using standard survival models from the literature (Siler 1979). Sampling bias is poorly controlled and it is difficult to identify variations in the estimated vital rates and the effect of variables (*e.g.* cause of death, area or sex). We provide here a complementary and updated demographic estimates which helps to fuel the debate on how to consider and study an elusive marine mammal population such as the common dolphin in the North-East Atlantic. In order to better control the bias in the representativeness of the strandings, we performed a stratified random sampling to select individuals (females and males). For each individual, where possible, we obtained age-at-death data using odontochronological methods on dental tissue. We then constructed another dataset of reproductive status from the analysis of all available gonad samples for both males and females. The data on age and reproductive-status-at-death range from 1997 to 2019. From these data, we obtained vital rates associated with survival and reproduction using a joint model (including survival and reproduction). The survival part is based on the model construction presented in Chapter 3. The reproduction part is based on an Accelerated Failure Time model construction. Vital rates were estimated in three ways: without effect, with covariates (sex and cause of death) and with random effect (years of death). Finally, we filled a Leslie matrix model with the obtained vital rates to obtain the population growth rate and to geometrically project its evolution.

4.2 Methodology: Stratified random sampling and Joint modelling

The methodology developed in this study implies five major actions (or steps):

- 1. Define the sampling plan
- 2. Acquire data from biological samples
- 3. Estimate vital rates (with covariates and random effects)
- 4. Build life-tables
- 5. Project the fate of the population

Sampling of a stranded population

A major problem with randomly selecting individuals for analysis from a stranded population is that representativeness bias is not controlled. Random selection can add representativeness bias to the already existing bias associated with the stranding filter. Ideally, age and reproductive-status-at-death distributions should be exactly the same between the stranded population and our sample. This would allow us to avoid adding bias and to be sure that the only bias associated with our results is due to the stranding filter. One way to control for this selection bias is to implement a stratified random sampling design. This is based on the choice of important criteria defining strata within which random sampling is carried out (Figure 4.2).

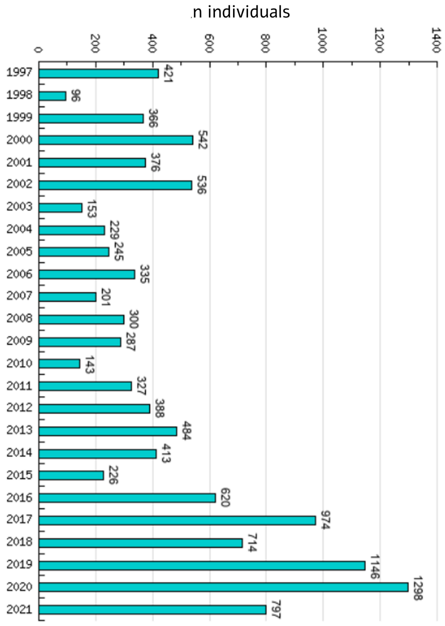


Figure 4.1: Strandings records on the Atlantic French seashore recorded by the "Observatoire Pelagis" between 1997 and 2021. The number of stranded dolphins has been increasing since 1997 with a record number of strandings in 2020. In the project presented, the time series extends to part of 2019. The whole of 2019 as well as 2020 and 2021 are presented to show the latest stranding estimates.
Data from Observatoire Pelagis website: `https://www.observatoire-pelagis.cnrs.fr/?lang=en`

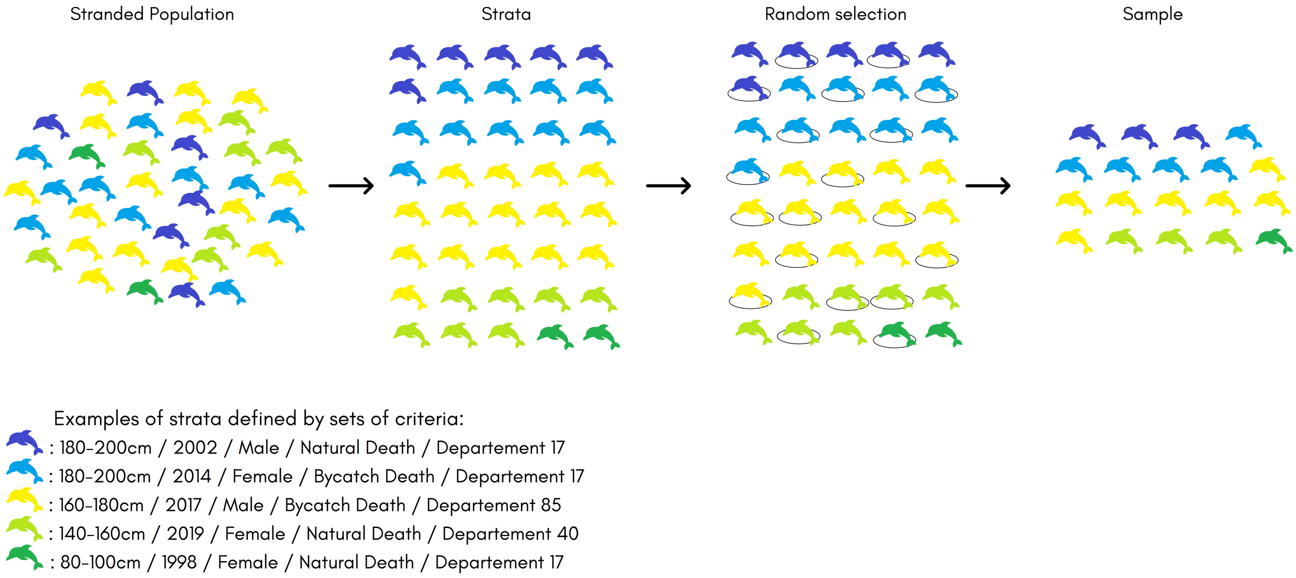


Figure 4.2: Diagram of the stratified random sampling. In this figure, the stratified random sampling method is illustrated. From the stranded population, each individual is assigned a value for the criteria of interest. These values are used to stratify the individuals. Within each stratum, random sampling is then carried out. The sample is obtained. The strata presented here and their associated criteria values are schematic. The number of strata is determined by the number of criteria values.

In order to maximise representativeness, a sampling design must be defined that takes into account several criteria that can influence the representativeness of demographic data. We used a statistical sampling method used in various scientific fields (*e.g* forestry ecology, polls surveys or psychology) that has never been applied to study marine mammal demography from stranded individuals. The objective is to define a sampling plan that will allow the selection of the most representative individuals of the stranded population, from which biological samples will be obtained to provide data on age and reproductive-status-at-death. The 3 main steps (Figure 4.4) are as follows:

- **1.** The first step is to define the need for representativeness. On what basis to select individuals. To select the individuals, we chose 5 criteria that can influence the distributions of the demographic parameters. This selection is made in a non-hierarchical way:
  The first is **length** since length is an indicator of age and reproductive status.
  The second is **year**, since year can provide information on a possible cohort effect or even a change in the value of vital rates over time.
  The third is **sex** since it can be an element influencing age-at-death and it is essential to respect the proportions observed in the stranded population.
  The fourth is the **cause of death** because it seems necessary to transcribe the mortality signal as observed in the field.

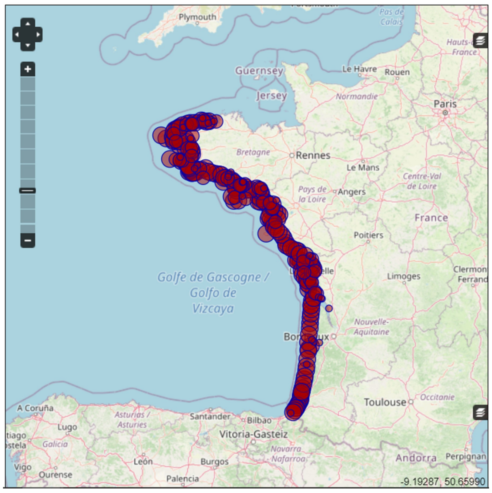


Figure 4.3: Map of all the stranded common dolphins records from 1997 to 2021. It can be seen that all strandings are recorded on the Bay of Biscay but none are recorded in the English-Channel.
Data from Observatoire Pelagis website: `https://www.observatoire-pelagis.cnrs.fr/?lang=en`

Examples of external examinations of stranded individuals to determine the cause of death of the animal are described Figure 2.19.

The fifth is the **location** that is not very important and can be removed, but it is intended to select individuals stranded all along the coast.

Having defined the criteria to be considered, it is necessary to calculate their proportion within the stranded population. The proportion of each criterion for the age-at-death dataset can be seen in Figure 4.8.

- **2.** Next comes the stratification step. For each stranded individual recorded in the stranding database, a value for each of the 5 criteria was assigned. Using the example in diagram 4.2, some individuals will have the following criteria values: 180-199cm, 2002, Male, Natural death, Department 17 while others will have: 180-200cm, 2014, Female, Bycatch death, French Department 17. These individuals share common criteria but do not belong to the same stratum because they differ by at least one criterion value. The stratification stage consists of classifying all the individuals in the stranded population database into different strata to ensure inter-stratum representativeness.

- **3.** Finally, random selection within each stratum is used to ensure intra-stratum representativeness. Individuals from the stranding database are selected on the basis of their criteria values but also on the availability of samples. Indeed, it is not possible to obtain teeth and gonads from all stranded individuals despite the existence of the National Stranding Network ("*Réseau National Echouage*" in French). Sample collection is dependent on the state of degradation of the animal (Figure 2.20).

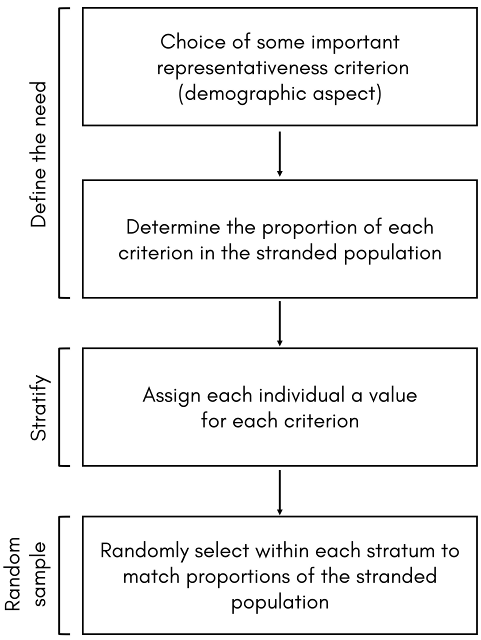


Figure 4.4: Main steps in stratified random sampling. This figure complements the diagram. It describes the important conceptual steps to recreate the sampling protocol.

In summary, the list of individuals in the age-at-death dataset is obtained by stratified random sampling. The list of individuals in the reproductive-status-at-death dataset is obtained by considering all available gonad samples.

Data acquisition through histology

Teeth: age-at-death dataset

The number of individuals with an age in the age at death dataset is 642. The methodology used to determine the age of an individual from its dental tissue involves a technique called odontochronology. This technique involves counting the annual layers in the teeth resulting from the incrementation of cementum and dentin in the dental tissue (Perrin and Myrick 1980). The deposition of these layers is mainly due to seasonal phenomena but other phenomena linked to the organism (stress) can cause the appearance of accessory growth layers (Hohn 2009). One year of life corresponds to 1 Growth layer Group (GLG) which consists of an alternating light and dark layer. This technique is considered valid for determining the age of common dolphins (Mannocci et al. 2012; Murphy et al. 2009).

The objective is to observe these growth layers. To do this, it is necessary to treat the teeth. The first step was to decalcify the teeth. Here the teeth were placed in a bath of concentrated DC3 acid. The decalcification time ranged from 3 to 48 hours depending on the size of the tooth. Then teeth have been cut using a freezing microtome in a longitudinal section plan, a cut known as "dolphin cut" (Bowen and Northridge 2010). For each individual, three teeth were removed, all from the mid-left jaw. Six sections were produced from each tooth for a total of 18 sections. These sections were then stained. The staining was carried out with toluidine blue (a frequently used stain) which allows the growth curves to be highlighted (Bowen and Northridge 2010). The stained sections were finally placed on slides for microscopic observation. Three slides per individual were produced, each with 6 sections. An example of the final product is available in Figure 4.5, which shows the growth curves at the apex, middle and base of the tooth for three individuals of different ages and without the same proportion of accessory striae.

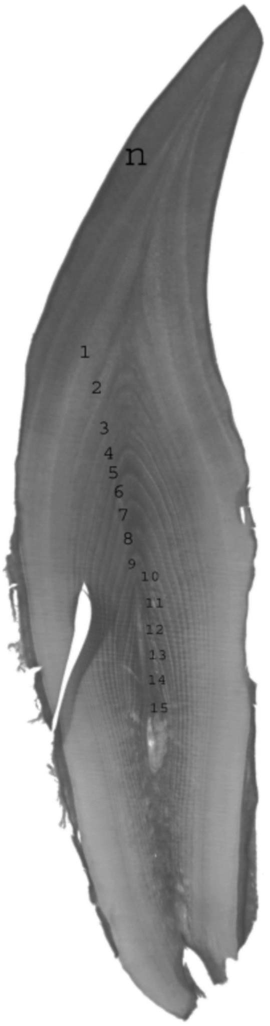


Figure 4.6: Growth layer groups (GLGs) in a common dolphin teeth. Years are depicted with numbers and neonatal line with "n". Photo from Murphy and Rogan (2006).

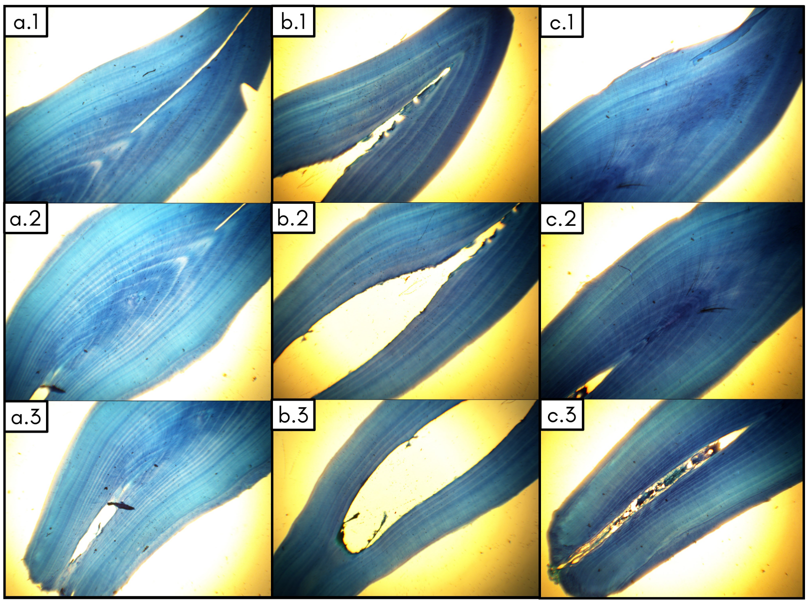


Figure 4.5: Tooth sections from three individuals in the age-at-death dataset. For each individual (a, b and c), Growth Layer Groups and accessory striae can be seen. The reading is done from the left or right side of the tooth. The age can be read on three areas for confirmation: the apex (1), the middle (2) and the base (3).

Two age determinations were made to construct the age-at-death dataset. In each case, three readers were required. One of the readers was common to both periods, the trainer with the most experience in age determination. For age determination that occurred during the project, if the difference between readers was less than 2 years, estimates were averaged. If the difference was more or equal to 2 years, readers were discussing to reach a consensus. If it was not possible, only age reading of the trainer was taken into account. All readings were made without prior knowledge of body length or sex.

Gonads: reproductive-status-at-death dataset

The number of individuals with age and reproductive status in the reproductive status dataset is 240. For all the individuals, age was also available. When the state of decomposition of the animal allowed collection of the gonads, the left and right gonads were sampled and preserved in 10% formalin with 10 volumes of ethanol. Reproductive status was assessed for both males and females. We also chose to consider males because the analytical framework allows allows for the inclusion of covariates (Rouby, Ridoux, and Authier 2021).
he size of the male testicles depends on the season with an increased size during the mating periods (May to September) (Evans and Teilmann 2009). It is hypothesised that this size adaptation is associated with spermatic competition (Murphy, Collet, and Rogan 2005). For this reason, macroscopic examination alone does not allow the reproductive status of the male to be determined. We sent the testicular samples to an independent histology laboratory which provided us with testicular histological slides. From these cross-sections, we determined the reproductive status based on the signs of spermatogenesis, including spermatozoa in the tubules and/or mature spermatozoa present in the epididymes (A. J. Westgate and A. J. Read 2007; Figure 4.7).

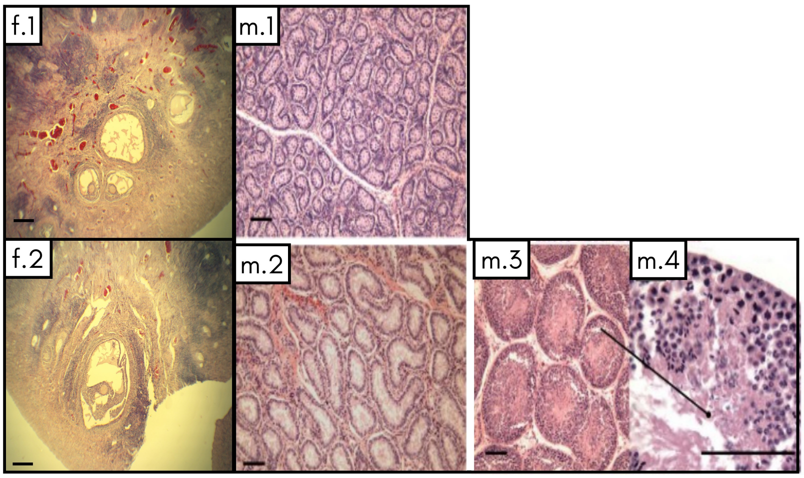


Figure 4.7: Histological sections of common dolphin gonads. The female gonads (ovaries) are indicated by the letter f. De Graaf follicles can be seen in the sections. The male gonads (testicles) are indicated by the letter m. **m.1**: immature individual with small underdeveloped seminiferous tubules and a relatively high degree of interstitial tissue. **m.2**: Mature but regressed testis. Small tubules and high amount of interstitial tissue. **m.3**: mature in production with increased tubule size and few interstitial tissues. **m.4**: higher enlargement of the mature tubule showing signs of spermatogenesis.
Black scale bar = 100 μm

For females, maturity was determined from the ovarian structures which are referred as *corpus*. Only the left ovary was observed as it is usually larger than the right one and contains twice as many *corpus*. The primary follicle, which contains an oocyte embryo, develops into a secondary and then a tertiary follicle before maturing into a "de Graaf" follicle. The oocyte is expelled into the fallopian tube when the follicle reaches the "de Graaf" stage. The follicle then deteriorates as a *corpus luteum* and finally into a scar on the ovary (R. J. Harrison and Ridgwa 1971) which are refereed to as *corpus albicans* (Figure 1 in Appendix 7.4). The concept of persistent *corpus albicans* have been questioned for the common dolphin and it is now assumed that it is not possible to estimate the number of gestation based on the presence of *corpus albicans* (Dabin et al. 2008). Table 4.3 summarises the determination of the reproductive status of females based on histological observation.

Table 4.3: Characteristics of the different reproductive stages.

Ovarian features	Reproductive state
No mature follicle	Immature
De Graaf follicle and no *corpus albicans*	Pubscent
De Graaf follicle and one or some *corpus albicans*	Resting mature
corpus luteum with or without a fetus	Pregnant
corpus luteum and productive mammary glands	Mature pregnant lactating

The definition of pubescent status is possible for both sexes and for several species of delphinids (Murphy, Collet, and Rogan 2005; Goodall et al. 1997; Rosas and Monteiro-Filho 2002; M. B. Santos et al. 2008). For females the age-at-first-reproduction is commonly assumed when there is a *corpus albicans* (Slooten 1991). Females are assumed to be pregnant as soon as they reach maturity (Mannocci et al. 2012) despite of the non-persistence of ovarian scares (*corpus albicans*) for the common dolphin (Dabin et al. 2008). Using pubescent status, we did not explore the age-at-first-reproduction (AFR) and age-at-sexual-maturity (ASM) as it is commonly done in the literature. We explored the access to puberty. I think that this parameter is more sensitive to life history changes. However, we still compute the proportion of sexually mature females as it is commonly done in the literature in order to better compare our observations with previous works on this population.

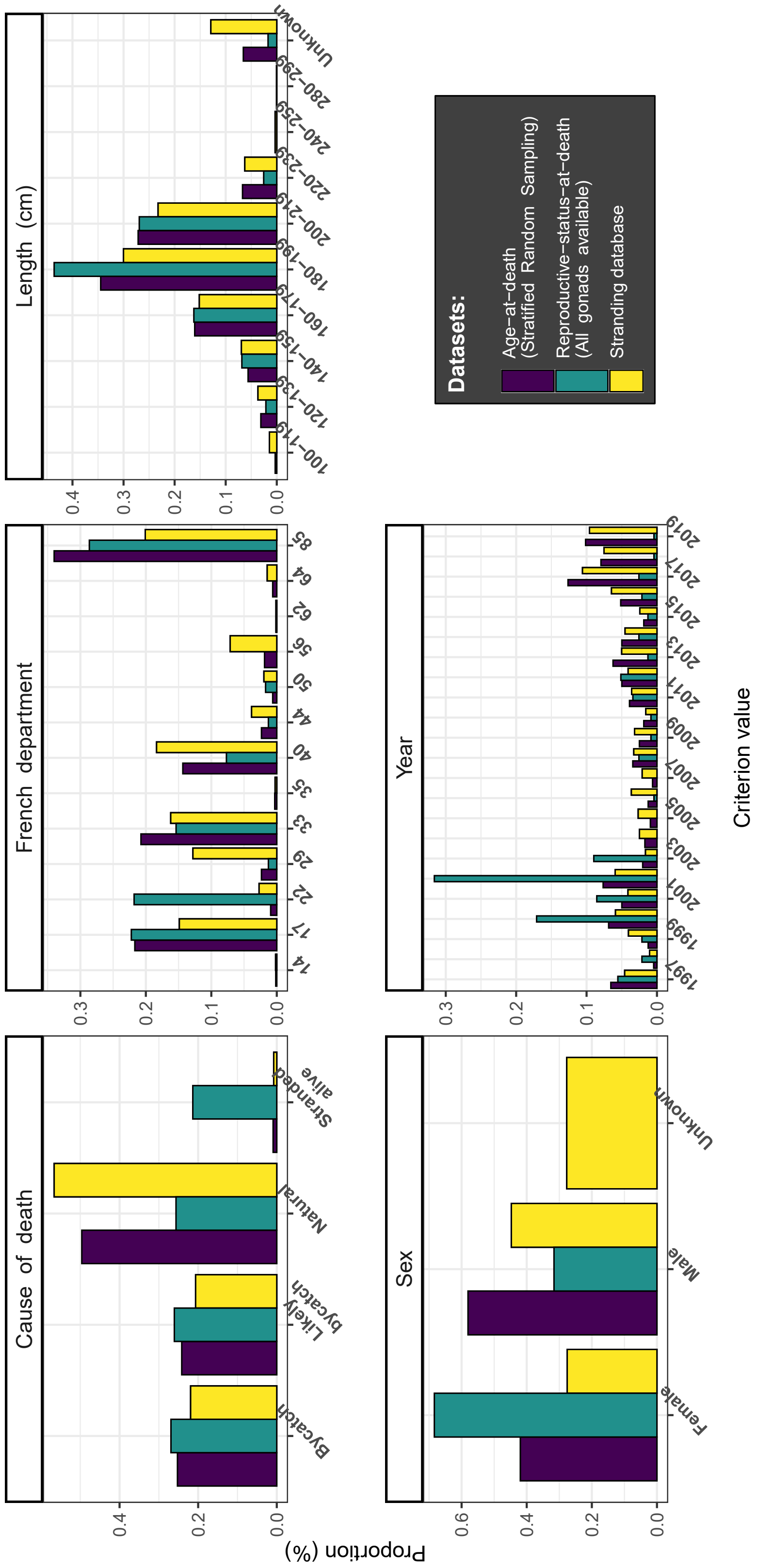


Figure 4.8: Comparisons of proportions of each criterion value for the stranding database and the two study datasets. The stranding database is shown in yellow. The age-at-death dataset in dark blue. The reproductive-status-at-death dataset in blue-green. Stratified random sampling allows for similar proportions between the age-at-death dataset and the stranding database, including cause of death, years, size and sex. Within the reproductive-status-at-death dataset, there is a large proportion of samples from the Biocet[a] program conducted in 2002. There is also a greater proportion of females than males, contrary to what is seen in strandings. Individuals of 180-199cm also seem to be over-represented. The causes of death are globally balanced but not representative of the stranding signal.

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[a] EU-funded BIOCET project (Bioaccumulation of persistent organic pollutants in small cetaceans in European waters: transport pathways and impact on reproduction, EVK3-2000-00027). See Pierce et al. (2008) for a study within this program.

Joint estimation of vital rates with a null effect, covariate effect and random effect

The previous steps have provided data on age and reproductive-status-at-death from which we can calculate vital rates. Usually, these vital rates are calculated from separate models. The Siler (1979) and Heligman and Pollard (1980) models are used to calculate vital rates associated with survival (Saavedra 2018). Logistic regression is used to calculate the vital rates associated with reproduction (Mannocci et al. 2012; Murphy et al. 2009). In the previous chapter, I described a new approach to survival estimation based on the Reed model (Reed 2011). We have developed a similar approach for estimating vital rates of reproduction by considering an Accelerated Failure Time model[3] (AFT) model. Rather than considering these models separately, we combined them into a joint model.

Cohort effect

The cohort effect is the proportion of the observed outcome that is due to the characteristics of the cohort.
Here, the cohorts are annual and have death as a common event. The cohort effect captures the effect of the common characteristics of individuals who died in the same year on the estimated vital rates.

Model selection

The estimation of the parameters of the two models is linked by the presence of random effects related to the year of death of the individuals. This random effect is analogous to a cohort effect (see margin-box for a definition). We considered 8 increasingly complex models. The first 2 do not involve the common cohort effect (no year effect). For each model, we computed the Widely Applicable Information Criterion (WAIC) and the Leave-One-Out cross-validation Information Criterion (LOOIC) as they allows to select the better model given the out-of-sample prediction (Vehtari, Gelman, and Gabry 2017). The better model to use is the one with the lowest WAIC or LOOIC. The selection given each model complexity is detailed in Appendix Table 1[4] . According to both WAIC and LOOIC, the better models were the 8 and the 7. From the perspective of statistical parsimony we used the model 7 as it is less complex than the 8 (no correlation between survival and reproduction estimation).

Table 4.4: Models specification. Model 1 and 2 are not joint models. Simple: a null effect, Cov: Covariate effect, Years: Random effect (joint modelling on Years), Cor: Correlation between random effects, Trend: Trend effect on random effects. WAIC and LOOIC are depicted in Appendix Table 1.

Model	Specification	Joint modelling
1	simple	No
2	cov	No
3	years	Yes
4	years + cor	Yes
5	cov + years	Yes
6	cov + years + cor	Yes
7	cov + years + trend	Yes
8	cov + years + trend + cor	Yes

We also used the approach commonly used in the literature to estimate survival and reproduction of common dolphins (*i.e.* Siler, Heligman-Pollard and logistic regression). I do not detail here the functions related to these approaches, but I describe them in Appendix 7.4. Only the models and functions associated to the joint modelling approach will be detailed. Functions' parameters are estimated using a Bayesian framework. From the previously obtained data, the times to the event (death or puberty) are used to estimate the parameters of the models. These parameters are then entered into each function to calculate vital rates. The details of

[3] 3: Parametric model that assumes that covariate accelerate or decelerate the reaching of the event.

[4] 4: For technical details of convergence and parameterisation see Appendix subsection 7.4

the estimated vital rates and the associated models are provided in Table 4.5:

Table 4.5: Vital rates information. For each important vital rate here, the mathematical notation, method of calculation and inclusion or not in the Leslie matrix model are detailed. Only age-specific survival and fecundity rate (female offspring) calculated from the joint modelling approach are used to inform the Leslie matrix. The fecundity rate is calculated using the proportion of mature females obtained from the joint modelling approach. The latter takes into account the pubescent status as a reference event.

Vital rate	Notation	Calculation	Use in the Leslie matrix model
Survivorship	l(x)	Siler & Joint model: Equation 4.2	No
Age-specific survival rate	S(x)	Joint model: Equation 4.3	**Yes**
Hazard rate	h(x)	Heligman-Pollard & Joint model: Equation 4.4	No
Proportion of mature females (with maturity status)	$P_M(x)$	Logistic Regression	No
Proportion of mature females (with pubescent status)	P(x)	Equation 4.6	No
Fecundity rate from puberty	$f_P(x)$	Equation 4.7	**Yes**

Although the approach involves joint modelling, each model is detailed separately. The join is provided by the random variable α_{it} (cohort effect) which is an individual effect (i) related to the year of death of the individual (t).

Survival part

The age-at-death data obtained from the stratified random sampling are detailed in Figure 4.9. Each age within this data distribution is used to inform the parameter x_{it}. Age-at-death dataset from Mannocci et al. (2012) is also used to compare the effect of sampling on the survivorship value since authors did not perform stratified random sampling but used all available age-at-death values.

The survival model is the following:

$$\log x_{it} = \mu + \sum_{j=1}^{p} \gamma_p X_{ip} + \alpha_t^1 + \sigma \times \epsilon_i - \frac{Z_i}{\beta} \tag{4.1}$$

It consists in modelling the logarithmic transform of x_i (which is the age-at-death for each individual i) assuming a normal-Laplace distribution for $\log x_i$ where μ is a location parameter; σ and $\frac{1}{\beta}$ are (positive) scale parameters; and Z_i are independent standard exponential deviates. The parameter $\frac{1}{\beta}$ quantifies individual frailty (Kannisto 1991; Reed 2011) or persistent demographic heterogeneity (Cam, Aubry, and Authier 2016). We specified the following distribution for residuals $\epsilon_i \sim \mathcal{N}(0,1)$ and $\frac{1}{\beta} > 0$ which

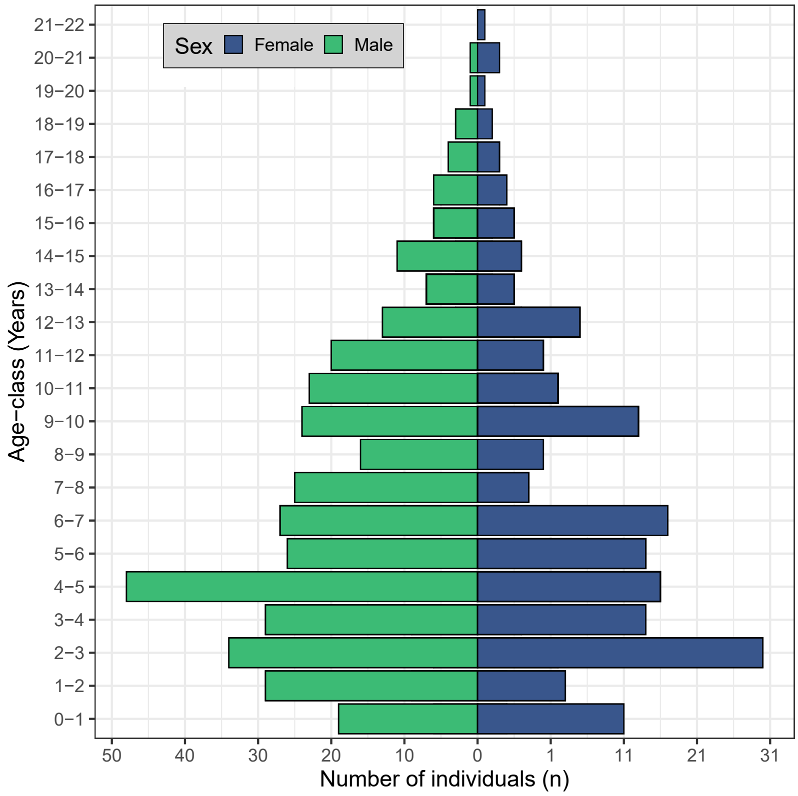

Figure 4.9: age-at-death data as an age pyramid by sex. The maximum age class is 21-22 years with some females of this age. The data seem to be characterised by a low representation of age groups 0-1, 0-2 and sometimes 7-8 and 8-9. Over-representation is also possible for ages 9 to 14. For comparisons, see Chapter 2 with two age distributions on the same population. In total, there are 642 individuals.

allows to accommodate a bathtub-shaped hazard rate curve which is the pattern expected for long-lived species of vertebrates in the wild (Choquet et al. 2011b). It is possible to incorpore p individual-level covariates X_{ip} (such as sex or cause of death) and random variables α_t (such as years). The superscript α_t^1 means that this is the random effect associated with survival model.

The vital rates associated with the survival component are:

- Survivorship $l(x)^5$ at age x with Φ^c as the cumulative density function of a standard normal distribution with $\Phi^c = 1 - \Phi$ (with Φ as the density function of a normal distribution):

$$
\begin{aligned}
l(x) = \Phi^c\left(\frac{\log x - \mu}{\sigma}\right) - \\
\exp\left(\beta(\log x - \mu) + \frac{\beta^2\sigma^2}{2}\right) \times \\
\Phi^c\left(\beta\sigma + \frac{\log x - \mu}{\sigma}\right)
\end{aligned}
\tag{4.2}
$$

To apply covariates and/or random and/or trend effects it is on the intercept μ:

$$\mu_{1997} = \mu + \alpha_{1997}$$

- Age-specific survival $S(x)^6$:

$$S(x) = \frac{l(x+1)}{l(x)} \tag{4.3}$$

5: the proportion of the population that survive at least to age x.

6: the proportion of the population at age x that reaches the age $x + 1$.

- Hazard rate $h(x)$[7] with R as the Mills ratio ($R = \frac{\Phi^c}{\phi}$) which is the ratio between the cumulative density function (Φ^c) and the probability density function of a standard normal distribution (ϕ) :

$$h(x) = \frac{\beta}{x} \times \frac{R\left(\beta\sigma + \frac{(\log x - \mu)}{\sigma}\right)}{R\left(\frac{(\log x - \mu)}{\sigma}\right) - R\left(\beta\sigma + \frac{(\log x - \mu)}{\sigma}\right)} \tag{4.4}$$

This approach is accurate to estimate survivorship with a sample size of 300 while for hazard rate it is better with at least 500 individuals (Rouby, Ridoux, and Authier 2021).

Reproductive part

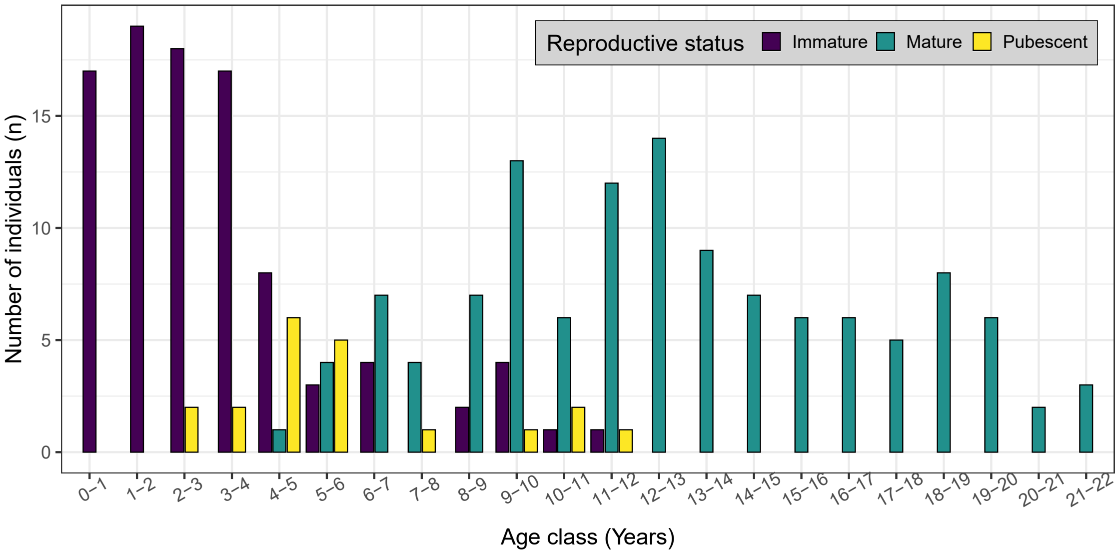

Figure 4.10: Distribution of reproductive status by age (regardless of sex). No immature individuals were founded after 11-12 years. Pubescent individuals are found from 2-3 years to 11-2 years of age with the largest proportion between 4 and 6 years. The first mature individuals are found at 4-5 years of age. For comparisons with other datasets from this population, see Chapter 2. In total, there are 240 individuals.

The reproductive model is the following:

$$\log x_{it} = \mu + \sum_{j=1}^{p} \gamma_p X_{ip} + \alpha_t^2 + \sigma \times \epsilon_i \tag{4.5}$$

It consists in modelling the logarithmic transform of x_{it} (which is age-at-death associated with a reproductive state) assuming a Weibull distribution for x_{it} and a standard Gumbel distribution $\epsilon_i \sim G(0, 1)$. The Weibull distribution used is a two-parameter distribution: α is the shape parameter which describes the distribution pattern of the risk of becoming sexually mature; and λ_i which is the scaling parameter defining the position of the

if $x_{it} \sim$ Weibull (α, λ)
$\log(x_{it}) \sim$ Gumbel (μ, σ) with $\alpha = \frac{1}{\sigma}$ and $\lambda = e^{-\mu}$

[7] Instantaneous probability of dying at time $t+dt$ given that and individual i has survived until time t

distribution curve. Residuals $\epsilon_i \sim G(0,1)$ which induces a Weibull law.
It is possible to include p individual-level covariates X_{ip} (such as sex or cause of death) and random variables. The random variable α_t^2 is the cohort effect associated to the reproductive model. Covariates inclusion allows to compute the proportion of mature females, which is the sex usually used in unisex animals dynamic populations, without subseting the dataset and lose information. Three reproductive status (*i.e.* model censoring states) are used to inform the model parameters estimation: Immature (right-censored), Pubescent (not censored, the most informative) and Mature (left-censored).

Vital rates associated with the reproductive component:

- Proportion of mature females $P(x)$ at age x with α as the shape parameter of the Weibull distribution ($\alpha = \frac{1}{\sigma}$ with σ as the standard deviation of the Gumbel distribution of $\log(\mathrm{x_{it}})$) and μ as the intercept of the Gumbel distribution:

$$P(x) = 1 - \left(exp \left(- \left(\frac{x}{exp\left(\frac{-\mu}{\frac{1}{\sigma}}\right)} \right)^{\frac{1}{\sigma}} \right) \right) \tag{4.6}$$

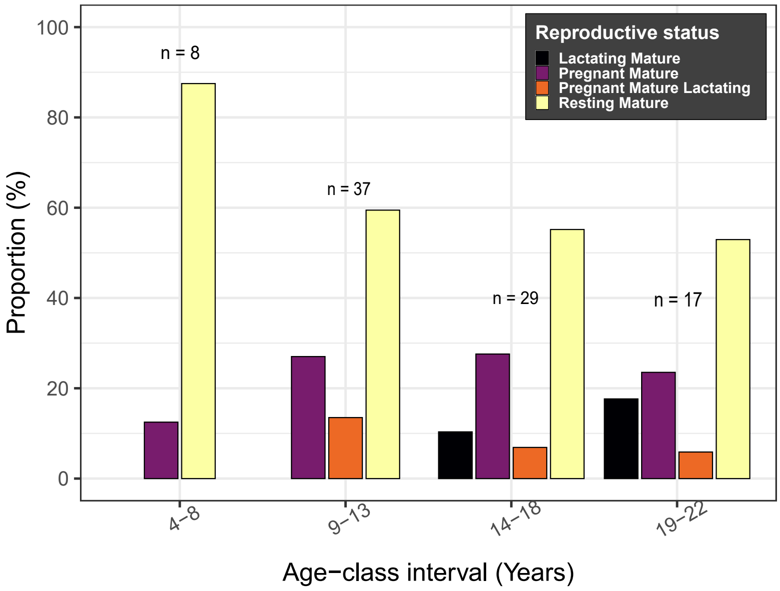

Figure 4.11: Reproductive status of females given four age-class interval. The total number of female used is about 91. For a comparison with other dataset, see Chapter 2.

- Gestation rate $G(x)$ at age x. The gestation rate was obtained considering 4 age-class intervals (4-8, 9-13, 14-18 and 19-22) as depicted in Figure 4.11.
  Gestation rate before 4 years is equal to 0 since no female was pregnant before 4 years. It is equal to 0.125 for 4-8 since one of the 8 mature females of this age was pregnant. It is

equal to 0.45 for 9-13 since 15 of the 37 mature females of this age were pregnant. It is equal to 0.35 for 14-18 since 10 of the 29 mature females of this age were pregnant. And It is equal to 0.30 for 19-22 since 5 of the 17 mature females of this age were pregnant.

- Fertility rate $f_P(x)$ at age x. The proportion of mature females (estimated with the pubescent status in the AFT modelling framework) is multiplied by the gestation rate (divided by two assuming a sex ratio at birth of 1:1) and multiplied by the age-specific survival rate considering the transition to the next age S_{x-1}:

$$f_P(x) = P(x) \times \left(\frac{G(x)}{2}\right) \times S_{x-1} \tag{4.7}$$

The proportion of mature individuals through the ages is obtained considering both sexes. To compute fertility rate, we used the proportion of mature females computed with the pubescent status (through the covariate inclusion). It is more accurate to use females for demographic modelling since it is considered as the limiting sex in the population and it is easier to measure the reproductive output than for males.

Leslie matrices and elasticities

The vital rates obtained above allow the construction of life tables. The tables and their construction are detailed in the supplementary material. Once vital rates have been obtained, including age-specific survival (S_x) and fecundity rates from pubescents (f_{P_x}), a Leslie matrix model can be filled in to obtain the population growth rate. This growth rate is then used in a geometric population dynamics model.

The matrix population model is the following:

$$\begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ N_3 \\ \dots \\ N_{24-1} \\ N_{24} \end{bmatrix}_{n+1} = \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ N_3 \\ \dots \\ N_{24-1} \\ N_{24} \end{bmatrix}_{n} \times \begin{bmatrix} f_{P_0} & f_{P_1} & f_{P_2} & f_{P_3} & \cdots & f_{P_{24-1}} & f_{P_{24}} \\ S_0 & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & S_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & S_2 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & S_3 & \dots & 0 & 0 \\ 0 & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & 0 & \dots & S_{24-1} & 0 \end{bmatrix} \tag{4.8}$$

Vector N gives the number of individuals in each age-class at time t and then at time $t + 1$. The previously estimated vital rates were combined into the matrix with the female age-specific survival rate $S(x)$ and the fertility rates from pubescents females $f_P(x)$. Female vital rates were obtained by including covariates without and with the random effect of year. The matrix model is therefore relative to female only. Before age class 5, the gestation rate is 0. No offspring are produced by females strictly under the age of 5.

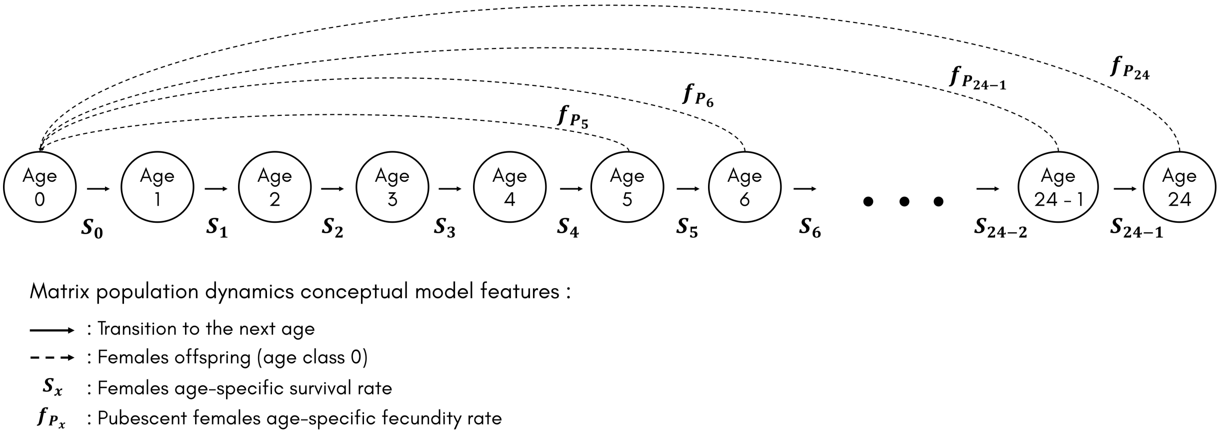

Figure 4.12: Conceptual model of the Female leslie matrix modelling approach. 24 age classes are modelled. After age class 24, the females die, so there is no survival rate for this class. Before age class 5, the gestation rate is 0. No offspring are produced by females strictly under the age of 5.

The population growth rate λ was computed as the asymptotic growth rate of the Leslie matrix and allowed to project the remaining population at time t ($N(t)$) taking into account the initial abundance at time t_0 ($N(t_0)$). The population's trajectory was projected through 100 years, from 2020 to 2120.

$$N(t) = N(t_0) \times \lambda^t \tag{4.9}$$

We also explored the relative changes in population's growth rate λ caused by a proportional change in one of the life cycle parameters, referred to as elasticities (de Kroon et al. 1986). The elasticities analysis may be used to improve and study the management of long-lived species (Crouse, Crowder, and Caswell 1987).

Baseline assumptions

- Stranded dolphin population is representative of the living population (regarding demographic features).
- Age and reproductive-status-at-death are representative of the stranded population.
- Each age-at-death is known and correctly reported.
- Each reproductive-status-at-death is known and correctly reported.

- Joint model is accurate to estimate vital rates and the survival and fecundity patterns are congruent for the species.
- The population growth geometrically and is not subject to migration.

4.3 Results: Vital rates and population growth rate

The first part of the results is related to the vital rates of the population. In this part, the first result highlighted is the comparison of survival estimates according to the sampling of age-at-death data. The second result highlights the patterns of survivorship and proportion of matures individuals without effect. The third result highlights the survivorship and proportion of matures individuals patterns with covariates. The fourth result highlights the survivorship and proportion of matures individuals patterns with random effects.

The second part of the result highlights the properties of the matrix model used. The first result highlights the projection of the evolution of the population (in percentage) without effect and with random effect. There is no covariate because the projection is always made from the sex covariate, to take into account the females only. The second result shows the value of the elasticities for survival and fecundity, by age and by year.

Common dolphin population vital rates

Survivorship difference according to sampling

We estimated survivorship from Mannocci et al. (2012) dataset ("All age-at-death available" Figure 4.13) and the dataset obtained in this project ("Stratified-random-sampling" Figure 4.13) using Siler (1979) and Reed (2011) models. This was done with the aim of testing the influence of stratified random sampling on the estimation of survivorship. As a reminder, Mannocci et al. (2012) did not use stratified random sampling. For the Mannocci dataset, the survivorship estimated is equal to that estimated in the Mannocci et al. (2012) study using the Siler model (Figure 4.13). Using the Reed model, there is a gap from the 0 to the 12 age-class (without taking into account the uncertainties). Then estimation are consistent and nearly overlapping. For the dataset collected in this study, both models estimated nearly the same survivorship across all age-classes even if there is a limited gap between 0 and 4 years (≈ 0.25).

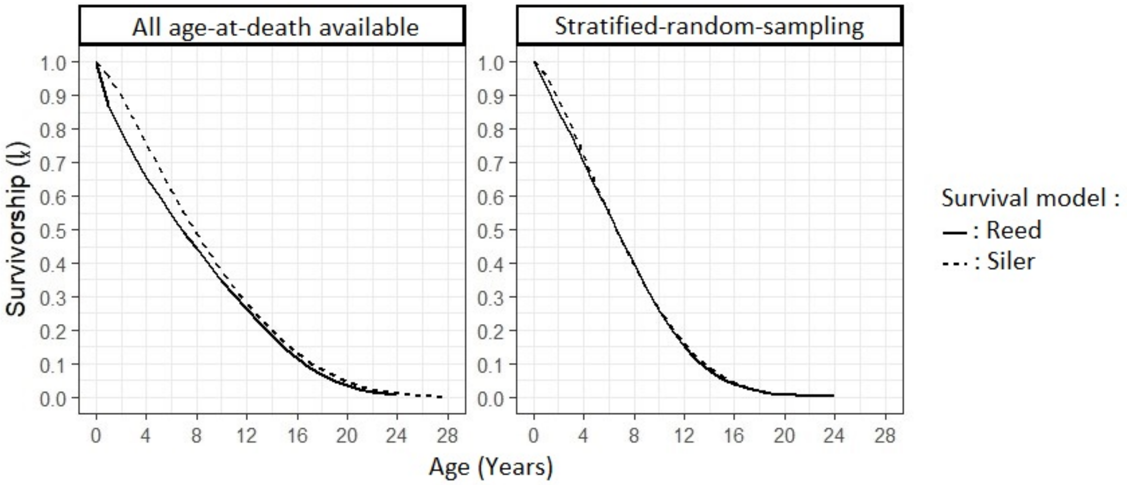

Figure 4.13: Survivorship estimation for each age-class on the two dataset types with Reed and Siler models. The estimation realised with the Siler model is displayed in black dashed line whereas the estimation using the Reed model is displayed in black solid line. For the dataset built using all the age-at-death available (Mannocci et al. 2012), there is a difference in survivorship estimates. This difference is much less marked, or even almost non-existent, for the dataset constructed from the stratified-random-sampling.

Survivorship and Proportion of mature individuals with a null effect

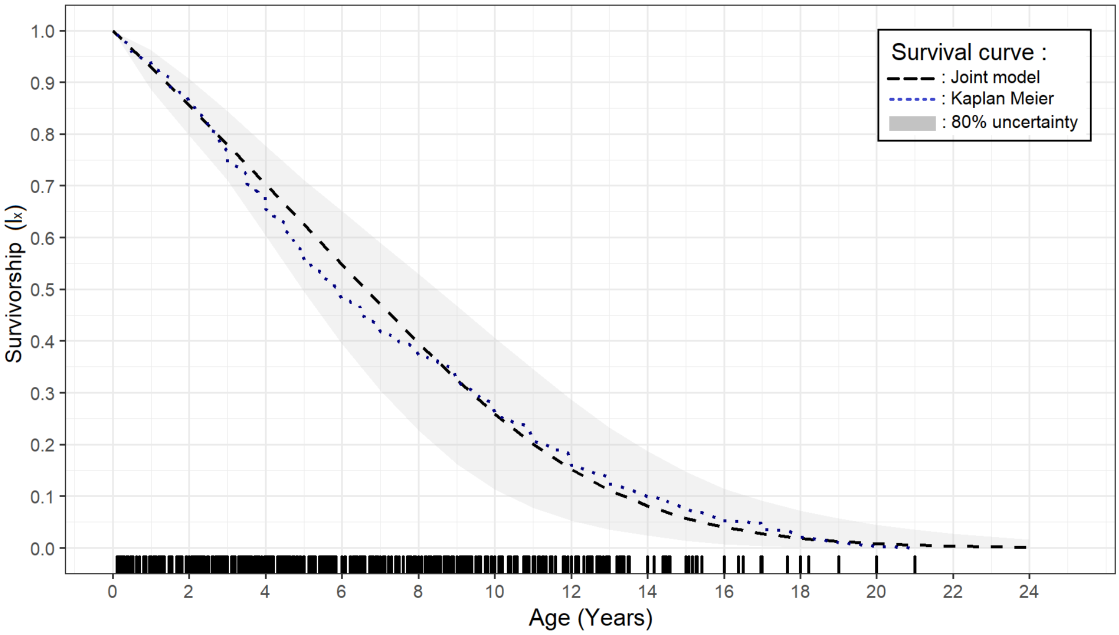

Figure 4.14: Survivorship estimated from the age-at-death dataset for each age-class. The blue dotted line corresponds to the observed survivorship estimated from the Kaplan-Meier estimator. The black dashed line is made from the Reed model. Uncertainty is displayed as the 80% uncertainty interval (*i.e.* Bayesian credibility interval).

The survivorship according to each age-class is highlighted in Figure 4.14. Availability of data by age is displayed in rug line. Observed survivorship from this data (obtained with Kaplan-Meier estimator) is showed in blue points. The confidence interval around the mean is a 80% confidence interval as it correspond to the Bayesian credibility estimate. The confidence estimate is at its widest value at 10 years admitted a survivorship uncertainty of 0.3. From 0 to 10 years, the survivorship decreases from 1 to 0.25. It is almost equal to 0 at 20 years. There is a gap between the observed and the estimated survivorships from 3 to 8 years with an higher value of estimated survivorship of about 0.05.

The proportion of mature females, estimated by the joint model using pubescent status as a reference, according to each age-class is highlighted in Figure 4.16. For comparison, the proportion of mature females estimated by logistic regression from the proportions of mature females at each age is shown in Margin-Figure 4.15. In Figure 4.16, availability of data is displayed in rug line. Black rugs are associated with immature and mature individuals (both sexes). Orange rugs are associated with pubescent individuals (both sexes). Raw proportions of mature females are displayed in both Figure 4.16 (grey dots) and Margin-Figure 4.15 (black dots). The estimated fitted curve with the Accelerated Failure Time (AFT) Weibull model is expressed as a dashed line. Likewise for survivorship, the 80% interval uncertainty around the estimation is displayed in grey. The estimated ASM taking into account the pubescent biological information through the AFT approach is about 5.3 years. The maturity difference between the two approaches is therefore about 2 years.

Figure 4.15: Proportion of mature females along age-class obtained through logistic regression. Black dots are the observed proportion for each age-class. The black solid line is the model fit. Data showed a null proportion of mature females from 0 to 4 years and a full proportion of mature females from 11 to 21. From 5 to 11, the proportion increases but the pattern in the data is noisy. Female Age at Sexual Maturity (ASM) is of 7.36 years (*e.g.* 50% of the population is estimated as mature).

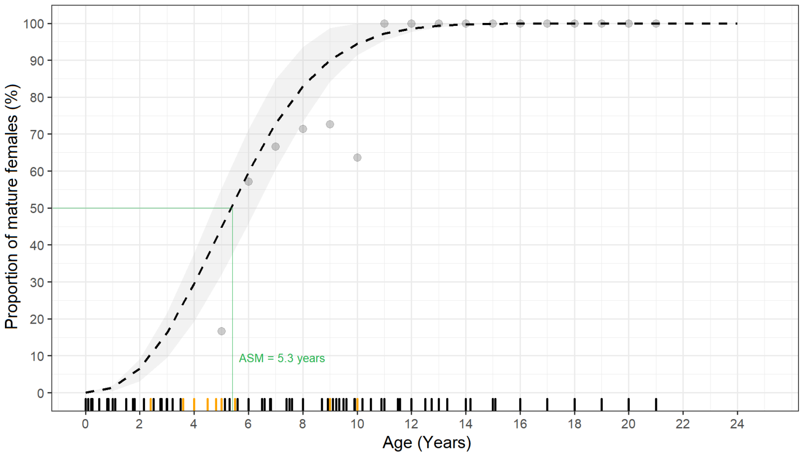

Figure 4.16: Proportion of mature females estimated with joint model for each age-class. The real data are displayed as grey dots and the estimated proportion done with the AFT Weibull approach is displayed as black dashed line. The 80% uncertainty around the mean estimated is displayed as a grey area.

Survivorship and Proportion of mature individuals with Covariates

The effect of the two covariates (Bycatch and sex) on survivorship is presented in Figure 4.17 horizontal panel A. The percentage of change between the two estimated survivorship

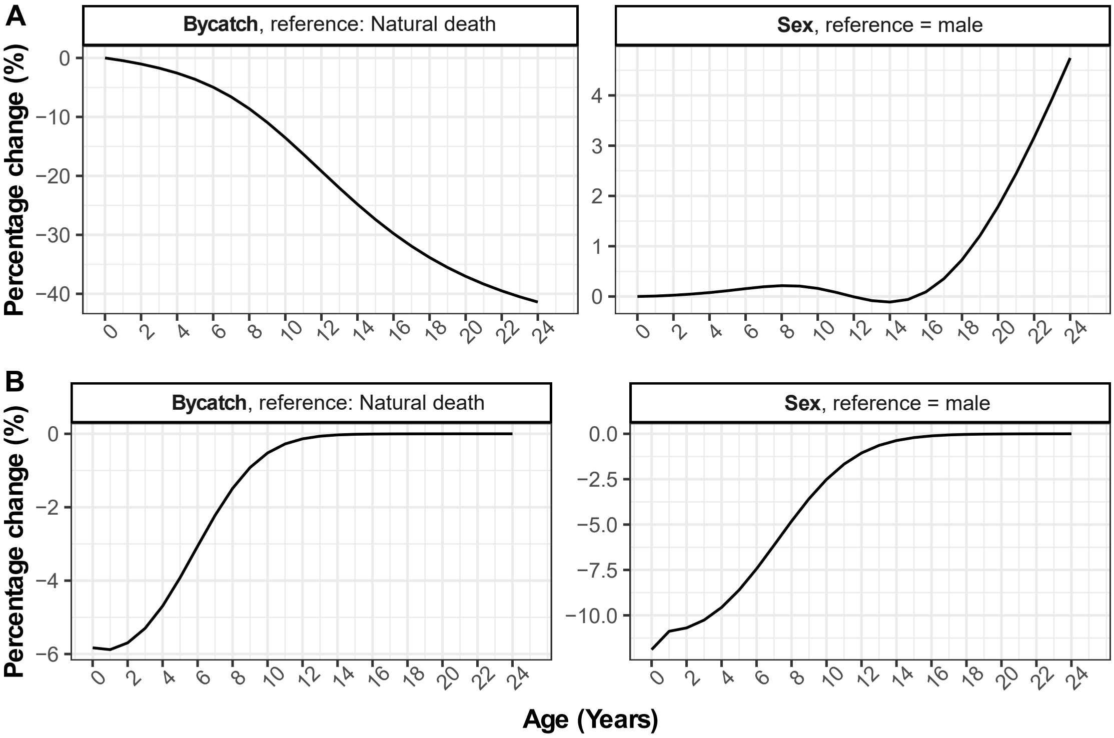

Figure 4.17: Percentage change between survivorship and fertility patterns for each covariate being tested.
A: Effect of covariates on survivorship. The difference in survival between captured and uncaptured individuals increases with age. It is about 15% at 10 years old and reaches 30% at 16 years old. Females seem to survive slightly better than males at the end of their lives, particularly from the age of 16. Their survival is about 3% better at 22 years.
B: Effect of covariates on proportion of mature individuals. The proportion of mature individuals appears to be higher in the younger age classes among the individuals caught. At 7 years of age, there are 2% more mature individuals. The females also seem to mature faster than the males. At 8 years of age, females are 5% more mature than males.

profiles is expressed in percentage. For Bycatch (or cause of death), the reference value is "Natural death". For sex, the reference value is "Male". It can be seen that the difference between profiles is more pronounced when the cause of death is taken into account in comparison to sex. By focusing on the effect of bycatch, it appears that the bycaughts individuals seem to survive less well than non-bycaught ones for all ages. The difference between bycaught and non-bycaught individuals in survivorship goes from 0 to 10% from 0 to 8 years to 10 to 30% from 8 to 16 years.
The effect of the two covariates (Bycatch and sex) on the sexual maturity attainment is presented in Figure 4.17 horizontal panel B. The percentage of change between the two estimated sexual maturity profiles are highlighted in the same way as before. It can be seen that bycaught individuals reach sexual maturity more quickly than non-bycaught ones. From the age of 13 to 14, however, there is no longer any difference. Sex also seems to have an effect on the estimation of the sexual maturity profile. Females seem to mature more quickly than males.

Survivorship and Proportion of mature individuals with Random effects

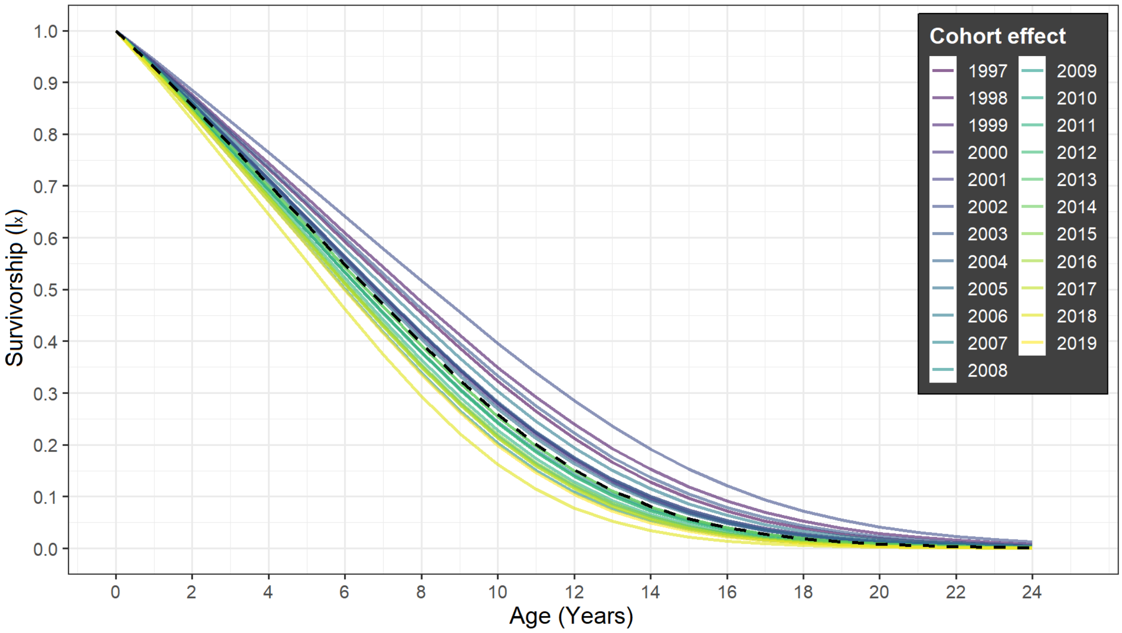

Figure 4.18: Cohort effect on survivorship. The black dashed line corresponds to the mean survivorship. Each coloured solid line of is a deviation around this mean (*i.e.* random effect) associated to a cohort.The cohorts share death as a common event. For example, the 2017 cohort includes all individuals who died in 2017 regardless of age. This cohort is associated with the lowest estimated survivorship. The highest estimated survivorship is for the 2002 cohort.

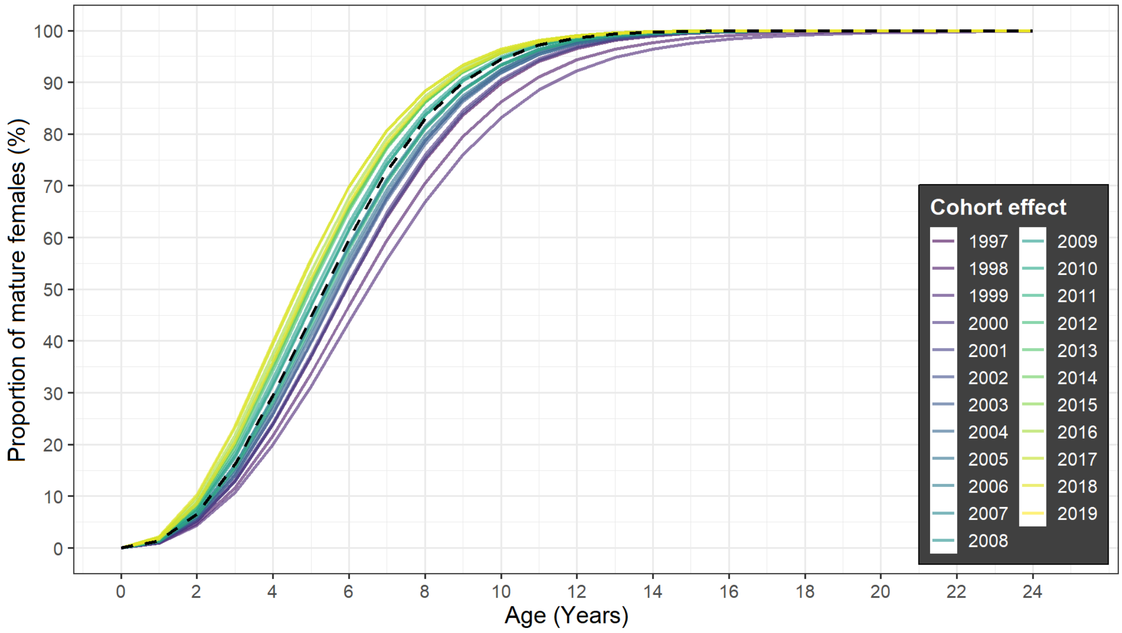

Figure 4.19: Cohort effect on proportion of mature females. The black dashed line corresponds to the mean proportion of mature females. Each coloured solid line of is a deviation around this mean (*i.e.* random effect) associated to a cohort. The cohorts share death as a common event. For example, the 2017 cohort includes all individuals who died in 2017 regardless of age. This cohort is associated with the earliest Age of Sexual Maturity. The latest Age of Sexual Maturity is estimated for the 2002 cohort.

Mean survivorship signal (dashed black line) and the deviation from this mean signal due to the random effect of the years (coloured solid lines) are available in Figure 4.18. The year associated with the highest survivorship is 2002 whereas the year associated with the lowest survivorship profile is 2017. Years before 2007 show a profile with a higher survivorship than the mean signal. After 2007, the survivorship was associated to lower values with the lowest values recorded for recent years after 2016.
Mean proportion of mature idnviduals signal (dashed black line) and the deviation from this mean signal due to the random effect of the years (coloured solid lines) are available in Figure 4.19. The year associated with the latest maturity (50 % of the population estimated as mature) according to age is 2002. The year associated with the earliest maturity according to age is 2017. Years from 2009 show a profile with a latest age-at-maturity than years after 2010 that show a profile with an earliest age-at-maturity.

Population growth rate and elasticities

The mean signal of the projected population abundance trajectory (in percent) between 2020 and 2120 from the estimated vital rates with the covariate "female" is presented in Figure 4.20. The mean estimated growth rate is about 0.868 which correspond to a population's extinction within 40 to 50 years.

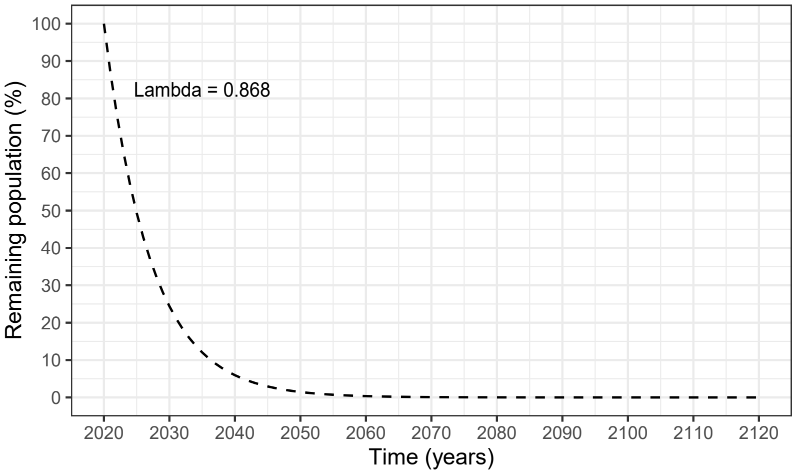

Figure 4.20: Remaining population from 2020 to 2120 given exponential geometric growth population model. The asymptotic growth rate is about 0.868. For a comparison with previously made population projections on this population, see Chapter 2.

The deviations induced by the annual random effects from the mean signal of the population abundance trajectory projection are presented in Figure 4.21. The cohort effect (years of deaths) deviations are displayed in colour likewise for survivorship and proportion of mature individuals. The year with the highest growth rate is 2002 with $\lambda = 0.928$ which corresponds to an extinction within 70 to 80 years. 2017 is the year with the lowest growth rate value ($\lambda = 0.848$) which corresponds to an extinction within

30-40 years. Years from 2012 show a faster extinction with much less population remaining over time compared to the years before 2012.

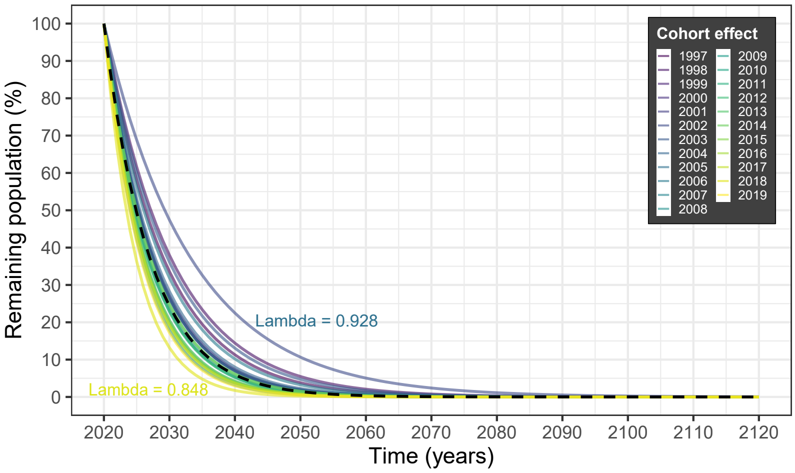

Figure 4.21: Cohort effect on population growth from 2020 to 2120. The population model admits a exponential geometric growth. The lowest asymptotic growth rate is observed for the 2017 cohort whereas the highest is observed for the 2002 cohort.

The mean proportional contribution to the growth rate, of each age-class for both survival and reproduction are displayed in Figure 4.22. For both facets, the mean signal is shown as a black dashed line and the deviations from the mean signal due to the random year effect are shown as solid coloured lines.
Regarding the survival component, the contribution decreases along the lifetime. The estimated contribution is at his highest from age 0 to 6 and then drops to 0 at age 22. From age 0 to 6, cohorts from 1997 to 2008 are associated to a lower contribution compared to the mean whereas years from 2015 to 2019 are associated with a higher contribution. From age 7 to 22 cohorts from 1997 to 2008 are associated to a higher value compared to the mean whereas cohorts from 2016 to 2019 are associated to a lower value for the same age-class interval.

Regarding the reproductive component, the contribution increases from age 1 to 8. The age-class which contributes the most to population growth rate is the 8^{th}. Then the estimated contribution decreases up to the age-class 22. The contribution of age classes before 6 is higher than the average for the years-of-death cohorts after 2010 and lower for cohorts before 2010. Then, from age 6 until age 10 cohorts with an higher value of contribution than the mean are cohort from 2016 to 2019 with a difference peak at year 8. These years are also associated to a lower contribution compared to the mean signal from age 12 to to 22. For cohorts before 2006 the contribution is lower than the mean from age 6 to 11. Then it is higher from age 12 to 22.

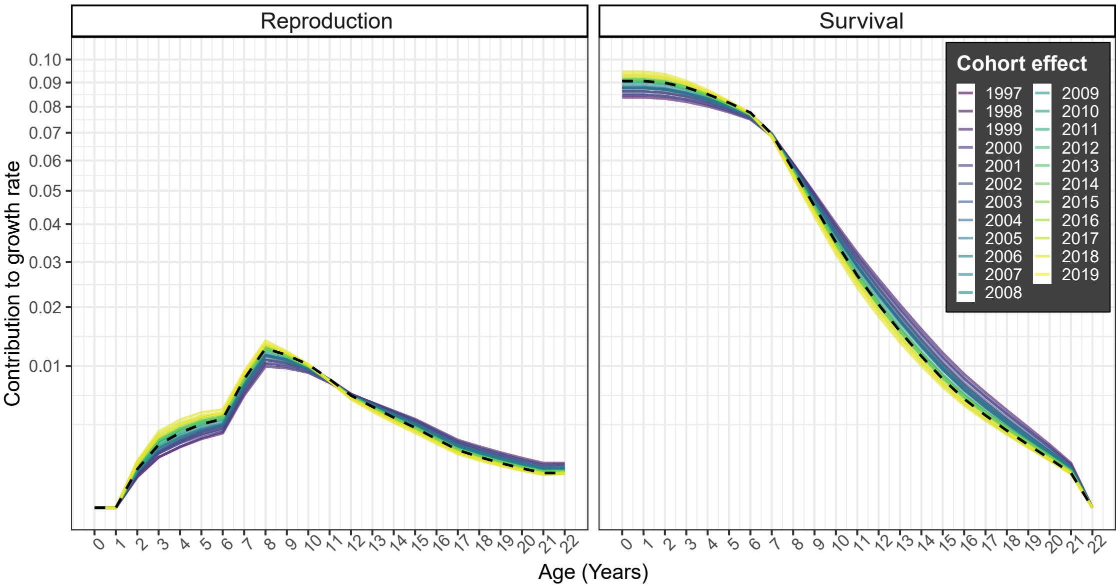

Figure 4.22: Cohort effect on elasticities of age-specific fecundity (Reproduction) and survival rates (Survival). Black dashed line corresponds to the mean signal and solid coloured lines correspond to the deviations around this mean signal. The age class whose reproduction contributes most to the growth of the population is the 8-year-old age class. The age classes whose survival contributes most to population growth are the younger age classes (0-6 years).
Age-specific survival rates are the vital rates that contribute most to the value of the growth rate (0.9 when adding up each elasticity). age-specific fecundity rates contributes slightly (0.1 when summing each elasticity). The contribution appears to be unequal across cohorts.
The 2017 cohort has the highest contribution to population growth from reproduction and survival of young age classes (3-8 for reproduction and 0-6 for survival). It is also the cohort whose reproduction and survival of adult year-classes (14 to 22 for reproduction and 10 to 20 for survival) contribute least to population growth. This pattern is reversed for the 1997 cohort.

4.4 Discussion: Important aspects and implication of the study

We obtained age-at-death data for individuals (females and males) selected by stratified random sampling. We obtained reproductive-status-at-death data for all individuals (females and males) for which we had gonad samples available.
We used these data to obtain vital rates associated with survival and reproduction. The vital rates were obtained using a joint modelling approach. This approach takes into account a random effect common to both survival and reproduction, relating to the year of death of each individual.
The vital rates that will be presented in this section are presented according to the inclusion of: a null effect, a covariate effect and a random year effect.
The rates obtained by this approach were used to inform a Leslie matrix model. The values used are those for females (via the sex covariate effect) without and with random year effect. Female fecundity is obtained from modelling the attainment of puberty. The value of the gestation rate induces a female offspring equal to 0 before 5 years.

The growth rate obtained from the Leslie matrix was used to project the evolution of the population without and with random year effect. The elasticity properties of the matrix(es) were calculated.

Representativeness bias and age distribution

The approach is based on a cross-sectional monitoring which is fundamentally related to strong assumptions difficult to meet. The most important to meet was addressed by (Caughley 1966) which is the necessity for the population to be at a stationary age distribution when using age-at-death recorded from strandings. The stationary age distribution is an age distribution that induces a stable population whose abundance does not increase or decrease over time. This stationary age distribution is a special case of the so-called stable age distribution (Caughley 1966). The stable age distribution emerges when the birth and death rates are fixed and the distribution of ages in a population are stable (Carey and Roach 2020, p. 128). Our age-at-death dataset does not appear to be representative of a so-called stable population for a delphinid (Mannocci et al. 2012; Barlow and Hohn 1984). Since the stationary age distribution (required as a baseline assumption) is a special case of a stable age distribution, it is likely that our age-at-death sample does not meet the baseline assumption.

Strandings are probably biased regarding the juvenile and the older senescent age-classes with fewer individuals than expected for a wild population.

The age classes that could be biased are the calves (0-2 years), adult (8-12) and older-senescent (> 19 years) (Barlow and Hohn 1984; Stolen and Barlow 2003). The representation of juveniles and older-senescent individuals may be influenced by drifting processes. They may be less buoyant than adults (Peltier et al. 2012) It is therefore possible that they sink more easily. The under-representation of calves in the dataset may also be explained by a more rapid decomposition, greater vulnerability to predation, scavenging, and lower detection probability of small-sized animals (Stolen and Barlow 2003).

The Over-representation of adults in the age-at-death dataset may be explained by three assumptions (Barlow and Hohn 1984):

- 1) Non stable age distribution resulting from a disturbance.
- 2) Inconsistent deposition of GLG during life.
- 3) Oversampling resulting from a filter before stranding.

Strandings are probably biased regarding the adults age-classes around 6 to 10 years with more individuals than expected for a wild population.

The second assumption is unlikely to be possible. For common dolphin it is commonly admitted that GLGs deposition is constantly 1 per year (Murphy and Rogan 2006). To validate or invalidate the first assumption, much more age data would be needed. It would be possible to see whether a change in representation for a given age class is repeated in subsequent years as individuals advance in age. In case of disturbance, it should propagates across years

regarding age-class distribution (Barlow and Hohn 1984). The third assumption could be possible if we consider an overmortality of these age classes due to the bycatch. As shown in Figure 4.17, the age classes most likely to have a drop in reduced survivorship (Age > 8 years) when the bycatch covariate is taken into account are also those that would appear to be over-represented in the dataset. This observation could support the validity of the third assumption.
To better accommodate the over-representation of adults and the under-representation of calves, it might be interesting to use a mixture model that allows to represent two hazard rate components (Rouby, Ridoux, and Authier 2021). The first specific to calves. The second specific to adults. Before testing this survival model, a simulation study should be conducted.

Contribution of stratified random sampling approach

The sampling plan seems essential to minimise bias in estimating population survival in cross-sectional analysis.

This study is the first to employ a stratified random-sampling framework while estimating the vital rates of a marine mammal population from stranding data. Usually, demographic studies from strandings use all age-at-death data available (Mannocci et al. 2012; Barlow and Hohn 1984; Stolen and Barlow 2003). The stratified random sampling is a way to satisfy both ecologist's and statistician's requirements for the representative dataset (Roleček et al. 2007). The advantage using this approach is that it allows to maximises the probability of best representing the age structure of the stranded population. It is important to match the stranding signal as closely as possible on the basis of criteria (that shape strata) influencing the demography and individual selection (such as cause of death). Such an approach is commonly used in fisheries studies (Holden and Raitt 1974; Cochran and William 1977; Lai 1993), forestry ecology (de Vries 1986) or human psychology and social sciences for which it is important to correctly represent age conditions in a population (Banerjee and Chaudhury 2010). As it is shown in Figure 4.13 survivorship results can vary a lot depending on the sample collected.

The sampling in the Mannocci et al. (2012) study was not controlled and estimated survivorships may vary. The dataset from (Mannocci et al. 2012) study were built using all the age-at-death data available. As it was shown in Figure 4.13, the estimated survivorship is not the same depending on the survival model used (Siler or Reed). There is a gap between the two curves from age 0 to about age 10. The dataset we built in this project was constructed using stratified random sampling. The survivorship estimates from this dataset are almost the same between the two survival models. It is therefore possible that by not controlling for sampling and taking all available age-at-death data, this reflects an additional bias that may influence the estimation of survival models. In the case where sampling is controlled, the estimated values are the same regardless of the models used. The stratified random sampling may help to reduce the sensitivity of the estimate to the age distribution.

We think that it is essential to perform a stratified random sampling (if sufficient data) in order to better represent the stranding signal. We propose a three-steps framework to minimise representativeness bias using strandings (also see Margin-Figure 4.4 and Diagram 4.2):

- 1) Define the need for representativeness by choosing relevant criteria and calculate the proportion of each in the stranded population
- 2) Stratify by assigning each individual a value for each criterion
- 3) Random sample individuals within each stratum to match proportions of the stranded population

This approach ensures that uncontrolled selection bias is not added to the sample or is at least minimised. The representativeness bias is therefore due solely to strandings.

Viability of the common dolphin population

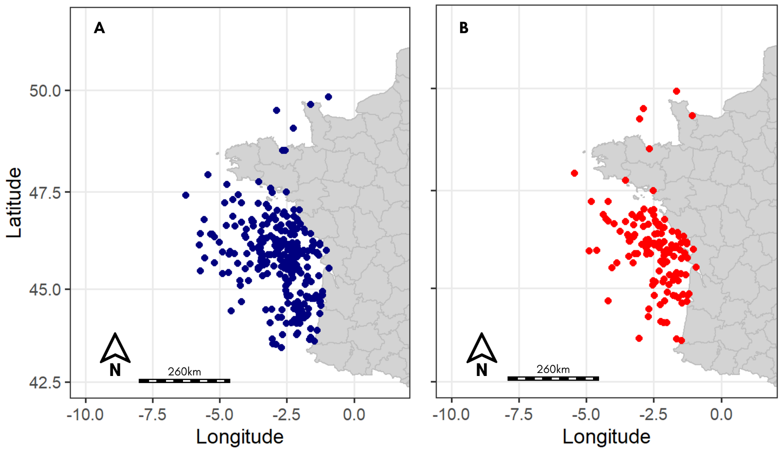

Figure 4.23: Death origin of the dolphins used in this study. The blue dots represent the age-at-death dataset. The red dots represent the reproductive-status-at-death dataset. The origin at death was obtained by using the MOTHY inverse drift model. The great majority of individuals died on the continental shelf of the Bay of Biscay.

The common dolphin population is currently considered as a single management unit by OSPAR whose population is panmictic (Murphy et al. 2021). In principle, the vital rates produced in this study should refer to the whole population (Benjamins et al. 2014). The samples used here (age-at-death and reproductive-status-at-death) were constructed from individuals stranded on the French coast. For some, it was possible to trace their supposed origin at the time of their death. This is achieved through the use of inverse drift models (Peltier et al. 2016). Almost all the individuals died on the continental shelf of the Bay of Biscay (Figure 4.23). This does not mean that they are uniquely tied to this area. But it is a possibility to consider if we assume the hypothesis put forward by Lahaye et al. (2005) and Caurant et al. (2009) which have highlighted the possible existence of two stocks that are tied to either the continental or the oceanic part of the Bay of Biscay. If individuals were restricted to this part of European waters, then it would be difficult to generalise the vital rates obtained at the scale of the OSPAR management unit. Conversely, it would be possible to use them to inform the descriptors of the MSFD which considers parts of the population's distributional range.

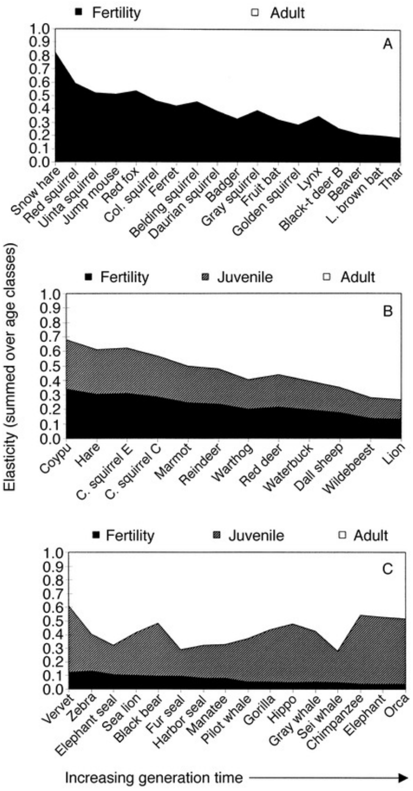

Figure 4.24: Stage-specific elasticities for mammal populations, grouped by age at maturity and ordered by increasing generation time. **A.** Age at first maturity = 1 yr; no juvenile stage. **B.** Age at first maturity = 2 yr; fertility elasticity = juvenile survival elasticity. **C.** Age at first maturity >2 yr. This groups correspond to species that exhibit a similar life history as the common dolphin. With delphinids in it and marine mammals. Fertility elasticities for those species are almost equals to the one that we founded for the common dolphin. Figure from Heppell, Caswell, and Crowder (2000).

It is possible that the bycatch pressure on the population is increasing and resulting in poorer survival. Since 2016, the number of stranded dolphins including bycaught individuals has been increasing almost constantly (Dars et al. 2020). The time series data we have used takes into account the year 2017. This year was marked by a very strong bycatch episode with a record number of stranded individuals (which will be exceeded by 2019 and 2020). This is the year in which survivorship is lowest, sexual maturity is reached most quickly and the population growth rate is lowest. It is therefore possible that the cohort effect observed is mainly due to an increase in bycatch pressure on this population. To compensate for this pressure, the population would tend to mature and pubesce more quickly as it is suggested by the cohort effect. The inclusion of the covariate "cause of death" may reinforce this assumption. As shown in the Figure 4.17, bycaught individuals survive less well that non bycaught ones and seem to mature more quickly. The external mortality force exerted by humans through bycatch could decrease the survival pattern of the common dolphin and speed up sexual maturation at the population level. An other interpretation of the survivorship difference between bycaught individuals and non bycaughts is sampling bias. The survival profile associated with bycaught individuals may be biased by the over-representation of bycaught individuals in the sample. The inclusion of the "cause of death" covariate would therefore limit the bias introduced by bycatch in the survival analyses.

By looking at the elasticity properties of the Leslie matrices (Figure 4.22), reproduction contributes only for 10% of the growth rate whereas survival contributes up to 90 %. This differential contribution is expected for a long-lived species like the common dolphin (Heppell, Caswell, and Crowder 2000). See Margin-Figure 4.24 for a comparison with other mammals and delphinids. The low contribution of reproduction to population growth (regardless of cohort) could explain why, despite the reduction in reproductive age, the growth rate is still decreasing.

Predicted but not observed extinction

Mannocci et al. (2012) projected the trajectory of the common dolphin population and predicted that the population would become extinct within 100 years at an average growth rate $\lambda = 0.945$. The average growth rate that we estimated in this study is lower with a value of $\lambda = 0.868$. Considering this rate, the population will go extinct within 50 years. This growth rate seems to vary between cohorts as highlighted by the projections taking into account random effects (Figure 4.21) but none of the years taken into account is associated with a projection as favourable as that of (Mannocci et al. 2012). Our time series covered years 1997 to 2019 whereas (Mannocci et al. 2012) used a time serie from 1972 to 2006. The difference may be due to a different cohort effect between these two time series. Different characteristics or pressures experienced by our cohorts between 2007 and 2019. Considering our time serie, the population's state seems worst in the recent years (2010 to 2019) with a growth rate that decreases from 0.928 in 2002 to 0.848 in 2017. According to our estimates and those of (Mannocci et al. 2012), a decrease should be observed. However, this does not seem to be the case according to the available abundance estimates (Appendix Table 1). It is possible that the population from the Bay of Biscay is a sink population receiving individuals from source stocks.

The most favourable growth rates we have estimated are associated with the earliest years (< 2005) and are close to Mannocci et al. (2012) estimates.

The population should have been declining for years, but that is not what we are seeing. It is possible that this is a sink population. This hypothesis will be discussed in more detail in the general discussion.

The basic assumptions made in this study may be unrealistic. Six main assumptions were made to conduct the study. The first assumption: "*Stranded dolphin population is representative of the living population*" may be unrealistic and lead to a mismatch between the growth rate obtained and the trend observed in the abundance surveys. The demographic rates of the stranded population may not be representative of the population at sea. Another baseline assumption that may account for the mismatch between the growth rate obtained and the observed abundance is the last one: "*The population growth geometrically and is not subject to migration*". This assumption suggests that the population grows or decreases geometrically (here exponentially) depending on the value of the growth rate. But the geometric population growth model used does not take into account migration phenomena which could be the cause of an apparent stationarity of the population in the Bay of Biscay.

Quantifying the bycatch | 5

The Common dolphin plays an important functional role in Bay of Biscay marine ecosystems as a top predator, but is threatened by bycatch, *i.e.* the incidental capture of non-targeted species in commercial and recreational fisheries. Bycatch has been increasing, and has been associated with a large number of winter strandings of dolphins on the French Atlantic coast since at least 2017. However, uncertainties around the true extent of common dolphin bycatch and the fisheries involved have led to delays in the implementation of mitigation measures. Current data collection on dolphin bycatch in France is with non-dedicated observers deployed on vessels for the purpose of national fisheries sampling programmes. These data cannot be considered as representative of all fisheries bycatch. This feature makes it difficult to use conventional ratio estimators, as they require a truly random sample of the fishery by dedicated observers. We applied a newly developed approach, regularised multilevel regression with post-stratification, to estimate total bycatch from unrepresentative samples and total fishing effort. The latter is required for post-stratification and the former is analysed in a Bayesian framework with multilevel regression to regularize and better predict bycatch risk. We estimated the number of dolphins bycaught for each week and ten ICES divisions from 2004 to 2020 by jointly estimating the bycatch risk, haul duration and the number of hauls per days at sea. The bycatch risk in pair trawlers flying the French flag was the highest in winter 2017 and 2019, and was associated with the longest haul durations. ICES divisons 8.a and 8.b (shelf part of the Bay of Biscay), were estimated to have the highest common dolphin bycatch. Our results are consistent with independent estimates of common dolphin bycatch from strandings. Our method shows how non-representative observer data can nevertheless be analysed to estimate fishing duration, bycatch risk and, ultimately, the number of bycaught dolphins. These weekly estimates improve current knowledge on the nature of common dolphin bycatch and can be used to inform management and policy decisions at a finer spatio-temporal scale than has been possible to date. Our results suggest that limiting haul duration, especially in winter, could serve as an effective mitigation strategy.

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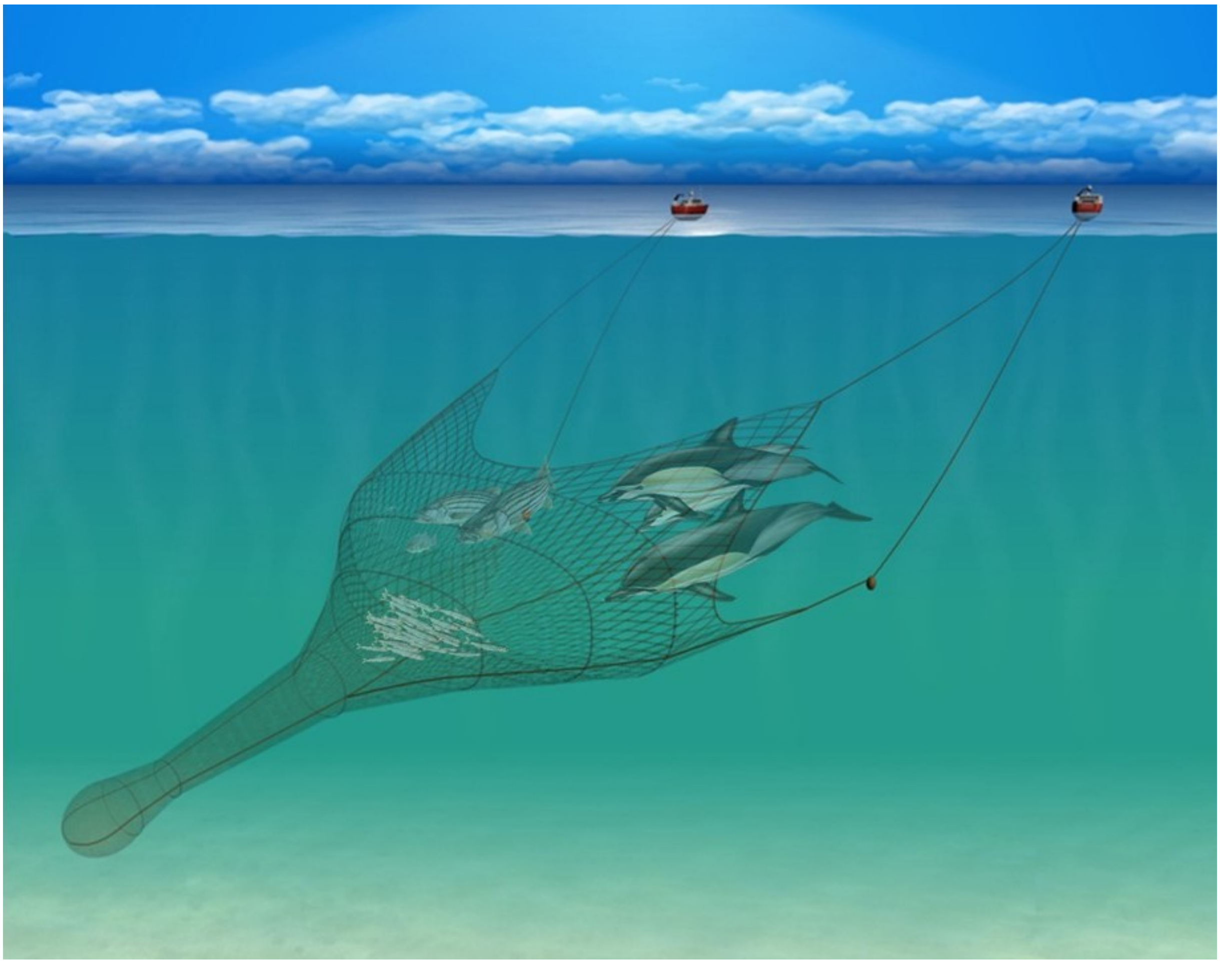
5.4 Discussion 123



Published works

This chapter is associated with three publications. The first is included as part of the introduction. The second is not included. The third constitutes the core of the chapter:

- **1.** Gilbert, L., Rouby, E., Tew-Kaï, E., Spitz, J., Peltier, H., Quilfen, V. and Authier, M. 2021. Spatiotemporal models highlight influence of oceanographic conditions on common dolphin bycatch risk in the Bay of Biscay. Marine Ecology Progress Series. 679:195-212. Doi:`https://doi.org/10.3354/meps13894`
- **2.** Authier, M., Rouby, E. and Macleod, K. 2021. Estimating cetacean bycatch from non-representative samples (I): a simulation study with regularized multilevel regression and post-stratification. Frontiers in Marine Science. 8:1459. Doi: `https://doi.org/10.3389/fmars.2021.719956`
- **3.** Rouby, E., Dubroca, L., Cloâtre, T., Demaneche, S., Genu, M., Macleod, K., Peltier, H., Ridoux, V. and Authier, M. .Estimating bycatch from non-representative samples (II): a case study of Pair trawlers and common dolphins in the Bay of Biscay. 2022. Frontiers in Marine Science. p:1946. Doi:`https://doi.org/10.3389/fmars.2021.795942`.

5.1 Introduction: About the bycatch phenomenon

Why does bycatch of common dolphins occur?

The structuring of multilevel trophic pelagic ecosystems is influenced by the presence of submesoscale and mesoscale oceanographic structures (Bakun 1997, 2006). These structures correspond to oceanic fronts (*i.e.* the frontier between two water masses of different density), upwellings (*i.e.* upward movement to the ocean surface of deeper cold usually nutrient-rich waters) and eddies (*i.e.* circular current of water). Upwellings contribute to the enrichment of the water column with nutrients through different processes, but regarding the eddies, it is the Ekman pump that is involved (Margin-Figure 5.1). In the event of a cyclonic wind (for the North Hemisphere) there will be a transfer of water from the centre to the periphery of the eddy, which will lead to an upwelling of cold water in the centre (Fieux 2019). Oceanic fronts support the enrichment of water with nutrients by the same process by allowing two different water masses to encounter and promote the retention of nutrients in a given area. If they are sufficiently stable over time, these structures allow the development of a whole trophic chain from phytoplankton, to zooplankton, to fish and finally to top-predators (Bakun 1997). Top predators, such as delphinids, integrate ecological processes at all levels of the trophic web through their dynamic distribution (Croll et al. 1998). A key element of delphinids distribution is the availability of fish, which is variable in space and time due to the oceanographic processes discussed above (Hyrenbach, Forney, and Dayton 2000).

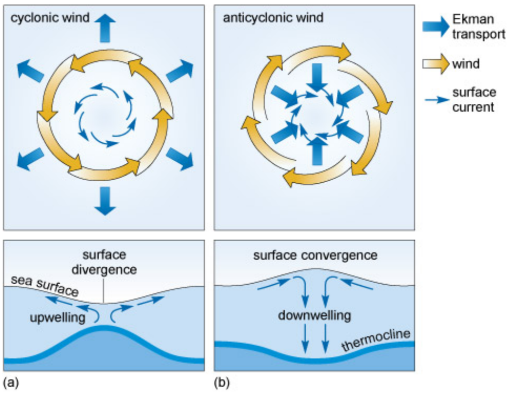


Figure 5.1: Ekman pumping. Horizontal divergence of the integrated Ekman transports gives rise to a vertical velocity at the base of the Ekman layer (*i.e.* "Ekman “pumping"):
A. Cyclonic winds drive upwelling (Ekman suction).
B. Anticyclonic winds drive downwelling (Ekman pumping).
Figure from Colling (2001). The book Fieux (2019) also provides information on this subject.

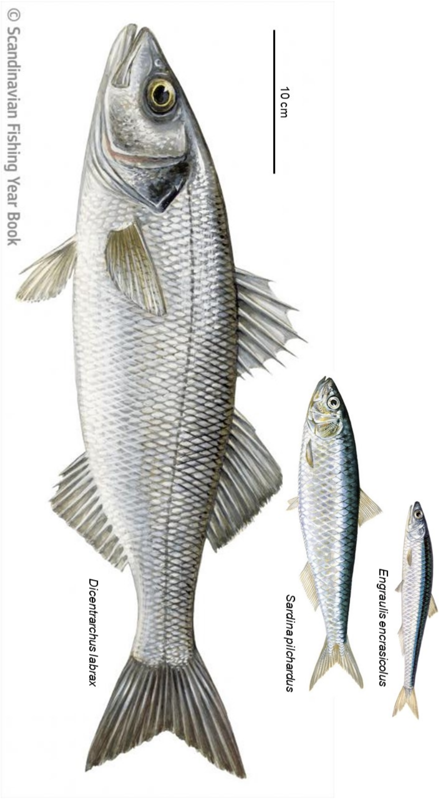


Figure 5.2: Drawings of fish important to the feeding ecology of the common dolphin.

The common dolphin is a top predator of pelagic ecosystems in the Bay of Biscay that feeds on a wide variety of fish species, some of which are targeted by fisheries (Pusineri et al. 2007; Meynier et al. 2008; Spitz et al. 2013), and whose presence depends on oceanographic conditions. The main fish species involved in dolphin-fisheries interactions are the sardine (*Sardina pilchardus*), the anchovy (*Engraulis encrasicolus*) (both are prey to the dolphin) and the seabass (*Dicentrarchus labrax*) (in trophic competition with the dolphin; Spitz et al. 2013; Figure 5.4 for an overview of the trophic chain). The latter species is targeted by the Pair trawlers (Margin-Figure 5.5), a *métiers* (*i.e.* the combination of gear, target species and fishing area) historically associated with bycatch of common dolphin in the Bay of Biscay (Peltier et al. 2021; as well as other fishing *métiers*). The occurrence of sea bass, and the fish on which the dolphin feeds, is indirectly conditioned by the availability of nutrients (such as phosphorus, nitrogen, potassium and iron). Nutrients have an influence on the development of phytoplankton

(Bakun 1997). The presence of phytoplankton (and the diversity of species associated with it) influences the presence of zooplankton that feed on phytoplankton (Lampert et al. 1986). If the persistence and retention of nutrients are sufficient, then the development of plankton will allow predators such as fish to feed (Beaugrand and P. C. Reid 2003). Finally, large fish and dolphins feed on smaller fish (Spitz et al. 2013) and pair trawlers target fish of commercial interest (Peltier et al. 2021).

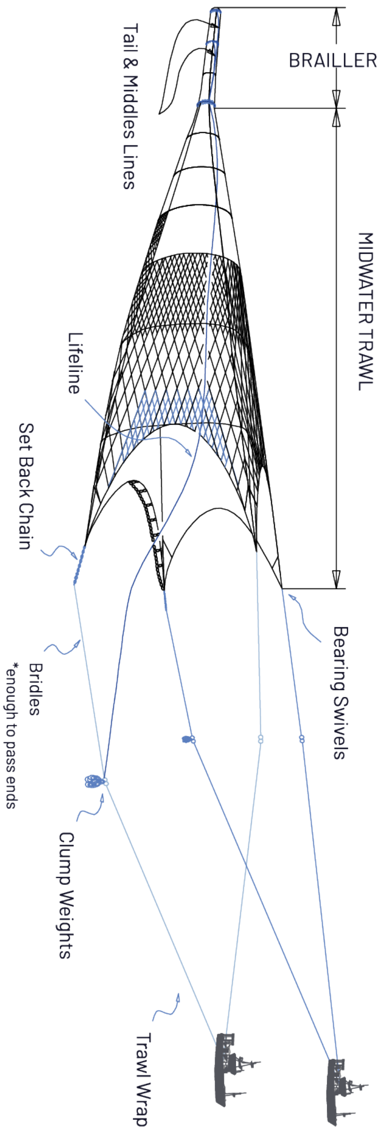


Figure 5.3: Scheme of pelagic pair trawler net.
Figure from `https://sng.ie/fishing/pelagic-old/`.

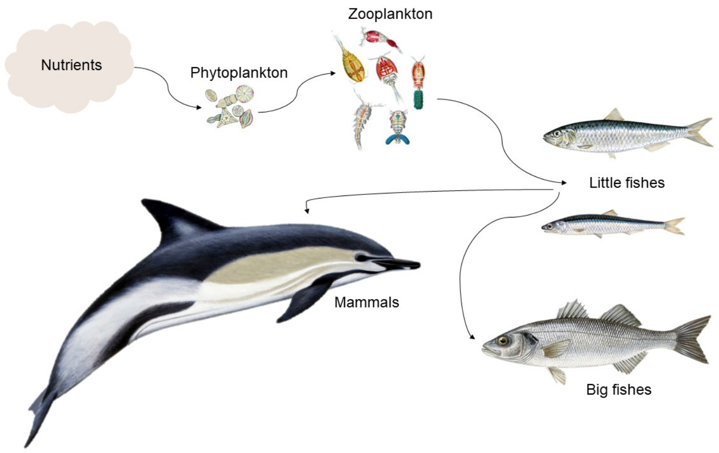


Figure 5.4: Diagram of trophic chain associated with common dolphin.

The proximal relationship between fish, dolphins and pair trawlers could drive the spatio-temporal variability of the bycatch pattern: fish distribution is notoriously variable in both space and time (Erauskin-Extramiana et al. 2019) and is governed by many factors from dynamic oceanographic conditions. Changes in local distribution and abundance of prey species might be a substantial driver of their simultaneous presence with common dolphins, commercial predatory fish and fisheries in localized areas. In order to investigate the link between oceanographic factors and dolphin mortality at sea, we coupled biological data which are related to reverse drift trajectories obtained from the bodies of stranded dolphins with incidental capture evidence and environmental data intrinsic to various physical processes at high and low frequency obtained thanks to the modelling services of the Shom[1] (Gilbert et al. 2021). We built a mortality estimation model to study the influence of sea surface temperature, turbulence force or eddy kinetic energy (*i.e.* Eddies occurrence) and mean surface temperature gradient (*i.e.* Frontal structures occurrence and intensity) over the years 2012 to 2018. The winter and summer oceanographic processes do not appear to be linked to the same mortality processes. In winter, the Bay of Biscay environment is characterized by a seasonal cross-shore (West to East) surface temperature gradient with lowest temperature close to shore and intense frontal activity parallel to the coast (North to South) (Yelekçi et al. 2017). These frontal structures are freshwater fronts, correlated to the mixing of oceanic

Two seasons of mortality with different oceanographic processes were highlighted:
Winter - Freshwater frontal structures.
Summer - Tidal frontal structures.

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[1] Service Hydrographique de la Marine Nationale: `https://www.shom.fr/`

waters and cold freshwater inputs from river plumes (Yelekçi et al. 2017). Their location and time line concur with observed patterns regarding bycatch mortality. Together with the effects of the associated oceanographic variables on the mortality index, results suggested these seasonal fronts may be targeted by both fisheries and common dolphins as areas where fish aggregate, thereby putting the latter at risk of bycatch by the former.
In July and August, the mesoscale dynamic activity of the Bay of Biscay is rather different than in winter. In summer, there are mainly fronts due to tidal flow (Yelekçi et al. 2017). Summer tidal fronts are quite consistent from one year to the next because they are correlated to a repetitive process (i.e. tides) (Yelekçi et al. 2017). In summer, the main frontal activity is a seasonal tidal front, called the Ushant front, located off western Brittany (Yelekçi et al. 2017). Its activity peaks in July and August (Yelekçi et al. 2017). The location of this typical tidal frontal structure concurred with the location of hot spots of fitted mortality index as well as with the location of bycaught common dolphin strandings, mainly occurring on the coast of the South Finistére region during the summer mortality season.

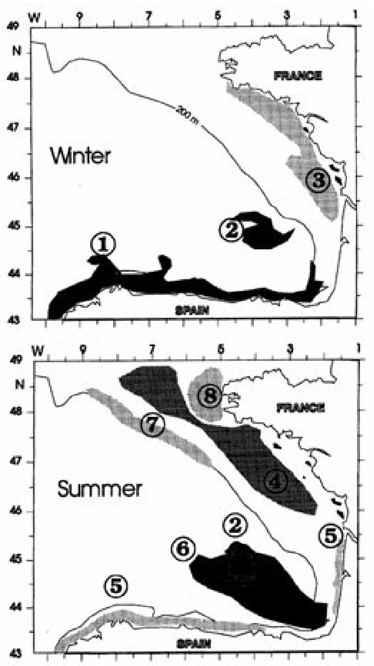

Figure 5.5: Seasonal variation in the main hydrographic structures in the Bay of Biscay. With: (1) winter warm slope current, (2) swoddies, (3) river plumes, (4) cold waters, (5) upwellings, (6) warm waters of Bay of Biscay, (7) slope current, (8) tidal currents.
Figure from Koutsikopoulos and Le Cann (1996).

These results suggest the influence of spatio-temporal oceanographic processes on common dolphin bycatch mortality in the Bay of Biscay. But the relationship should not be over-interpreted as the model indirectly linked oceanographic processes to common dolphin mortality. While this study aimed to explore the "why" question, it is important to answer the "how much" question. Especially in the context of the Habitat Directive and the MSFD.

Bycatch observation and quantification

In France, the monitoring of cetacean bycatch in fisheries is non-dedicated (Cornou et al. 2018) (observers are non-dedicated to the bycatch observation), and the collected data are described as non representative, which makes it difficult to estimate the bycatch risk. The bycatch risk is the probability of catching at least one dolphin in a haul. From the calculation of the bycatch risk, it is possible to estimate the number of common dolphins bycaughts for a given year in a given ICES[2] division. This estimation is carried out mainly in the Working Group on Bycatch of Protected Species[3] (WGBYC). Traditionally, using the observer data, the way to quantify the bycatch risk per Day at Sea (also refer as "bycatch rate" per day at sea) is to use a ratio-based estimator. A day at sea is defined as any continuous period of 24 hours (or part thereof) during which a vessel is present within a division and absent from port (Anonymous 2016). The number of bycaught dolphins is estimated[4] as the

[2] `https://www.ices.dk/Pages/default.aspx`

[3] `https://www.ices.dk/community/groups/Pages/WGBYC.aspx`

[4] The total bycatch $\hat{\Upsilon}$ of species (i) by region (r) is estimated as the sum of the observed specimens (y_i) to observed Days at Sea (x), time total fishing Days at Sea (X) summed over ICES areas (a) of interest:
$\hat{\Upsilon}_{ir} = \frac{\sum y_{iar}}{\sum x_{ar}} \times \sum X_{ar}$

product of the ratio of the sum of observed bycaught individuals to observed days at sea, times total fishing days at sea summed over ICES division of interest (ICES 2019, p. 58). This ratio-estimator is a design-based approach of the estimation of bycatch and is referred as a Bycatch risk Assessment (BRA) by WGBYC. The accuracy of the approach is largely dependent on the representativeness of sampling protocol (notably the observer scheme design). Due to the low observer coverage, the non dedicated-sampling protocol, the non-representativeness of observer dataset and the small number of hauls with few common dolphin bycatch, estimates based on ratios appear unreliable (Babcock, Pikitch, and Hudson 2003; Course 2021; Authier, Rouby, and Macleod 2021). An other way to quantify bycatch is to use strandings (Peltier et al. 2016).

It is impossible to use the classical ratio-estimator approach on onboard observer data to obtain the number of dolphin bycaught at fine spatio-temporal scales.

The use of strandings can be referred as model-based estimate since it implies a modelling-framework. Here it will be referred to as "stranding-based" estimates to better flow with the rest of the chapter, including the discussion. This approach is based on the drift reconstruction trajectory of the stranded individual using the MOTHY model[5] ("*Modéle Océanique de Transport d'HYdrocarbures*") from *Méteo France*. Then the estimated mortality in each year is corrected by the probability of being buoyant. This correction allows to estimate the number of dead dolphins, included those that sank and were not found ashore (Peltier et al. 2016). Using this approach, it is not possible to discriminate the involvement of each fishing métier in the mortality of common dolphins. To fill this gap, the use of observer data is very important, even if biased. Some model-based recent improvements allows to minimise the impact of the representativeness bias. For example, Luck et al. (2020) recently used a modelling framework to estimate the corrected bycatch probability and then use the fishing effort to extrapolate to the whole fishing fleet. Recently, Authier, Rouby, and Macleod (2021) adapted the use of a the regularized multilevel regression with post-stratification to infer more accurately bycatch rates at finer spatio-temporal scale than it is actually done.

Strandings are used to obtain the number of dolphin bycaught on a monthly basis. The estimation is done by inverse drift modelling. ICES estimates are currently made in this way.

[5] `http://www.meteorologie.eu.org/mothy/`

Stranding based estimates do not allow the number of catches per *métiers* to be estimated on a fine spatial and temporal scale.

There is a need to obtain bycatch estimates at a fine spatial and temporal scale and to use data from at-sea observers. In addition to estimates of the number of dolphins bycaught, estimates must be made for the variables associated with bycatch. The spatial and temporal scale must be fine enough to allow for inter- and intra-annual differences within ICES divisions. In this chapter, I present how we quantified the bycatch risk, haul duration, number of hauls per Days at Sea and number of bycaught dolphins from biased observer data . We quantified these parameters for each week from 2004 to 2020 within 10 ICES division to better represent variations in bycatch spatio-temporality using the approach of (Authier, Rouby, and Macleod 2021). This study involves firstly

We used Multilevel Post-Stratification to obtain the number of dolphins bycaught by PTM on a weekly basis from 2004 to 2020 in ten ICES divisions. We also estimated the bycatch risk, mean haul duration and number of hauls per Day at Sea on the same basis.

the analyse of historical bycatch monitoring data collected by onboard observers (from 2004 to 2020) on pair trawlers flying the French flag (hereafter called "PTM")[6] which is called Obsmer[7] ("*Observation des captures en mer*"). This dataset is the one considered as biased. From this dataset we estimated the bycatch risk, the haul duration and the number of hauls per Day at Sea. Then, we used a fishing effort dataset computed using the SACROIS algorithm[8] and the median number of bycaught dolphin by haul to estimate the number of bycaught dolphins per year and ICES divisions. Both dataset were provided by IFREMER[9] ("*Institut Français de Recherche pour l'Exploitation de la Mer*"). After presenting the involved data and the broad-lines of the applied methodology, I will compare the estimates made in this study with those of the stranding-based estimates.

5.2 Methodology: Quantify the bycatch parameters

In this section, the methodology used to estimate bycatch parameters (*i.e.* risk, duration and number of hauls) is detailed. First, a review of the materials available to perform the analyses is made. Then, a review of the methods is presented in outline.

Materials

ICES divisions, fisheries and study area

The North-East Atlantic ocean can be geographically divided differently depending on the focus (for example focusing on fisheries management or on ecosystems). ICES defines some ecoregions to refer to ecosystems in its ecosystem-based management approach (EBM) and divisions to give an overview of the fisheries related aspects in these ecoregions (ICES 2021b; Figure 2.11 in Page 34 Chapter 2).

The Bay of Biscay, the English Channel and part of the Celtic seas are ecoregions associated to a high variety of fishing gears, *métiers* and targeted species. These areas are associated with submesoscale and mesoscale oceanographic processes, such as eddies, river plumes and tidal fronts, that enhance ecosystem productivity and result in high availability of fishes, including commercial species (*e.g.* European seabass *Dicentrarchus labrax*, Sardine *Sardina pilchardus* or Anchovy *Engraulis encrasicolus*). Pelagic trawl fisheries, as pair-trawlers, are active within all of these areas and mainly target the anchovy, sardine, seabass and hake in divisions 8a and 8b (ICES 2020a). The study area for the estimation of common

[6] Pair-Trawlers flying the French flag are referred as "PTM" for the rest of the manuscript.

[7] `https://sih.ifremer.fr/Ressources/Obsmer`

[8] `https://wwz.ifremer.fr/sih_eng/Debarquements-effort-de-peche/Sacrois`

[9] `https://wwz.ifremer.fr/`

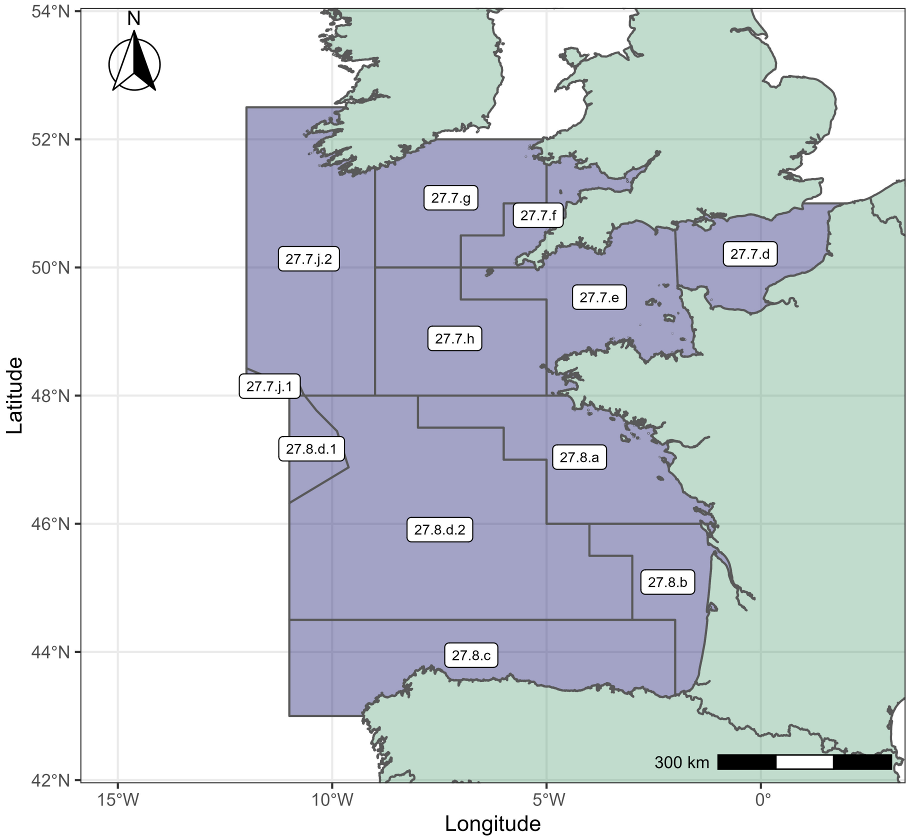

Figure 5.6: Study area in the North-East Atlantic ocean, with ICES divisions overlayed.

dolphin bycatch by the PTM takes into account 10 ICES divisions (Figure 5.6). Depending on the bathymetry, it is possible to classify these divisions as oceanic or neritic. Divisions 7.d, 7.e, 7.f, 7.g, 7.h, 8.a, 8.b and 8.c are related to neritic ecosystems while division 7.j and 8.d are related to oceanic ecosystems.

Datasets

Two main source of data[10] were used. The first source of data that was used is a dataset called Obsmer. This dataset is collected as part of an onboard observer program set up within the Data Collection Framework of the Common Fisheries Policy and carried out by IFREMER, under the supervision of the Directorate of Fisheries and Aquaculture ("*Direction des pêches maritimes et de l'aquaculture*", DPMA). Onboarding ObsMer observers' primary duty is to register the length and weight composition of catches. Still, they have to report any bycatch if they witness such events. Obsmer data on PTM covers 4, 484 hauls between 2004 and 2021, of which 82 were associated with a bycatch event of at least 1 and up to 50 common dolphins.

Obsmer provides the geographic position, timing, and du-

[10] Two dataet are used. Obsmer contains the information about byctach at the fine spatio temporal scale. It is the biased dataset. SACROIS contains the information about the true fishing effort of PTMs from 2004 to 2020 on a weekly basis. It is the population-level data assumed as true.

ration of hauls. Although Obsmer is aiming at a coverage of 10% and 5% of fishing effort for (level-3 *métier*) PTM for vessels of more than 15 meters and less than 15 meters respectively. Effort is quite low overall, ranging from 0.0 to 11% of Days at Sea (DaS; Table 5.1). The number of observed hauls with at least one bycatch record is very small: the yearly percentage of observed hauls with a bycatch event never exceeded 4.5% and was 0 in nearly half of the surveyed years. Obsmer data on PTM are an unrepresentative sample of hauls, largely because allowing an observer remains largely at the discretion of skippers (Babcock, Pikitch, and Hudson 2003; Benoît and Allard 2009).

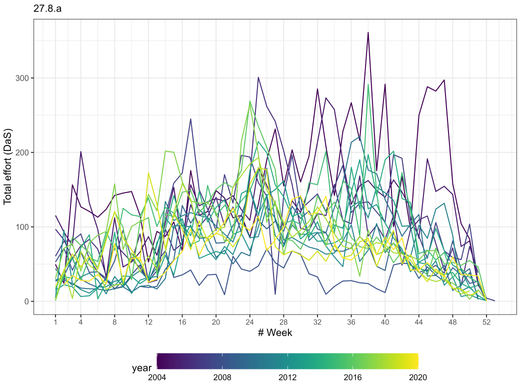

Figure 5.7: Total weekly PTM fishing effort in Days at Sea for each year in division 27.8.a. The raw data suggest significant inter-annual variation but a common pattern. Total effort appears to increase between week 1 and week 28 before declining.

The second dataset provides monthly estimates of total fishing effort in each division. This dataset is generated from the algorithm SACROIS developed by Ifremer and integrates data from Vessel Monitoring System, log-books and landing statistics (for boats longer than 18 meters from 1^{st} of January 2004 and longer than 15 meters from 1^{st} of January 2005; (Système d'Information Halieutique 2017)). The SACROIS algorithm is interesting for two main points: (1) it allows to correct errors that could exists in the integrated dataset due to recording or collecting errors ; (2) it reconstitutes métiers during fishing trip as there are not recorded in logbooks nor fish market data (Cornou et al. 2018). The SACROIS dataset provides the best available estimates of total effort, in Days at Sea (DaS), between 2004 and 2020 (Table 5.1). There are also refusals from skippers due to administrative and security reasons. Skippers must apply for permission to take observers on board and even if they decide to apply, permission may be refused for safety reasons (*e.g.* not enough space or rails not high enough).

These two datasets[11] are complementary to address the following challenge: is it possible to quantify bycatch parameters (such as bycatch risk, haul duration, number of hauls and number of dolphin bycaughts) from a non-representative sample ? The sample Obsmer contains the information on marine mammal bycatch at micro-level (*i.e.* on a haul resolution basis). This source of data allows to estimate the bycatch parameters (Luck et al. 2020). On the other hand, the fishing-vessels effort data from SACROIS provides the spatialized effort data at the scale of the whole fishing fleet (macro-level component). These population-level data on effort allows the post-stratification of bycatch risk estimated from observer data to obtain the number of bycaught dolphins at the level of the whole fleet (Authier, Rouby, and Macleod 2021). Descriptive statistics of both datasets are displayed in Table 5.1. Used in tandem, both datasets allow using regularized multilevel regression with post-stratification to estimate cetacean bycatch from non-representative samples (Authier, Rouby, and Macleod 2021).

11: Obsmer provides the micro-scale information while SACROIS provides the macro-scale information.

Table 5.1: Descriptive statistics for Obsmer and SACROIS data displayed for each year.
The bycatch events observed seem to be recurrent since 2007. The year associated with the highest level of observed bycatch is 2009 with 50 dolphins.
Total observer coverage of fishing effort is rarely more than 5%. The maximum PTM fishing effort covered in Days at Sea is 10.9% in 2008.

Dataset	Obsmer						SACROIS
Year	**Hauls**	**Average Duration (hours)**	**Bycatch events**	**Median nb of dolphins**	**Max. nb of dolphins**	**DaS (Coverage %)**	**Total Effort (DaS)**
2004	4	2.80	0	-	-	4 (0.0)	8 530
2005	5	4.26	0	-	-	4 (0.0)	8 790
2006	122	4.62	0	-	-	90 (1.1)	7 853
2007	727	3.89	6	1.5	5	401 (6.4)	6 305
2008	554	4.81	6	1.5	4	328 (10.9)	3 011
2009	464	5.50	20	2	50	326 (7.4)	4 413
2010	305	3.52	1	4	4	159 (3.5)	4 486
2011	173	3.99	2	3	3	86 (2.1)	4 001
2012	210	3.58	4	4	8	96 (2.4)	4 005
2013	128	3.81	2	5.5	9	75 (1.8)	4 192
2014	114	4.44	0	-	-	78 (1.9)	4 136
2015	136	2.77	1	2	2	78 (1.7)	4 597
2016	156	4.75	5	3	10	106 (2.3)	4 603
2017	196	5.23	12	2	20	124 (2.6)	4 835
2018	184	3.85	1	1	1	102 (2.8)	3 613
2019	438	5.45	11	2	8	289 (7.4)	3 139
2020	123	3.69	2	2	3	70 (4.0)	1 686

Methods

The modelling framework involved two steps. First, it is necessary to both estimate the bycatch risk and the duration of hauls for each haul i, ICES division j, week t and year k. Also, it is possible to estimate the number of hauls per day at sea at the week, division and year scale. This is done with the Obsmer dataset. Then, it is necessary to rescale these estimations at the entire fleet level to estimate the number of bycatch events and number of bycaught dolphins for the same levels. This post-stratification is done with the SACROIS dataset.

Estimations were carried out in a Bayesian framework using programming language `Stan` (Carpenter et al. 2017b) called from `R` v.4.0.1 (R Core Team 2020) with library `Rstan` (Stan Development Team 2020). `Stan` uses Hamiltonian dynamics in Markov chain Monte Carlo (MCMC) to sample values from the joint posterior distribution (Carpenter et al. 2017b). Four chains were initialised from diffuse random starting points and run for a total of $2,000$ iterations, discarding the first $1,000$ as warm-up. Default settings for the No-U-Turn Sampler (NUTS) were changed to 0.99 for `adapt delta` and 15 for `max treedepth` (Hoffman and Gelman 2014). We fitted a total of 6 models of differing complexity (see Margin-Table 5.2 for specification and article in Appendix 7.4 for model selection): we compared models assuming either a gamma or a log-normal likelihood for haul duration, and models assuming additive effects

Model	likelihood for duration	Specification
$\mathcal{M}_6$	gamma	ICES division × week × year
$\mathcal{M}_5$	log-normal	ICES division × week × year
$\mathcal{M}_4$	gamma	ICES division + week × year
$\mathcal{M}_3$	log-normal	ICES division + week × year
$\mathcal{M}_2$	gamma	ICES division + week + year
$\mathcal{M}_1$	log-normal	ICES division + week + year

Table 5.2: Models specification.

versus interactive effects of week, year and divisions. Model fitting was carried out on the supercomputer facilities of the "Mésocentre de calcul de Poitou Charentes (Université de Poitiers/ISAE-ENSMA/La Rochelle Université)". Codes are available at `https://gitlab.univ-lr.fr/mauthier/cdptmbycatch`.

Modelling Bycatch risk, duration of hauls and number of hauls

The objective of this part of the modelling framework is to model the bycatch risk and the haul duration at the haul level and the number of hauls per day at sea using only the Obsmer dataset. The problem with trying to estimate the value of these parameters is that we do not know how to interpolate between the observed points. Lets start with an example. In the Margin-Figure 5.8, we see that we only have 6 data points (for weeks $t = 3, 4, 10, 24, 46$ and 53). This number is reduced to 4 for a given year k and is reduced to 3 for a given division j in a given year k (Figure 5.10 to see the data depletion associated with stratification). We do not know how to fit a line between those points. And even less is known about how to extend the estimation of these profiles beyond the weekly scale to estimate by week for each year in each division. We only have some observations at the haul level scale i for the bycatch risk and the haul duration and we also have the number of hauls. Obsmer data are sparse (Margin-Table 5.3) and the stratification of these data increases sparseness (Figure 5.9).

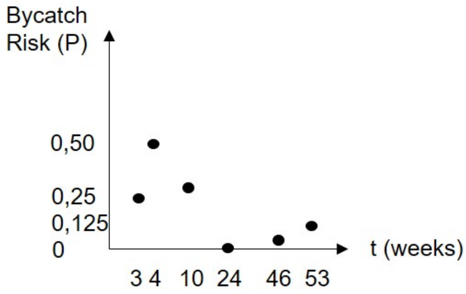

Figure 5.8: Diagram of bycatch risk per weeks. This diagram shows how sparse the data available on the collection by observers is.

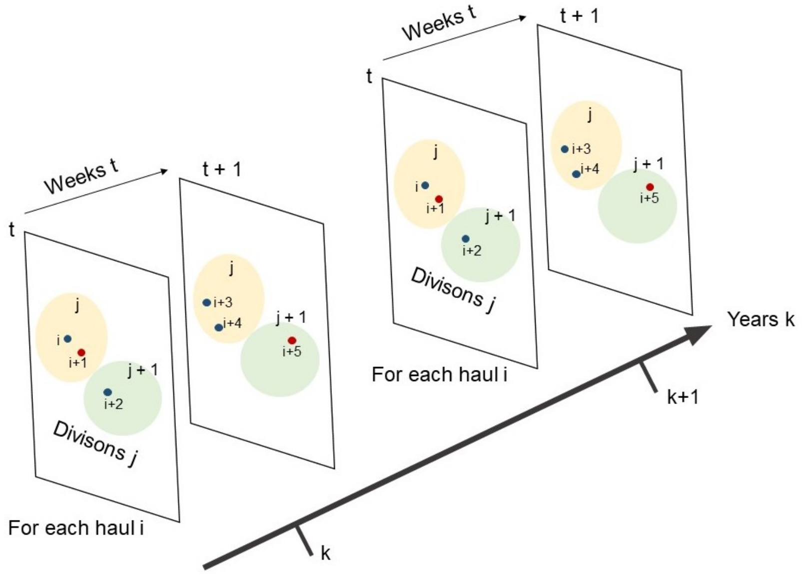

Figure 5.9: Diagram of stratification. This diagram shows the stratification of the data. The dots represent trawl hauls. Red dots are those with at least one bycatch event. The blue dots are those with no bycatch events. The lines are stratified by week, division and year.

To interpolate between the observed data points, we used firstly a random walk and then Gaussian Process. See Görtler, Kehlbeck, and Deussen (2019) for an interactive web-page explanation of Gaussian Processes. The vector $\boldsymbol{\epsilon}$ aggregates the mean weekly effects (on the linear predictor scale, *e.g.* logit scale for

Haul (i)	Duration (hours)	Bycatch	Week (t)	Year (k)	Division (j)
1	1.5	No	2	1	2
2	5	Yes	2	1	2
3	5	No	5	10	8

Table 5.3: Dummy dataset to illustrate the typical sparseness in Obsmer data.

bycatch risk) which are modelled with a first order random walk to ensure some smoothness in between-week variations (Figure 5.10; Authier, Rouby, and Macleod 2021).

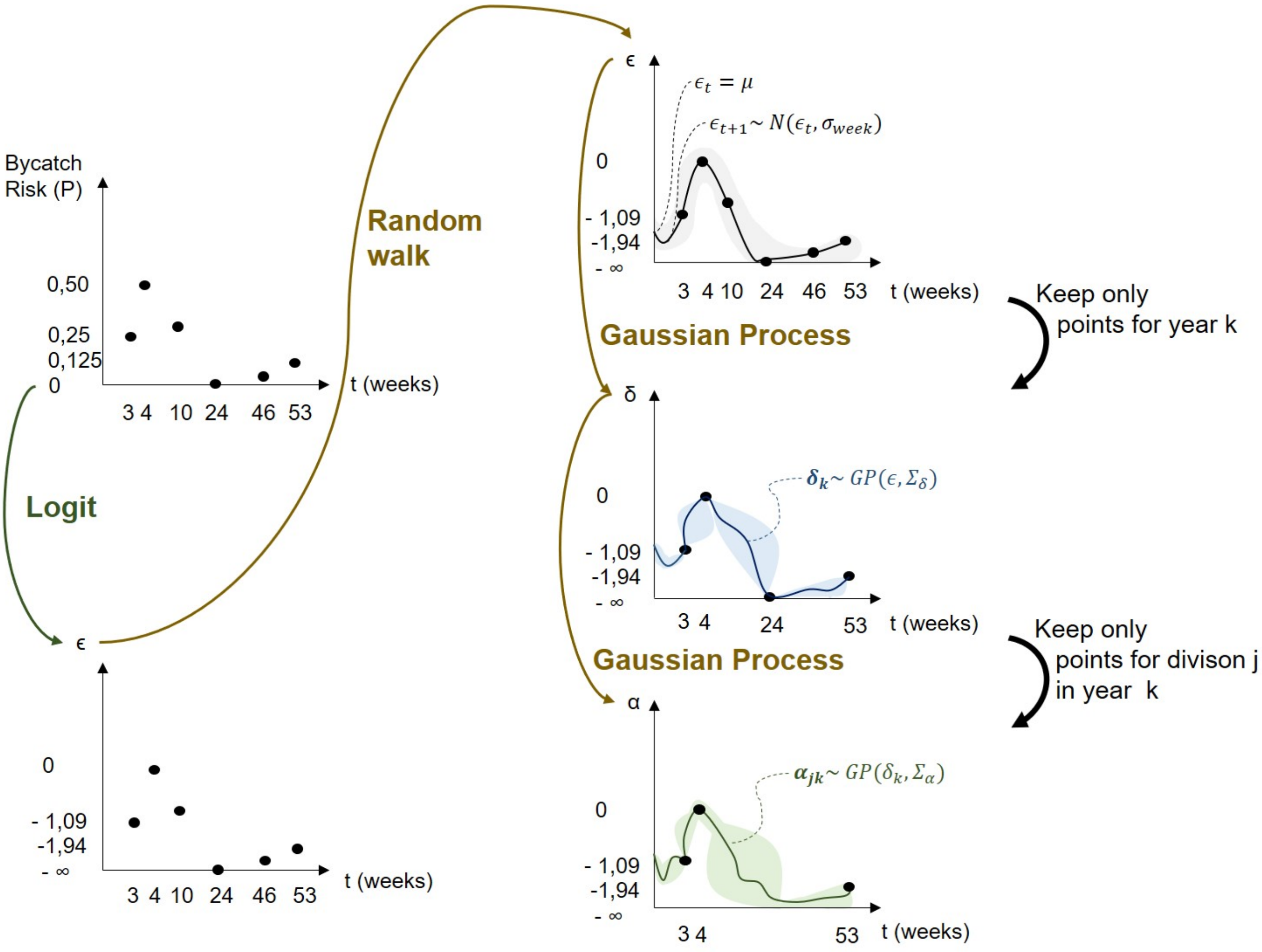

Figure 5.10: Diagram of the estimation process. This diagram is based on the example of the bycatch risk. It could also be based on the other two estimated parameters, which are: The Haul and the number of Hauls per Days at Sea.
The raw bycatch risk data are logistically transformed (logit function) in order to place the estimate on a continuous scale and not between 0 and 1. Each data point corresponds to a haul. A first estimate of the risk in one year (week 1 to 53) is modelled by a random walk of order 1.
The first stratification is performed and the value of each risk profile for each year k is estimated from a Gaussian process whose mean is the previous weekly risk profile.
The second estimation then takes place and the value of the risk profile for each division j within each year k is estimated by another Gaussian process whose mean is the previous Gaussian profile.

From the observed data points, it is possible to infer the bycatch risk profile for each strata using a Bernoulli model (*i.e.* logit scale; Figure 5.10). As it is depicted bellow on Equations 5.1, the intercept of the fitted curve corresponds to ϵ_t and is equal to μ.

The first order random walk then allows to estimate the following weekly value with a normal distribution: $\epsilon_{t+1} \sim \mathcal{N}(\epsilon_t, \sigma_{\text{week}})$ and so on until the 53^{rd} week.
From this overall profile (*i.e.* the vector $\boldsymbol{\epsilon}$), a first Gaussian Process allows to estimate the bycatch risk profile for year k, $\boldsymbol{\delta_k}$. Conceptually, the idea is to model $\boldsymbol{\delta_k}$ as a deviation from the mean profile $\boldsymbol{\epsilon}$. This can be described as modelling a random effect except that curves rather than scalars are being modelled here. The profile is estimated with the Gaussian Process as follows: $\boldsymbol{\delta_k} \sim \mathcal{GP}\,(\boldsymbol{\epsilon}, \boldsymbol{\Sigma}_\delta)$ with $\boldsymbol{\Sigma}_\delta$ as the covariance matrix.
From this year-specific profile (*i.e.* the vector $\boldsymbol{\delta_k}$), a second Gaussian Process allows to estimate the profile of $\boldsymbol{\alpha_{jk}}$ which depends on the year k and on the division j (Figure 5.10). The profile is estimated with the Gaussian Process as follows: $\boldsymbol{\alpha_{jk}} \sim \mathcal{GP}\,(\boldsymbol{\delta_k}, \boldsymbol{\Sigma}_\alpha)$ with $\boldsymbol{\Sigma}_\alpha$ as the covariance matrix.

$$\begin{cases} \boldsymbol{\alpha_{jk}} \sim \mathcal{GP}\,(\boldsymbol{\delta_k}, \boldsymbol{\Sigma}_\alpha) & \\ \boldsymbol{\delta_k} \sim \mathcal{GP}\,(\boldsymbol{\epsilon}, \boldsymbol{\Sigma}_\delta) & \\ \epsilon_t = \mu & t = 1 \\ \epsilon_{t+1} \sim \mathcal{N}(\epsilon_t, \sigma_{\text{week}}) & t > 1 \end{cases} \tag{5.1}$$

Simpler models without such interactions, and with only additive effects, were also fitted to the data. The simplest model included only additive random (unstructured) effects (dropping the superscript for convenience):

$$\begin{cases} \boldsymbol{\alpha_{jkt}} = \epsilon_t + \delta^*_k + \alpha^*_j & \\ \boldsymbol{\alpha^*_j} \sim \mathcal{N}\,(0, \sigma_{\text{division}}) & \forall\, j \\ \boldsymbol{\delta^*_k} \sim \mathcal{N}\,\left(0, \sigma_{\text{year}}\right) & \forall\, k \\ \epsilon_t = \mu & t = 1 \\ \epsilon_{t+1} \sim \mathcal{N}(\varepsilon_t, \sigma_{\text{week}}) & t > 1 \end{cases} \tag{5.2}$$

To simplify the equations, I did not include the superscripts in the Equations 5.1 but there are three alphas $\boldsymbol{\alpha^1}, \boldsymbol{\alpha^2}, \boldsymbol{\alpha^3}$ and three deltas $\boldsymbol{\delta^1}, \boldsymbol{\delta^1}, \boldsymbol{\delta^1}$. The superscript ^{1} refers to the bycatch risk, the ^{2} to the haul duration and the ^{3} to the number of hauls.

The Bycatch risk p_{jkt} is modelled as follow with y_{ijkt} corresponding to bycatch event (0 or 1) of the i^{th} haul for each ICES statistical division j in week t of year k. The occurrence of a bycatch event is modelled as the logit transform of α^1_{jkt} in a binary outcome, provided by the Bernoulli law. Depending on the bycatch risk, a

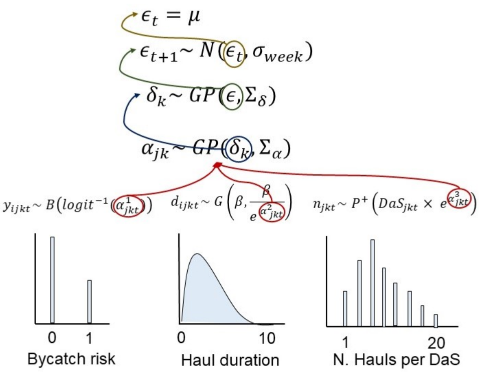

Figure 5.11: Diagram of the interaction between the equations in the estimation. The value of μ gives the intercept for the weekly risk profile.
The vector $\boldsymbol{\epsilon}$ corresponding to the weekly risk profile.
This vector is the mean estimate of the first Gaussian process for each year k. The estimate provides a risk profile for each year $\boldsymbol{\delta_k}$.
From this annual vector, a final Gaussian process takes it as an average to estimate the profile of each division j within each year k: $\boldsymbol{\alpha_{jk}}$.
The values of this vector are then used to inform the estimation of the bycatch parameters.

bycatch event can occur as:

$$\begin{aligned} y_{ijkt} &\sim \text{Bernoulli}\left(\mathrm{p}_{jkt}\right) \\ &\sim \text{Bernoulli}\left(\text{logit}^{-1}\left(\alpha^{1}_{jkt}\right)\right) \end{aligned} \tag{5.3}$$

The fishing duration d_{ijkt} at the haul level i is modelled for the same levels jkt with a Gamma distribution $\mathcal{G}$ of shape parameter β and scale parameter $\frac{\beta}{\bar{d}_{jkt}}$. The parameter $\bar{d}_{jkt}$ is associated to the second alpha as: $\bar{d}_{jkt} = e^{\alpha^{2}_{jkt}}$. This law allows the representation of continuous non negative value which is appropriate for a fishing duration. :

$$\begin{aligned} d_{ijkt} &\sim \mathcal{G}\left(\beta, \frac{\beta}{\bar{d}_{jkt}}\right) \\ &\sim \mathcal{G}\left(\beta, \frac{\beta}{e^{\alpha^{2}_{jkt}}}\right) \end{aligned} \tag{5.4}$$

and the number of hauls n_{jkt} for the same levels jkt per Days at Sea DaS_{jkt} is modelled assuming a zero-truncated Poisson likelihood (by definition, a DaS implies at least one haul). The parameter λ_{jkt} is associated to the third alpha as: $\lambda_{jkt} = e^{\alpha^{3}_{jkt}}$. This distribution allows the representation of non negative and non null discrete events number which is appropriate for a number of fishing hauls. :

$$\begin{aligned} n_{jkt} &\sim \mathcal{P}^{+}\left(\text{DaS}_{jkt} \times \lambda_{jkt}\right) \\ &\sim \mathcal{P}^{+}\left(\text{DaS}_{jkt} \times e^{\alpha^{3}_{jkt}}\right) \end{aligned} \tag{5.5}$$

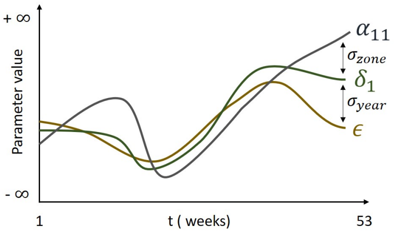

Figure 5.12: Diagram of the deviation when estimating the profile of the parameter of interest. What causes the profile to deviate is the variance due to the year effect (σ_{year}) and the variance due to the division effect (σ_{zone}). These two variances are included in the variance covariance matrices Δ.

The smoothness in $\boldsymbol{\alpha_{jk}}$ and $\boldsymbol{\delta_k}$ is controlled via the covariance matrices $\boldsymbol{\Sigma}_\alpha$ and $\boldsymbol{\Sigma}_\delta$ respectively as:

$$\begin{cases} \boldsymbol{\Sigma}_\alpha = \Delta_\alpha \boldsymbol{\Omega} \Delta_\alpha, \quad \Delta_\alpha = \begin{bmatrix} \sigma_{\text{zone}} & 0 & 0 \\ 0 & \ddots & 0 \\ 0 & 0 & \sigma_{\text{zone}} \end{bmatrix} \\ \boldsymbol{\Sigma}_\delta = \Delta_\delta \boldsymbol{\Omega} \Delta_\delta, \quad \Delta_\delta = \begin{bmatrix} \sigma_{\text{year}} & 0 & 0 \\ 0 & \ddots & 0 \\ 0 & 0 & \sigma_{\text{year}} \end{bmatrix} \end{cases} \tag{5.6}$$

Equations 5.1 and 5.6 allow to model an interaction between week, year and division. The joint model defined in Equations 5.3, 5.4 and 5.5 includes a time-varying component at the week-scale with an interaction with year and division.

As it is showed in Equation 5.6, there are two important component to build the covariance matrix. The first is Δ which corresponds to the variance matrix either for α (diagonal of σ_{zone}) or for δ (diagonal of σ_{year}). These σ are controlling the magnitude of variations from a mean profile (Margin-Figure 5.12 for a diagram).

The second is Ω, which is the correlation function between the variance matrixes. It is the correlation between week t and week $t^{'}$. This function is a Matérn correlation function of order $\frac{3}{2}$ and range parameter fixed to $\frac{3}{2}$ as: $\Omega\left(t, t^{'}\right) = \left(1 + \frac{2\sqrt{3}\times d(t-t^{'})}{3}\right) \times \exp -\frac{2\sqrt{3}\times d(t-t^{'})}{2}$ where $d(t-t^{'}) = |t-t^{'}|$ is the temporal distance (in weeks) between weeks t and $t^{'}$. The choice of the range parameter induces a temporal correlation of 0.05 after 4 weeks (Margin-Figure 5.13 and Figure 5.14; Authier, Rouby, and Macleod 2021).

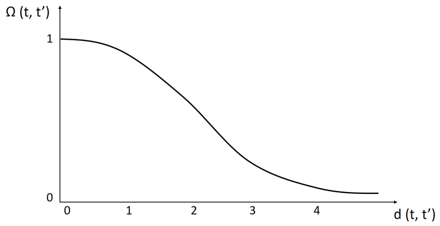

Figure 5.13: Diagram of autocorrelation independance. The omega-covariance function admits independence after 4 weeks.

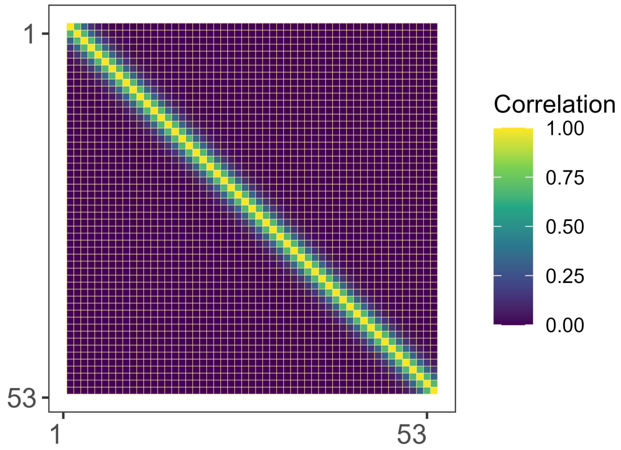

Figure 5.14: Graphical representation of the assumed correlation matrix $\boldsymbol{\Omega}$. The correlation is equal to 0 after 4 weeks.

The methodology is shown in the Directed Acyclic Graph Figure 5.15 taking for example the bycatch risk estimation. We have information about bycatch risk from the dataset Obsmer. From the estimations of hyperparameters (notably μ and σ_{week}) we can estimate the others. Finally it is possible to fit the bycatch risk profile (such as the haul duration and the number of hauls per Day at Sea) with a Bernoulli model (as in equation 5.3).

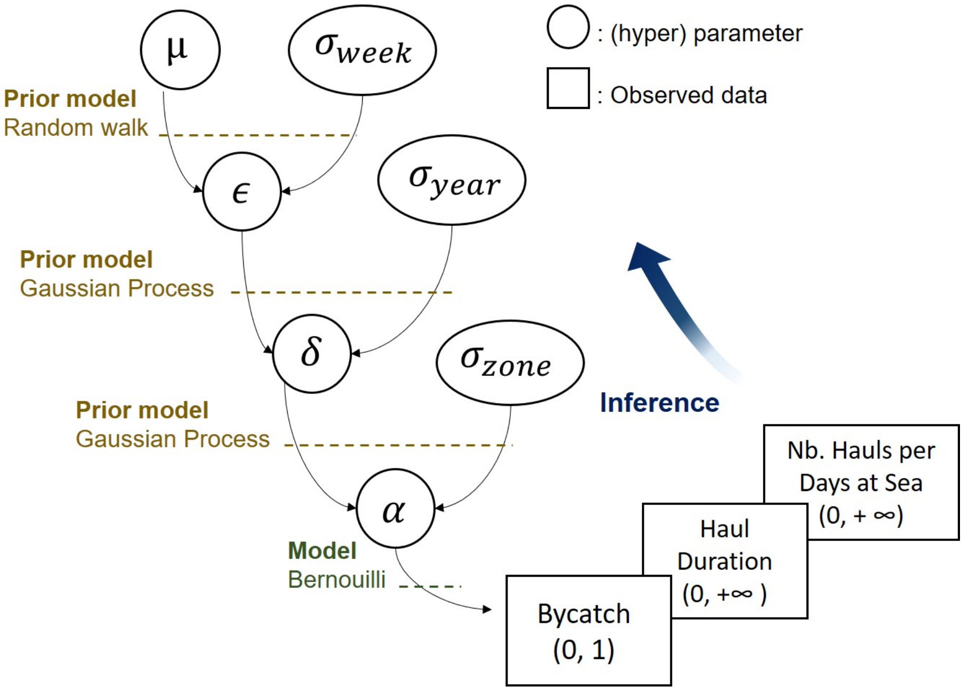

Figure 5.15: Directed Acyclic Graph of the methodology. The observed data are the basis of the statistical inference. Each parameter can be a hyperparameter of the others. For example, μ is a hyperparameter of the whole process while α is a simple parameter. Each parameter, or hyperparameter, is estimated from the previous one and a small deviation σ induced by stratification.

Modelling assumptions

- **1.** Bycatch risk, fishing duration and number of hauls per Days at Sea may be correlated. The correlation is induced at the week level via parameter $\boldsymbol{\alpha}$.
- **2.** There is a temporal Independence after 4 weeks.

Estimating the total number of hauls and bycatch events

The goal of this part of the modelling framework is to scale-up the estimated bycatch risk and the haul duration at the haul level and the number of hauls per day at sea at the fleet level using the fishing effort dataset (Days at Sea). It allows to estimate the total number of unobserved hauls $\hat{\text{N}}_{jkt}$ and the number of bycatch events $\widehat{\text{Bycatch}}_{jkt}$ for each week t, year k and division j.

The number of unobserved hauls N_{jkt} that happened in ICES statistical division j in week t of year k can be estimated from the number of observed DaS in Obsmer ($\text{DaS}_{jkt}^{\text{Obsmer}}$) and from total effort $\text{DaS}_{jkt}^{\text{tot}}$ (and accounting for zero-truncation):

$$\hat{\text{N}}_{jkt} = \frac{\hat{\lambda_{jkt}}}{1 - e^{-\hat{\lambda_{jkt}}}} \times \left(\hat{\text{DaS}}_{jkt}^{\text{tot}} - \text{DaS}_{jkt}^{\text{Obsmer}}\right) \tag{5.7}$$

The total number of bycatch events in ICES statistical division j in week t of year k is estimated as the sum of events observed in Obsmer ($\text{Bycatch}_{jkt}^{\text{Obsmer}}$) and the number of unobserved hauls multiplied by bycatch risk ($\hat{p_{jkt}}$):

$$\hat{\text{Bycatch}}_{jkt} = \text{Bycatch}_{jkt}^{\text{Obsmer}} + \hat{N_{jkt}} \times \hat{p_{jkt}} \tag{5.8}$$

Similarly, for each year, the number of common dolphins bycaught in PTM can be estimated using the observed number of bycaught dolphins in Obsmer, the estimated number of unobserved hauls (Eq. 5.7), bycatch risk and either the median number of dolphins involved in a bycatch event (Table 5.1, or the grand median of $m = 2$ for years with no observed bycatch event). We used the median to attenuate the influence of some bycatch events involving up to 50 dolphins (Table 5.1). These estimates are thereafter referred to as model-based estimates.

Baseline assumption for post-stratification

The total fishing effort data are accurate.

Comparison with strandings

One difficulty while estimating the number of bycaught dolphins is that it is difficult to ground-truth. The sample provided by Obsmer, a non-dedicated observer scheme of marine mammal bycatch, may not be representative of all bycatch. In addition it provides very sparse data, with less than 100 observed events over 17 years when strandings have reached several hundreds per week in recent years (ICES 2020b) (for all causes of death). The number of stranded common dolphins with evidence of bycatch can be used to estimate the total bycatch mortality with reverse drift modelling (Peltier et al. 2016) used in international working groups (ICES 2020b). Reverse drift modelling corrects for at-sea drift conditions, but cannot inform on which fishing gears was responsible for bycatch[12] . Hence, strandings-based estimates are considered here as total estimates of bycatch, and can be used to partially ground-truth model-based estimates of bycatch by PTM.

These model-based estimates use data independent from strandings, but they should not exceed stranding-based estimates. Secondly, whether model-estimates correlate with stranding-based ones is of interest to shed light on the increased mortality reported in the Bay of Biscay (Peltier et al. 2021). For each year we checked the magnitude of model-based estimates against stranding-based ones, and computed Pearson's correlation coefficient between the

[12] While it is possible to spot bycatch evidence as it is shown in Figure 2.19 in Chapter 2, it is very difficult to identify fishing gear involved. Sometimes it is possible to see the mesh marks of the net and assume the type of net. But this remains very exploratory and qualitative.

two time-series at the month level. To account for drift, these correlation were computed with and without a lag of 2 weeks when aggregating model-based estimates at the month level.

5.3 Results: Estimation of variables and number of dolphins bycaught

Bycatch risk, haul duration and number of hauls per Days at Sea

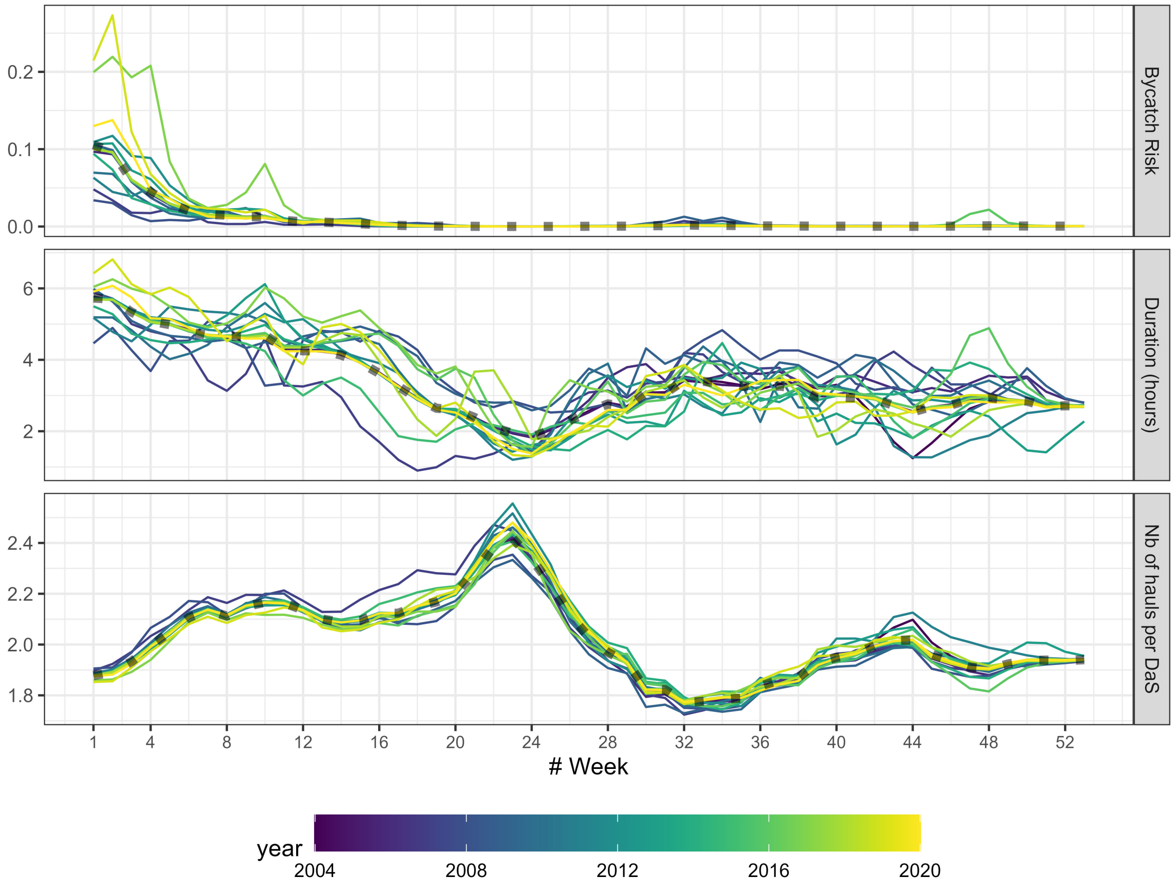

Figure 5.16: Model-based estimates (posterior medians) regardless of division. Estimates were made for bycatch risk, haul duration and number of hauls per DaS of pair-trawlers flying the French flag operating in the study area. Each colour represents a different year (parameters α_{jkt} in Eq. 5.1) and the dotted black line the yearly average (parameters ϵ_t in Eq. 5.1).

Haul duration, hauls per DaS and bycatch risk per haul (Eqs. 5.7 and 5.8) were jointly estimated. Their temporal variations are displayed on Figure 5.16 for each week between 2004 and 2020. Haul duration was the highest in week 1 with a posterior median estimate of 5.8 hours that decreased to 4.0 h in week 16, before dropping to 2 h in week 24. Haul duration increased up to 3 hours in week 32 and plateaued until the end of the year. Remarkable years were 2008 and 2014 with the lowest haul durations estimated

from week 1 to 24. Other remarkable years were 2017, 2019, and 2020 with the longest haul durations estimated from week 1 to 10. In 2016, an increase in haul duration was estimated in week 48 (5 h vs 3 h on average across years).
Bycatch risk was maximum in week 1 (around 0.1) and decreased to almost 0 from week 8 onwards. 2017, 2019 and 2020 were the years with the highest estimated bycatch risk in the first 8 weeks. In particular, risk was as high as 0.20 in 2017 for the first four consecutive weeks of the year. Two years prior to 2012 were associated with an increased risk between weeks 30 and 36. Year 2016 showed a rise in bycatch risk in week 48. The weeks in the highest risk years were also those with the longest hauls. The estimated number of hauls per DaS varied little from year to year, but varied substantially within a year.

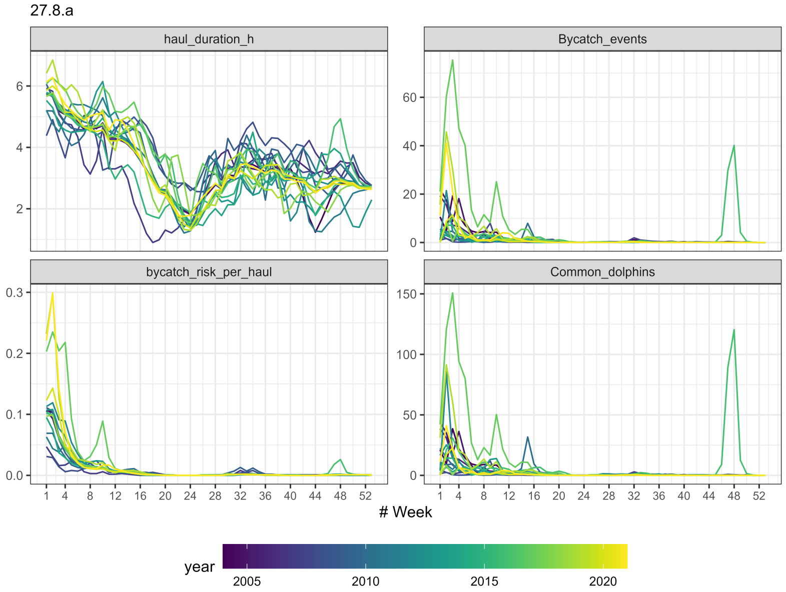

Figure 5.17: Temporal patterns for division 27.8.a. The temporal pattern is displayed for 4 variables: haul duration (hours), bycatch events (n), bycatch risk per haul (probability), common dolphins bycaught (n).
The estimated haul duration is the highest from week 1 to 20. The lowest at week 24 and then it remains stable from 32 to the end.
The estimated bycatch risk is highest between weeks 1 and 8 and is highest for years beyond 2016.

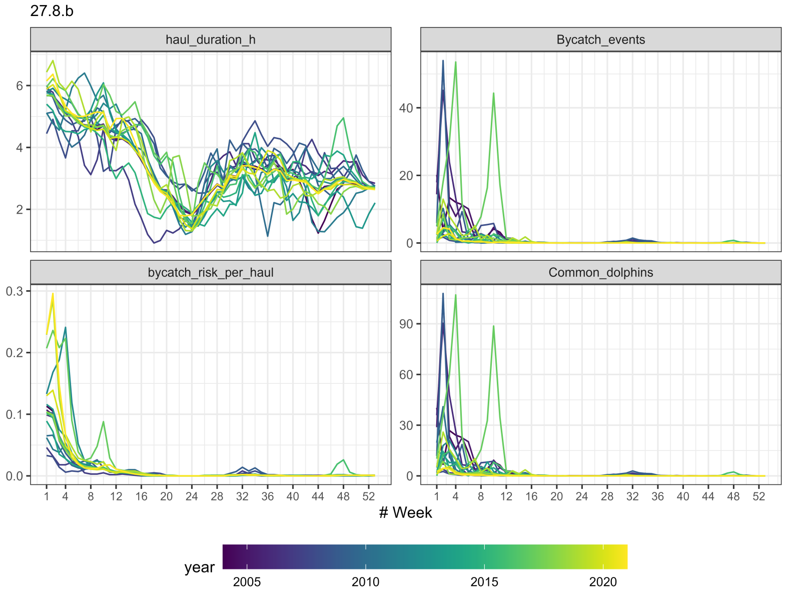

Figure 5.18: Temporal patterns for division 27.8.b. The temporal pattern is displayed for 4 variables: haul duration (hours), bycatch events (n), bycatch risk per haul (probability), common dolphins bycaught (n).
The estimated haul duration is the highest from week 1 to 20. The lowest at week 24 and then it remains stable from 32 to the end.
The estimated bycatch risk is highest between weeks 1 and 8 and is highest for years beyond 2016 and the year 2012.

There were noteworthy differences between divisions regarding bycatch risk (Figures 5.17 and 5.18). The overall signal was similar to the one observed on Figure 5.16 with the highest risk values estimated between weeks 1 and 8. Risk in 2017 and 2019 was higher by a factor 5 in week 1 compared to other years. After week 8, this difference disappeared. With respect to divisions, division 8.a. was the one with the highest bycatch risk, with an estimate as high as 0.50 in winter 2017 and 2019. For division 27.8.a, estimated bycatch events were more numerous from week 1 to 8 with high peaks for years > 2016. There was also a peak for year 2016 in week 48. The estimated number of common dolphins presented the same pattern as the number of bycatch events. For division 27.8.b, estimated bycatch events were more numerous from week 1 to 12 with a high peak for 2009 and 2012. There were two peaks for 2016, one in week 4 and one in week 10. The estimated number of common dolphins presented the same pattern as the number of bycatch events.

Number of Bycaught dolphins

Year	Neritic 7			Neritic 8			Oceanic			Total		
2004	0	48	248	0	177	876	0	1	10	0	227	1134
2005	0	56	302	0	235	1101	0	2	15	0	293	1417
2006	0	77	378	0	208	923	0	0	3	0	286	1303
2007	15	45	102	0	29	111	1	2	8	16	77	219
2008	1	18	63	11	46	125	0	0	4	12	65	190
2009	10	94	248	172	315	568	0	1	6	183	412	820
2010	0	119	537	4	112	454	0	0	3	4	232	994
2011	9	128	359	0	61	270	0	1	7	9	191	635
2012	22	233	667	0	129	511	0	3	13	23	366	1190
2013	13	315	1086	0	105	442	0	5	25	13	426	1552
2014	0	33	158	0	50	224	0	0	3	0	84	384
2015	0	14	71	2	78	368	0	1	8	2	94	446
2016	0	15	76	55	255	852	0	0	3	55	270	929
2017	0	18	61	156	600	1355	0	0	1	156	618	1415
2018	0	2	15	1	31	147	0	0	2	1	35	163
2019	0	12	40	59	203	391	0	1	6	59	216	441
2020	0	6	27	4	50	159	0	0	5	4	57	190

Table 5.4: Model-based estimates of common dolphin bycaught in PTM in the study area. Divisions 7.j and 8.d are labelled 'Oceanic', divisions 7.defgh are labelled 'Neritic 7' and divisions 8.abc are labelled 'Neritic 8'. Estimates (posterior median) are reported with the lower and upper bound of a 80% credibility interval (Louis and Zeger 2009)

The estimated total number of bycaught dolphins for each year is reported in Table 5.4. The study area was further divided into three strata: a neritic stratum in ICES subarea 7 (divisions 7.defgh) and another in subarea 8 (division 8.abc); and an oceanic stratum spanning subareas 7 and 8 (divisions 7.j and 8.d). Estimates were the lowest in the oceanic stratum of the study area, and the largest in the neritic stratum spanning ICES subarea 8. The largest bycatch estimate was in 2017, with a posterior median of > 600 common dolphins bycaught in PTM operating in the neritic stratum spanning ICES subarea 8. There were large between-year variations in estimates, ranging from less than a hundred (in 2018) to more than one thousand (in 2017). Uncertainties around model-based estimates were also large. Weekly profiles for the estimated number of common dolphins is also available for both divisions 8.a and 8.b in Figures 5.17 and 5.18.

Comparison and correlations with strandings

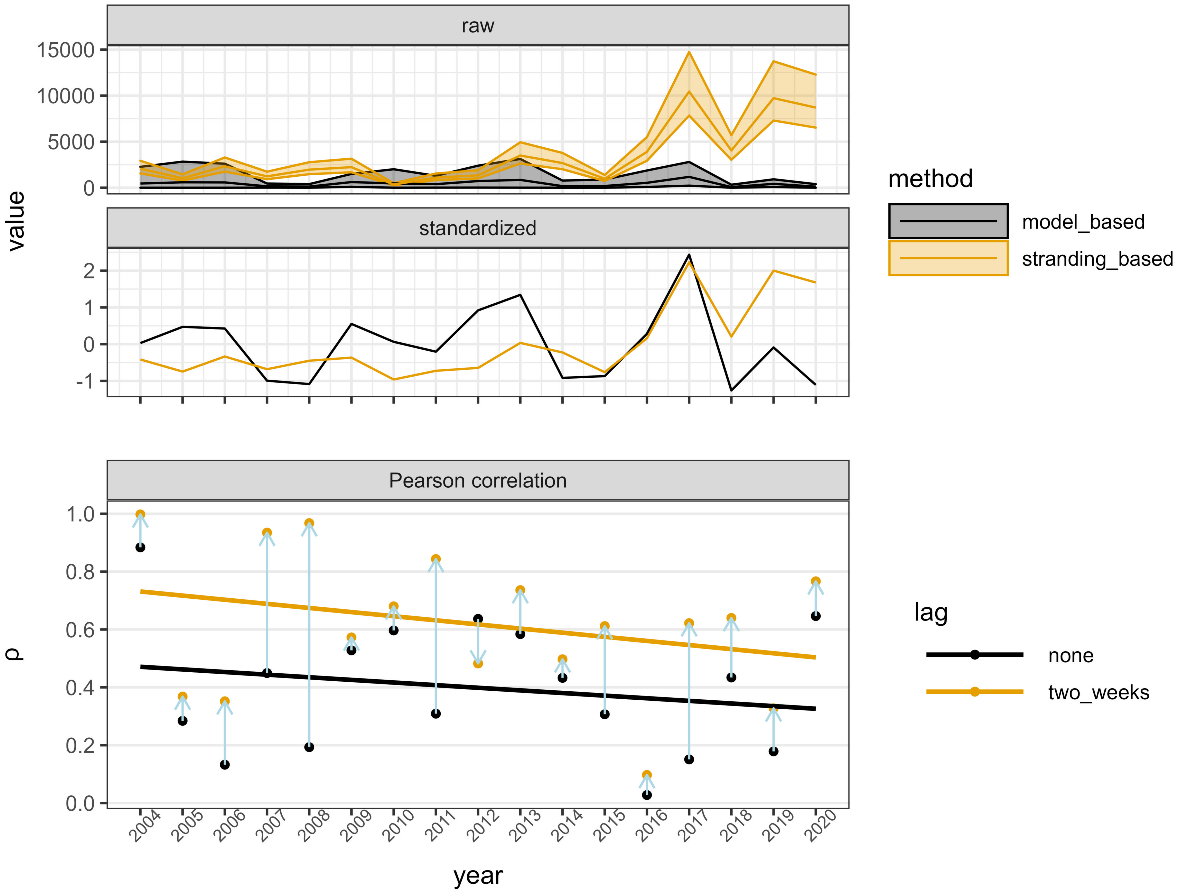

Figure 5.19: Comparison of model-based (orange solid line) and stranding-based estimates (dark violet solid line) of common dolphin bycatch. Upper panel: raw estimates with uncertainty intervals (80% for model-based estimates and 95% for stranding-based estimates); middle panel: standardized (mean centered and unit variance) estimates. Bottom panel: year-level and month-level (within each year) correlation were computed. At the within year (between month level), correlations were computed with and without a two-weeks lag. Change in the magnitude of the Pearson correlation coefficient is shown with an arrow.

Strandings data were used to estimate common dolphins mortality due to fisheries (Peltier et al. 2016) for each month from 1990 to 2020. Stranding-based estimates aggregate mortality due to all fisheries and do not distinguish between gears or métiers. Nevertheless, we correlated stranding-based estimates with our model-based estimates of mortality from PTM flying the French flag within each year (Figure 5.19). Correlations were computed on raw and standardized (mean centered and unit variance) values

(Figure 5.19).

Model-based estimates of bycatch by PTM were always below stranding-based estimates (which do not allow to disaggregate by *métiers*) except for 2010 (Figure 5.19). In 2010, model-based and stranding based estimates were 465 and 343 with a large overlap in credibility interval. Correlations between the two time-series were always positive. The estimated correlation decreases from 0.45 in 2004 to 0.35 in 2020 (profile without lag). The estimated correlation decreases from 0.75 in 2004 to 0.5 in 2020 (profile with lag; Figure 5.19). The temporal trend in within year correlation was negative over the study period.

5.4 Discussion

Variations of bycatch risk and number of bycaught dolphins

The estimated bycatch risk pattern shows some variations between and within years. This risk directly influences the estimated number of bycaught dolphins which also displays some variations. Here, a discussion about these variations for both components is proposed.

Inter-Year variations

The variation of bycatch risk, and subsequently of the number of bycaught dolphins, between years may be linked to ecological factors. Bycatch can be viewed as the resultant of two components that are the fishing activity and the dolphin presence (Margin-Figure 5.20). The oceanographic processes may influence the two components to enhance the encounter probability between fishing engines such as PTM and common dolphins (Gilbert et al. 2021). The highest estimated bycatch risk values were reported for the eight or ten first weeks of each year within each division of the study area 5.16. We can speculate that the years associated with a high bycatch risk were also those of notable spatial overlap favoured by particular oceanographic processes. Fishing activities and their operational conditions can also influence bycatch risk. For example, the setting of quotas on particular fish may cause operational changes in certain seasons. Market effects can also have an impact on fishing activity. If a particular fish is too devalued, it will no longer be targeted. These aspects will not be discussed in detail here as they are multifactorial and are more a matter of fisheries management.

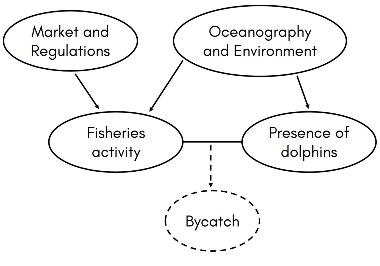

Figure 5.20: Simple diagram of bycatch phenomenon components.

Variations in the number of bycaught dolphins between years can also be explained by other factors than the bycatch risk. They are model-based estimates obtained through the bycatch risk, total fishing effort (Days at sea) and the median number of bycaught dolphins per year. The two latter parameter may be the source of the variation between years of the number of bycaught dolphins. For example, the (posterior median) estimate is of > 600 dolphins in 2017 and it downs to < 100 in 2018. Total effort in DaS in the Bay of Biscay (divisions 8.a and 8.b) in the first ten weeks of 2017, when bycatch risk was highest, is twice the value of total effort in 2018. The median number of dolphins involved in a bycatch event is 2017 was also twice the number in 2018 (2 and 1 respectively, Table 5.1). The bycatch risk being equal for the ten first weeks of these two years, the estimate for 2017 is expected to be at least four times that of 2018.

Variations in the estimated number of bycaught dolphins through the model-based approach can be related to the estimated number of bycaught dolphins obtained from the strandings estimations. Stranding records are an independent source of data for estimating the number of bycaught dolphins (Peltier et al. 2016). Reverse drift modelling allows to infer the death location of each stranded dolphin showing bycatch evidence for each month between 1990 and 2020. Observed stranding numbers for each month can be corrected by both stranding and buoyancy probabilities (Peltier and Ridoux 2015). Reverse drift modelling cannot disaggregate estimates by métiers or fisheries but it provides an independent estimates of total mortality due to bycatch in the study area. The bycatch mortality estimated for the PTM should be lower than the total estimated from strandings. This was verified for all years save for 2010, but uncertainties were large and credibility intervals had a large overlap. By looking at the correlations between estimated number of bycaught dolphins for the stranding-based and the model-based approaches, it appeared that the correlations were significant between the two estimated series, especially after accounting for a lag due to drift (Figure 5.19). The magnitude of the correlation decreased between 2005 and 2020. One interpretation is that of a change in the relative contribution of PTM in total dolphin mortality over time, with PTM having a smaller impact on common dolphins in recent years compared to the 2000s.

The mortality trend obtained by the model based approach seems to be rather constant while the stranding based trend seems to increase in recent years. This suggests that the increase in mortality estimated from the strandings is not due to PTMs.

The correlation between the two trends is stronger when considering a 2-week delay in stranding-based estimates. This correlation decreases over the period considered. The contribution of PTMs to total bycatch mortality may be lower than before.

Within-Year variations

For each year, the bycatch risk was estimated to be higher in the winter part of the years (*i.e.* week 1 to 10). This pattern is largely congruent with the pattern seen in strandings of common dolphins in the Bay of Biscay (Dars et al. 2020). A limitation of stranding data is that it does not allow to discriminate between fishing gears (Peltier and Ridoux 2015). The Obsmer data in contrast included

geolocalized bycatch events, with a spatial resolution at the level of ICES divisions kept for analysis. For the PTMs flying the French flag, we could identify divisions 8.a and 8.b from week 1 to 10 for nearly each years as the ones with the highest risk of bycatch.
For each year, the number of bycaught dolphins can also be estimated at the ICES division level for each year by the ICES Working Group on Bycatch (WGBYC). Using data collected by onboard observers collected between 2005 and 2017, bycatch rates for ICES divisions on the continental shelf of the Bay of Biscay were estimated with ratio-estimators (ICES 2019). These estimates are not produced at the week-level, but (ICES 2019) also identified divisions 8.a and 8.b as the ones with the highest bycatch in mid-water trawls for common dolphins over the period 2005-2017 (Page 120). ICES (2019) estimated yearly rates ranging between 0.285 to 0.372 dolphins per DaS and warned against extrapolation given the low observer coverage). Our model-based approach overcomes this limitation (Authier, Rouby, and Macleod 2021) and allowed to identify, within each year, that weeks 2 to 6 were the ones with the highest bycatch numbers for both divisions 8.a and 8.b. This results were concomitant with the seasonal stranding pattern observed each year on the French seashore (that is, winter strandings; Peltier et al. 2013): around 80% of all common dolphin strandings on the French Atlantic seashore is observed between the end of January and the beginning of March.

The current ICES mortality estimates do not make a fine spatial-temporal distinction. Our approach allows this distinction to be made for PTMs.

A key feature of our model-based approach is how it leverages correlations between bycatch risk, haul duration and number of hauls per DaS (Figure 5.16). Some of the correlations are expected, such as the negative correlation between haul duration and the number of hauls per DaS. If more hauls are performed in a Day at Sea, so they are to be shorter and vice versa. However, average haul duration is not constant within a year, with the variations reflecting change in the commercial fish species targeted by PTM at different time of the year. These variations at the week-level were quite substantial, and were taken into account when estimating bycatch in our model. There was a positive correlation between haul duration and bycatch risk, with at least a two-fold increase in the later when haul duration exceeds 5 hours (Figure 5.16). This was particularly evident in weeks 1 to 5 in 2017 and 2019 and week 48 in 2016. The latter was due to a single fishing trip with 5 hauls that lasted > 10 hours, each of which resulted in a bycatch event. We recommend, in light of the within-year pattern in haul duration (Figure 5.16), to investigate management actions and mitigation measures on limiting haul duration in winter to assess whether bycatch may also be reduced. The ability of our approach to propose more refined recommendations is a considerable advantage to reduce the impact of bycatch on the common dolphin population. However, it must be balanced against the fact that it has some

There seems to be a correlation between the fishing duration and the bycatch risk with a threshold effect. Beyond 5 hours of fishing, the bycatch risk is greatly increased. Restricting fishing duration may be a mitigating measure.

limitations.

Benefits and limitations of the method developed and used

The case study presented in this chapter is based on the application of the Authier, Rouby, and Macleod (2021) approach. This approach was developed to deal with low quality on-board observer data. A crucial assumption associated with this approach is the availability of accurate fishing effort data to perform the post-stratification step. The measure of effort chosen was the DaS, according to the current practice of international working groups. (*e.g.* ICES 2019). This guided the joint modelling of haul-level risk, haul duration and average number of hauls per DaS. This modelling choice has proved successful for PTM but cannot be developed to the same extent for other *métiers*, in particular for passive gears such as gillnets and trammelnets. In the latter case, a better measure of towing effort is soak time which takes into account the length and height of the net. This information can be difficult to collect, making it difficult to obtain an accurate measure of effort. This makes post-stratification difficult, but it is essential for the application of the model-based approach. The model developed for PTM may not necessarily transfer seamlessly to other *métiers*.

Figure 5.21: Photo of Pinger used in Bay of Biscay.
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Since 2021, PTM flying the French flag are required to use deterrent acoustic devices (pingers[13]). If these devices are efficient to reduce bycatch risk, this may be taken into account in the model, by adding a covariate in Equation 5.3. This requires post-stratification with the covariate using a fishing effort that explicitly takes the covariate into account. Currently, the model can implicitly account for the effect of pingers because it accounts for variations in bycatch risk from year to year and within a year. The large-scale deployment of pingers in 2021, if effective in reducing risk, will result in a lower estimated risk than in previous years. In other words, the model does not necessarily have to take into account all covariates at the haul level, as long as the objective is prediction rather than explanation (Authier, Rouby, and Macleod 2021). Explicit consideration of the pinger effect is only necessary to make sense of variations in risk between and within years, but not necessarily to estimate these variations.

While Authier, Rouby, and Macleod (2021) concluded on increased accuracy of using regularized multi-level regression with post-stratification to estimate bycatch with observer data, they also found that estimate precision was low. This was also the case in this study (Table 5.4). A simple way to increase precision is to include Electronic Remote Monitoring observations in Equations 5.7 and 5.8. Doing so would result in increased precision as a

[13] `https://www.mer.gouv.fr/protecting-cetaceans-annick-giradin-present`

greater number of hauls (and possibly DaS) would be monitored. Even if the estimate precision is low, it may provide a sufficient precision to inform management procedures algorithms conjointly to other data sources and biological indicators.

Implication for conservation

The large additional mortality due to anthropogenic activities on North-East Atlantic common dolphin population triggered a dedicated working group on emergency measures in 2020: the workshop on fisheries emergencies measures to minimize bycatch of short-beaked common dolphins in the Bay of Biscay and harbour porpoises in the Baltic Sea (WKEMBYC) took place remotely in spring 2020 (ICES 2020b) and informed an ICES advice that same year (ICES 2020c). This advice led to an infringement procedure issued in July 2020 against France for failing its obligations under the Habitats Directive which lists the common dolphin as a species requiring full protection on its Annex IV. The same day, the Paris Administrative Court of Justice condemned the French government for failing to transpose and apply in a timely manner the dispositions of the Habitats Directive and of Technical Measures regulating fisheries[14] (in French). Following the unprecedented number of strandings in 2017, a national working group with fishermen, their representatives, government officials, Non-Gouvernmental Organizations and academics was initiated to address the bycatch issue (Peltier et al. 2021). One recommended action was to improve estimates of bycatch due to high-risk métiers, and to develop adequate methodologies to analyse data from non-representative samples (Authier, Rouby, and Macleod 2021). The present work reports on a case study on PTM and operating for a large part in the Bay of Biscay, and to a lesser extent in the Celtic seas. Model-based estimates can (i) provide information on pressures on common dolphins, as required by the MSFD (EU 2008/56); and (ii) take into account the ICES recommendation to develop estimation methods to make best use of data already collected to inform timely management (ICES 2020c). In the next chapter, we will see how it is possible to combine both estimated number of bycaught dolphins and demographic indicators to inform conservation algorithm and provide adapted tolerable bycatch thresholds.

[14] `http://paris.tribunal-administratif.fr/content/download/172866/1715763/version/1/file/1901535.pdf`

Conservation Biology and Management Procedures

6

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The North-East Atlantic population of common dolphins is affected by bycatch which threatens its viability. The status of the population is of concern in relation to the conservation objectives set by the Habitats Directive and the MSFD. The conservation objectives are the basis for establishing management strategies. These management strategies determine the thresholds beyond which the conservation objectives will not be met. In the case of the common dolphin population, these thresholds are those of bycatch, or removals. The challenge is therefore to define management objectives that correspond to bycatch limits in order to build management strategies that will allow the population to achieve the conservation objectives. ASCOBANS has proposed as an interim conservation objective "to restore and/or maintain stocks/populations at 80% or more of carrying capacity". Based on this objective, OMMEG proposed the following quantitative conservation objective for marine mammals in European Waters: "a population should be able to recover to or be maintained at 80% of carrying capacity, with probability 0.8, within a 100-year period". Appropriate management strategies must therefore be defined to achieve this conservation objective for the common dolphin population. In this chapter we will determine the appropriate management objectives, *i.e.* the removal threshold. This study is part of a Management Strategy Evaluation approach that takes into account as much uncertainty as possible to provide relevant threshold. This approach involves the implementation of an operating model based on a Pella-Tomlinson population dynamics and a Leslie Matrix fed by estimated the vital rates in Chapter 4. A control rule based on the removal limit algorithm is applied to define the bycatch threshold at each time step during the 100 years simulated in the management strategy evaluation. A performance statistic is obtained at the end of the 100 simulated years. This statistical indicator, coupled with the use of real data, will ultimately allow to decide on the bycatch threshold to reach the OMMEG conservation objective.

Publication in prep.

This chapter is associated with one publication:
Rouby, E. and Genu, M. Setting Bycatch thresholds for common dolphin through Management Strategy Evaluation. In prep.

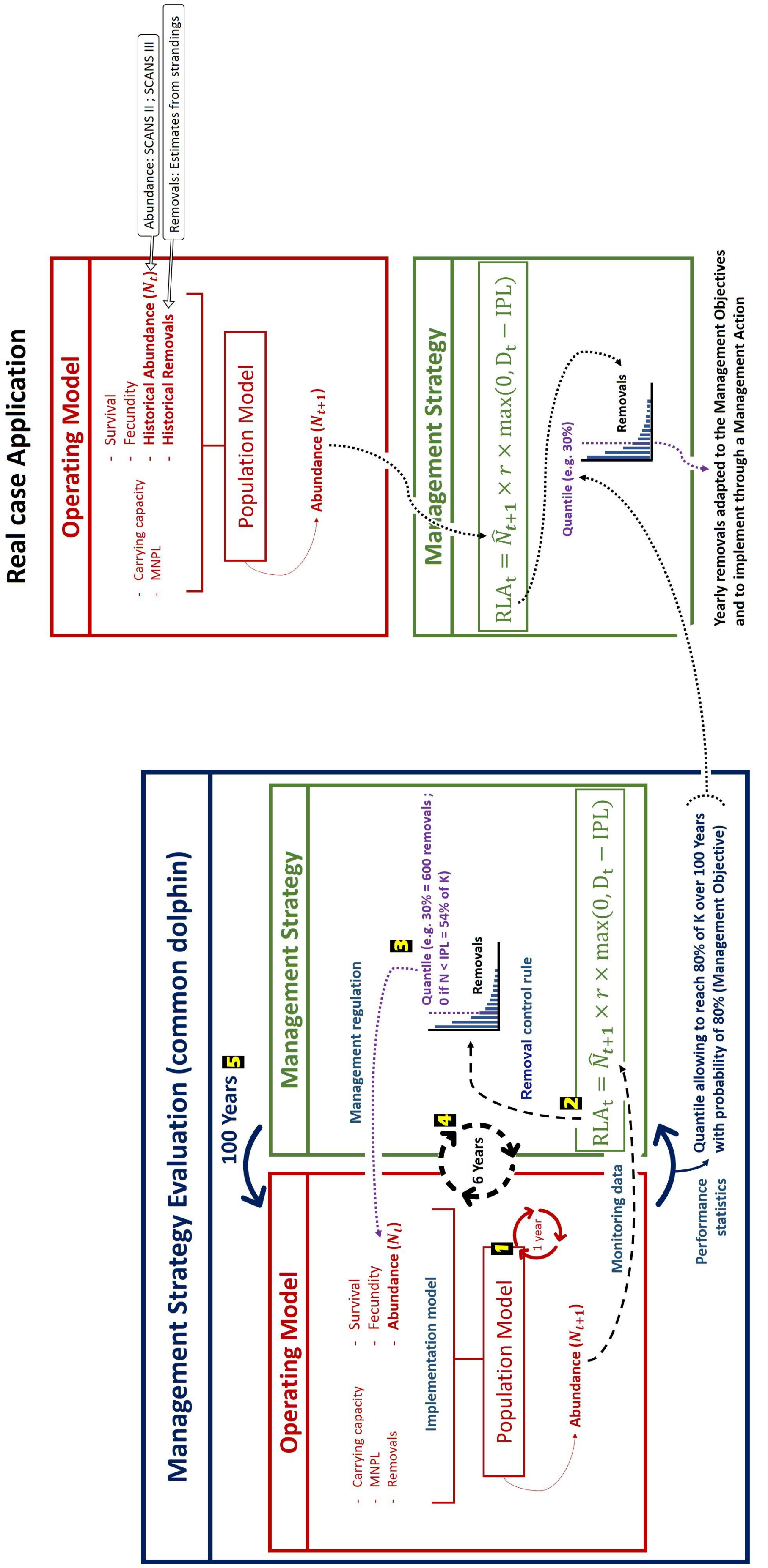

Figure 6.1: Flowchart of the whole MSE and Application case approaches. MSE runs for 100 years and allows the selection of a quantile. The application case runs for 1 year using real historical data and allows to obtain a distribution of removals. The quantile selected in the previous MSE framework is applied on the distribution to select a removal value.

6.1 Introduction: Conservation biology and Management procedure

In Chapter 5, we quantified the bycatch pressure exerted by PTM on the common dolphin population. In Chapter 4, we have seen that the bycatch pressure (any fishing *métier*) seems to decrease the survival within the population and to lead to a decline in its growth rate. Bycatch is actually one of the major threats to marine mammals (Avila, Kaschner, and Dormann 2018) particularly for small-sized cetaceans (Reeves, McClellan, and Werner 2013; Gray and Kennelly 2018; Brownell Jr et al. 2019; Rogan, A. J. Read, and Berggren 2021) and is currently impacting the common dolphin population (Peltier et al. 2016) to a point of non-viability (Mannocci et al. 2012). The conservation of marine mammal populations requires understanding and assessing the consequences of bycatch (Wade et al. 2021). Two examples of unsuccessful conservation cases associated to bycatch were mentioned in General introduction Page 7 with both the Baiji and the Vaquita and it is necessary to avoid similar situations for other populations. To do so, it is necessary to define conservation actions to promote the viability of marine mammal populations, in our case the common dolphin. Abundance indices are used to detect declines but once a decline is detected it is often too late to prevent the population from going extinct or it takes longer to recover to initial conservation status (Wade 1998; Gerrodette 1987; Cooke 1994; R. Williams, A. Hall, and Winship 2008; Authier et al. 2020). This is a reactive approach that is not precautionary (see Margin-Figure 6.2 for diagram; A. J. Read 2010). The development and use of pro-active conservation tools is of interest to prevent the extinction of the North-East Atlantic common dolphin population. An example of a pro-active conservation tool is the Potential Biological Removal[1] (PBR) developed as part of the implementation of the Marine Mammal Protection Act (MMPA) (Wade 1998).

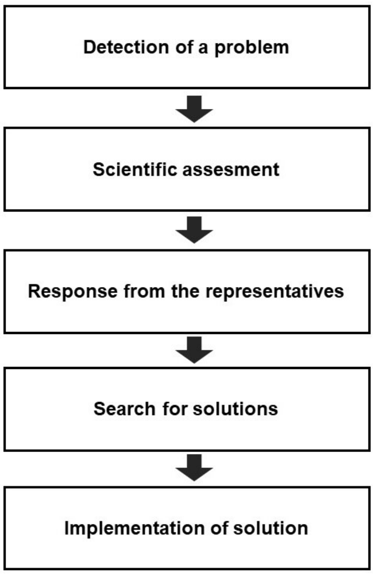

Figure 6.2: Classical conservation approach. The classical approach involves 5 steps (A. J. Read 2010). This approach is not proactive and may lead to viability problems for dolphin populations (Wade 1998).

The MMPA is one of the pioneering texts in terms of managing marine mammal populations from a conservation perspective[2] and it defines clear conservation objective (hereafter CO). The three CO retained by the MMPA are: 1) Maintain the population above its Maximum Net Productivity Level (MNPL); 2) Allow the population to recover close to its carrying capacity (K); 3) Allow the population to recover considering a growth rate close to its maximum possible (Wade 1998). MMPA defines clear quantitative CO and lays out management objectives and remedial measures to meet the CO. The quantitative CO for the MMPA is the following: "a population will remain at, or recover to, its MNPL (typically 50% of the population's carrying capacity), with 95% probability, within a 100-year period." In the case of European waters, there is

[1] PBR = $0.5 \times R_{max} \times N_{min} \times F_r$ with R_{max} as the maximum theoretical or estimated productivity rate of the population, N_{min} the minimum population estimate in number of animals and F_r the recovery factor.

[2] For more information on the MMPA: https://www.fws.gov/international/laws-treaties-agreements/us-conservation-laws/marine-mammal-protection-act.html

a lack of both: 1) a legally-binding CO for marine mammals and 2) management objectives with respect to human-induced mortality (ICES 2020c; Rogan, A. J. Read, and Berggren 2021). No clear and quantitative CO are defined regarding the impact of removals[3] on marine mammals population in European Waters. To address this, ASCOBANS defined a fixed percentage of the abundance of marine mammals population as a threshold to set the CO regarding bycatch in European waters (as mentioned in Chapter 2 Page 35). ASCOBANS passed two resolutions to set removal limit of marine mammal populations:

- **1.** "Unacceptable interactions" are, in the short-term, a total anthropogenic removal above 1.7% of the best available abundance estimate (Resolution 3.3 passed in 2000).
- **2.** Bycatch reduction have to be reduced to less than 1% of the best available population estimate as an intermediate precautionary objective (Resolution 3.3 and Resolution 5.5 passed in 2006).

This fixed percentage abundance approach have been used by the European Commission (EC) to assess the capacity of European member states to achieve the "Good Environmental Status" required by the MSFD. This fixed percentage approach has the advantage of being very simple in its use and easily understood. To apply it, at least one abundance survey covering the area associated with the population to be conserved and estimates of bycatch removals is required. It remains limited for two main reasons: 1) Inability to take into account life-history traits and 2) Does not take into account potential errors and biases (Winship 2009). Abundance estimates may not be synchronised with bycatch estimates, limiting proactive conservation initiatives. A more conservative approach is to define explicit bycatch thresholds as management objectives in relation to quantitative CO. The OSPAR Marine Mammal Expert Group (OMMEG) provided quantitative interpretation of the ASCOBANS interim objective “to restore and/or maintain stocks/populations to 80% or more of the carrying capacity” (ASCOBANS 2000). The quantitative CO defined by OMMEG in European waters in the context of the MSFD is the following: "a population should be able to recover to or be maintained at 80% of carrying capacity, with probability 0.8, within a 100-year period.". Explicit bycatch thresholds can be produced in relation to this quantitative CO.

In contrast to the USA, for which the MMPA defines a clear CO, Europe does not have a defined quantitative CO despite the ASCOBANS resolutions. OMMEG has provided a quantitative interpretation of the objectives set by ASCOBANS.

A management strategy is an agreed-upon set of rules for determining thresholds beyond which a CO runs the risk of not being met with unacceptably high probability (Winship 2009; Punt 2006; Bunnefeld, Hoshino, and Milner-Gulland 2011; I. C. Kaplan et al. 2021). Management strategy defines management objectives in the form of thresholds. Evaluating the relevance of management strategies (Management Strategy Evaluation, MSE) to

Conservation and management objectives should not be confused. A conservation objective is a goal to be achieved. It does not change. A management objective is a means to achieve the conservation objective. It is adaptable and can be reevaluated.

[3] Removals are bycaught dolphins removed from the population.

achieve COs is an issue that can be addressed through modelling and simulations (Cooke 1994; Hilborn and Mangel 2013). MSE requires generative models that generate (synthetic) data that are similar to observed data and it also requires real currently available data. Models associated with MSE are data-generating mechanisms. They can simulate a population dynamic taking into account removals effect (*i.e.* Bycatch effect) in addition to natural processes such as density dependence. These models allow scientists to assess the performance of management measures in hypothetical scenarios in order to set efficient management objectives. The management objectives will be assessed using real observable and available data (*i.e.* abundance and bycatch data with their uncertainties). Taking into account uncertainty at several levels (*e.g.* underlying model, potential biases and observed data) is of importance to measure the robustness of management strategies and choose the better one. A good management strategy should cover all aspects of management in accordance with pre-specified objectives. The thresholds regarding conservation of marine mammals are removal limits. A removal limit is an annual maximum number of animals whose removal would not result in excessive depletion of the population. MSE requires several components, including (list from Genu et al. (2021)):

The application of a management objective (*e.g.* removal limit) is a management strategy. The management objective is implemented through a strategy. To assess the adequacy of strategies, the MSE framework can be used. This framework involves the definition of an operational model and a control rule.

- **1.** One or Several Unambiguous quantitative CO.
- **2.** A data simulator (or operating model) to emulate the dynamics of the marine mammal population and the effects of anthropogenic activities on this population.
- **3.** A control rule, whose computation accounts for the expected quantity and quality of observable data, to set a removals limit beyond which the impact of human activities runs the risk of failing the aforementioned CO.
- **4.** Performance metrics (or performance statistics), necessarily context-dependent and reflecting the trade-off between the potentially multiple CO defined previously.

These elements are necessary to project forward in time the population dynamics (*i.e.* the number of animals at each time step according to population models operating within the data simulator). For each management strategy the control rule is applied. Finally the performance metrics are monitored and assessed with respect to the CO. Items 1. and 4. should be agreed by all stakeholders and scientists should not be expected to set the CO (Mangel et al. 1996). Items 2. and 3. are more relevant to scientists whose task is to test a wide range of realistic scenarios in order to protect the management strategy against uncertainties and potential biases in the available data. MSE involves a tune *via* simulations. Tuning in the MSE context means to: find, with a large number of simulations, parameter values of the control rule that meet the CO (Genu et al.

2021).

We used an MSE framework to conduct exploratory analyses to define a removal limit (*i.e.* management objective) that meets the conservation objective set by OMMEG.

There is a need to produce sustainable bycatch thresholds for the common dolphin population through an approach that takes into account uncertainty by involving several types of data. This approach should be part of a management strategy evaluation process to enable the chosen bycatch limit to meet the conservation objectives set by OMMEG in European waters. In this chapter we will see the MSE procedure applied to the case of the common dolphin in the Bay of Biscay. This application is made in order to define bycatch thresholds for this population calculated according to the achievement of the quantitative CO set by OMMEG from the work of ASCOBANS. The work carried out in demography on the common dolphin (Chapter 4) makes it possible to inform the population dynamics model constituting the operating model of the procedure. The recent development by Genu et al. (2021) allows for the calculation and redefinition of management objectives during the process. In line with the steps outlined above, we will start by choosing the CO for this population (OMMEG CO). Then we will see the implementation of the operating model (Pella-Tomlinson, General introduction Page 12). Then we will detail the control rule (Removal Limit Algorithm, RLA) and finally the choice of a performance statistic (Quantile that define removals). These steps are described in the baseline scenario case (no bias in abundance and bycatch estimates). We will then explain the robustness trials that aim to measure the effectiveness of the management strategies in achieving the CO when bias is introduced (bias in abundance or bycatch estimates). After selecting the most appropriate performance statistic for the common dolphin through simulations, we will use this statistic to define a bycatch threshold. This definition is based on the use of real data in the procedure. This work was carried out in close collaboration with Mathieu Genu whose role was to code all the analyses as part of the development of the RLA package to implement the procedure described in this chapter. This work is a preliminary analysis and does not yet aim to give a limit. The work was carried out taking into account the Bay of Biscay which does not correspond to the extent of the management unit recognised for the common dolphin population. This choice was made to allow the use of current data from the Bay of Biscay and to start exploratory analyses. The following sections present the method and preliminary results.

6.2 Methodology: Management Strategy Evaluation (MSE)

Demographic adjustment to make the population stationary

The vital rates obtained in Chapter 4 do not allow the population to be viable (Figure 6.4 with constant effect = 0). To enable it to be viable an adjustment on survival was made through the adding of a constant. Several values were tested from 0.1 to 2.0 and the one that allows the population to be stationary was 0.65 (Figure 6.4). This constant was then added in the joint modelling[4] and allows the estimation of age-specific survival rates (see Figure 6.3) that allow the population to be stationary. Using age-specific survival rates without adjustment, the population becomes extinct. The adjustment is made to obtain a stationary population. The adjusted age-specific survival rates are assumed to be representative of the natural survival of the population.

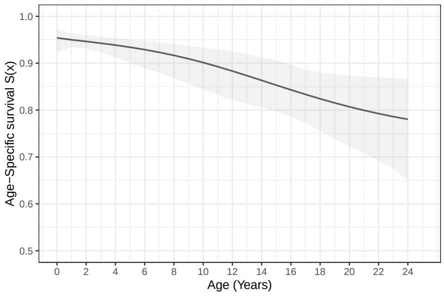

Figure 6.3: Age-specific survival rates obtained taking into account the constant effect on survival.

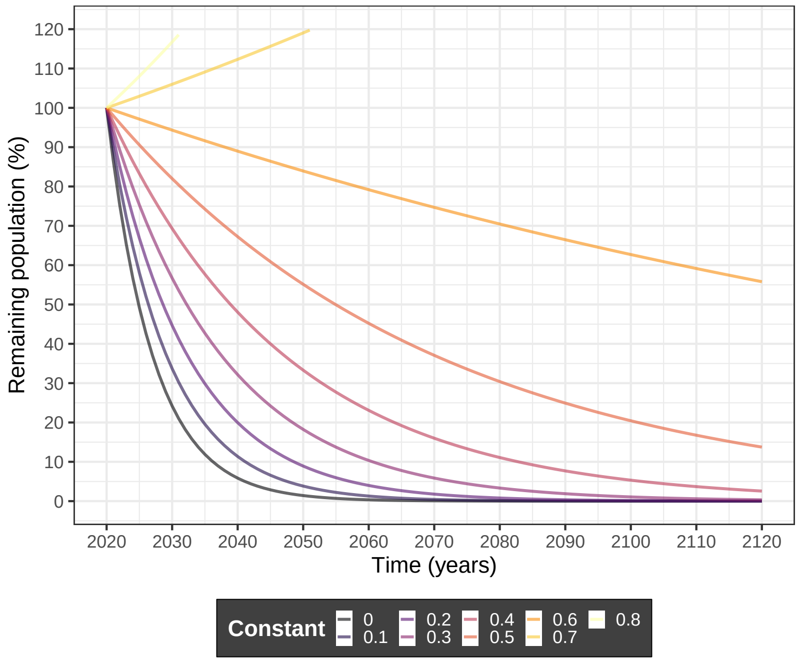

Figure 6.4: Remaining population over 100 years with constant effect on survival. The constant effect was applied to found the value for which the population remains stationary. With a survival intercept to which is added a constant effect equal to 0.65, the population remains stationary over time. This effect is then used in the estimation of the survival model to obtain the age-specific survival rates of a stationary population which will be used to inform the Pella-Tomlinson population dynamics model.

MSE base case scenario

Item 1. Choice of conservation objective

The conservation objective used here for the common dolphin population in the Bay of Biscay is that of OMMEG: "attain or maintain the population at an abundance equal to 80% of its carrying capacity (*i.e.* K) over 100 years with a probability of 80%"

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[4] The constant effect (c) on estimation is applied on the survival model from Chapter 4 with a logarithmic transform to be consistent with the modelling of age-at-death x_{it}.

$$\log x_{it} = (\mu + \log c) + \sigma \times \epsilon_i - \frac{Z_i}{\beta} \quad (6.1)$$

(OMMEG 2021), to be in line with ASCOBANS Resolutions 3.3 and 5.5.

Item 2. Operating model and Pella-Tomlinson population dynamics

The operating model is the functional part of the Management Strategy Evaluation framework. The operating model corresponds to the true-state of Nature, the state of our common dolphin population that changes every year. The population's state is define through its abundance and its depletion level relative to its carrying capacity. Changes are done through the arrival of newborns, the birth rate, the sex ratio, the proportion of the population that is mature, the age-specific survival (and implicitly mortality) that contributes to the removal of individuals and the removals on the population due to bycatch. No migration is assumed and taken into account.

The population model is age-aggregated with a maximum lifespan for the common dolphin population set at 24 years. The population model is based on a Pella-Tomlinson density dependence process (Pella and Tomlinson 1969):

$$\mathrm{N_{t+1}} = \mathrm{N_t} + \mathrm{r_{max}} \times \mathrm{N_t} \times \left(1 - \left(\frac{\mathrm{N_t}}{K}\right)^{\theta}\right) \tag{6.2}$$

Parameters of Equation 6.2: $\mathrm{N_t}$ as the abundance at time t, $\mathrm{r_{max}}$ as the maximum population growth rate, K as the carrying capacity and θ as the shape parameter.

Here, the MNPL is determined by θ. In the case of $\theta = 1$, population dynamics is given by a logistic growth curve with MNPL $= \frac{K}{2}$. The value of the birth rate at time t (b_t) is density dependent. Birth rate is the mean number of offspring per female assuming a sex ratio of 1:1. For example, a birth rate of 0.5 signify that each female produce 0.5 newborns per year. So 1 newborn is produced every two years by each female. Birth rate at time t is expressed as follows:

$$\begin{aligned} \text{birth rate}_t &= b_k + (b_{\max} - b_k) \times \left(1 - \left(\frac{N_t}{K}\right)^{\theta}\right) \\ &= b_k + (b_{\max} - b_k) \times \left(1 - (D_t)^{\theta}\right) \end{aligned} \tag{6.3}$$

Birth rate (b_t) calculation on Equation 6.3 depends on the birth rate at carrying capacity b_k, the maximum birth rate b_{max}, the real simulated population size at time t (N_t) and the carrying capacity K. The depletion level of the population is assumed as: $\frac{N_t}{K}$ and corresponds to the abundance of the population expressed in percentage of K.

The number of newborns in the population is the sum of the product of the population birth rate b_t, the age-specific abundance (N_{a_t}) calculated with the age-specific survival and the age-specific proportion of mature females M_{a_t} in the population.

$$\mathrm{newborns_t} = \sum b_t \times N_{a_t} \times M_{a_t} \tag{6.4}$$

The population model updates the total abundance N_t and the age-specific abundance N_{a_t} within a time-step of 1 Year. Each year the processes on the population dynamic are applied as:

- 1) Anthropogenic mortality is applied through bycatch removals on each age-classes of the population.
- 2) Natural mortality is applied through the age-specific survival rate on the population.
- 3) Animals reproduce through the age-specific fecundity rate and the abundance of age-class 0 is populated.
- 4) Increment the time by one year.

Processes on the population are shown in Figure 6.5 in the operating model block. The conceptual diagram of population dynamics from the demography chapter (Chapter 4) is taken up and adapted for the current study.

Since the initial depletion level of the population is unknown, 6 initial depletion levels were simulated simultaneously. The aim is to cover the population dynamics given several initial depletion intervals[5] The population model runs for 6 years. After 6 years, the first control rule (Removal Limit Algorithm) is applied.

Item 3. Control rule with the Removal Limit Algorithm

The control rule corresponds to the Removal Limit Algorithm (RLA) which is expressed as follows:

$$\begin{aligned} \mathrm{RLA_t} &= \hat{N}_t \times r \times \max(0, D_t - \mathrm{IPL}) \\ &= \hat{N}_t \times r \times \max(0, \left(\frac{N_t}{K}\right) - \mathrm{IPL}) \end{aligned} \tag{6.5}$$

Parameters of the Equation 6.5. RLA_t is the bycatch threshold at time t, r is the population growth rate, D_t is the depletion level of the population at time t and the IPL is the Internal Protection Level.

$\mathrm{RLA_t}$ is the outcome, the maximal tolerable threshold removals that must be applied to the population in order to reach the CO. It is a management objective that set the removals applied each year on the operating model. It is reassessed each cycle of 6 years since every 6 years a survey campaign is simulated to fill in the value of $\hat{N}_t$, the estimated abundance of the population (in the base case scenario) .

The estimation of $\mathrm{RLA_t}$ is carried out in a Bayesian framework. Its posterior distribution is obtained from the estimate of the posterior distribution of both D_t and r (Genu et al. 2021). From the posterior distribution of $\mathrm{RLA_t}$ a value must be chosen. It is the tuning part of the MSE. The tuning is a decision analysis. A quantile value within the posterior distribution is chosen in accordance with the achievement of the CO. A diagram illustrating the effect of quantile choice is shown in Figure 6.6. The choice of quantile allows

[5] Interval for initial depletion levels (% of K) are: (0.3, 0.4] ; (0.4, 0.5] ; (0.5, 0.6] ; (0.6, 0.7] ; (0.7, 0.8] ; (0.8, 0.9].

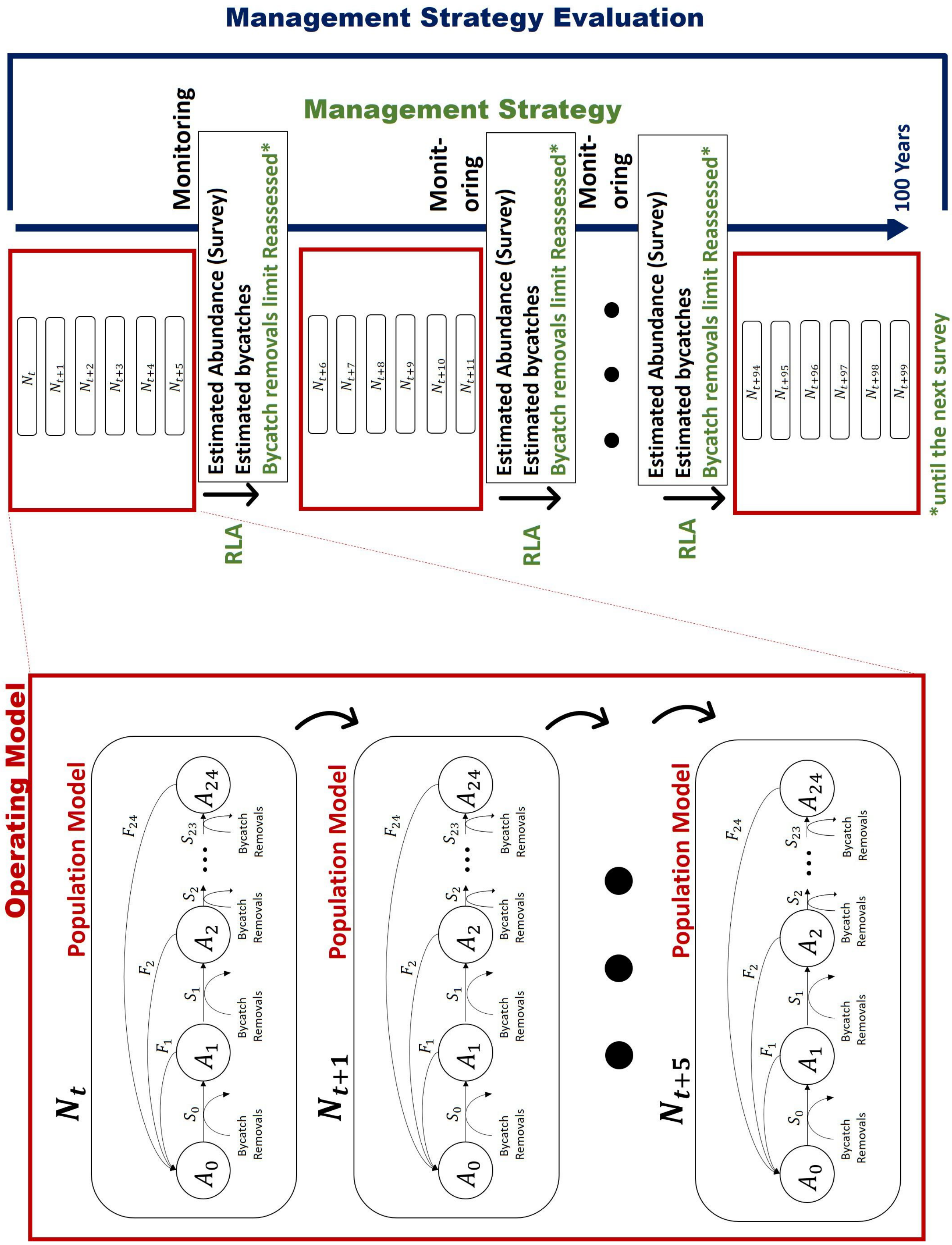

Figure 6.5: Diagram of the Management Strategy Evaluation associated with common dolphin population. The diagram shows both process (here blocks) that make up the Management Strategy Evaluation. The first is the operating model. This process involves a population dynamic that runs every year for 100 years. The second is monitoring in relation to the definition of the management strategy. Abundance monitoring is carried out every 6 years and bycatch monitoring every year. For each 6-year cycle a new bycatch limit is defined.

to set management objectives: the tolerable bycatch threshold is calculated by choosing a quantile from the Equation 6.5.

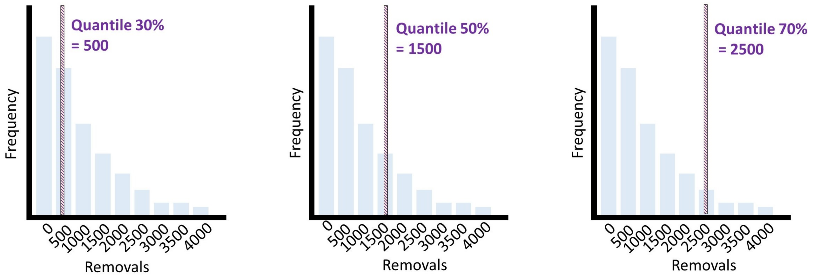

Figure 6.6: Diagram of tuning. The frequency of removals thresholds is depicted as a posterior distribution. The choice of quantile affects the definition of the management objective. Given the posterior distribution of $\mathrm{RLA_t}$, a quantile value of 30% involves a tolerable bycatch threshold of 500 individuals per year. A quantile value of 70% involves a tolerable bycatch threshold of 2500 individuals per year. The choice of the quantile value therefore defines the management objective. This choice is made in order to achieve the CO.

One important element is the presence of the Internal Protection Limit (IPL). The IPL is set to 0.54 = 54% of K. If the abundance of the population at time t, $\mathrm{N_t} < \mathrm{IPL}$, so $\mathrm{RLA_t} = 0$. This protection is set in order to limit removals to 0 if the population is too much depleted. One essential assumption of this part is that the removal limit is always respected (in the base case scenario) for the 6 next years.

The steps constituting the items of the operating model can be completed with those of the control rule:

Operating model:

- 1) Anthropogenic mortality is applied through bycatch removals on each age-class of the population.
- 2) Natural mortality is applied through the age-specific survival rate on the population.
- 3) Animals reproduce through the age-specific fecundity rate and the abundance of age-class 0 is populated.
- 4) Increment the time by one year.

Control rule:

- 5) From the estimated abundance and simulations estimate the distribution of possible removals.
- 6) From this distribution, determine the value corresponding to the quantile applied.

Item 4. Performance Statistic, Quantile for setting Removals

Originally, the Management Objective set by ASCOBANS was translated by the OSPAR Expert Group on Marine Mammals (OMMEG) into the following: After 100years, the depletion level of the population should be equal to 80% of its carrying capacity with a probability of 80%. At the end of the simulated 100 years, the depletion level of the population is established. If it is above 80%, the management strategy is assessed as viable. But it is necessary to choose one. The choice is performed on quantiles. The management strategy which is retained to be applied is the one associated to the maximum value of quantile that allow to reach the management objective. For example, if quantile 0.2 is associated to a depletion of 90% after 100 years and the quantile 0.3 to a depletion of 82% after 100 years, the retained quantile will be 0.3. Because it allows to reach the management objective set by OMMEG under ASCOBANS. The selected quantile can then be applied in the Management Strategy Application as it will be depicted latter. Figure 6.1 summarises all the steps needed to apply the MSE for the base case scenario which is the case where we suppose that we can fully trust our abundance and bycatch estimation data. However, it is not always necessarily the case. This is why we can take into account some bias in these estimations.

Robustness trials

We considered an abundance estimate bias and a bycatch estimate bias in order to represent some cases when we can not trust the data (abundance and bycatch) that we have. The interest of using these bias scenarios in addition to the base case scenario is that it allows to be more cautious while choosing a quantile to perform the real case Application and finally obtain removal limit threshold.

The first bias scenarios are based on the abundance estimate. As depicted in Figure 6.1 and Diagram 6.5, an abundance estimate is done every six years (simulating a SCANS campaign) and from this abundance estimate, the new removal limit is set and and revised six years later. We studied the case when abundance is underestimated by half (*e.g.* 120,000 dolphins estimated instead of 240,000) and the case when abundance is overestimated by half (*e.g.* 360,000 dolphins estimated instead of 240,000). We choose this values since they cover the confidence interval of SCANS II + CODA and SCANS III surveys[6] which is approximately equal to 0.4.

The second bias scenario is based on an underestimate of the bycatch. The population model updates the abundance of each age-class depending partly on bycatch removals which are carried out on each age-class. If the management strategy is conducted with the total abundance obtained from the population dynamic model given a set of removals without bias (base case scenario), the removal limit set during the management strategy will be set according to the bycatch removals assumed as true. But it is possible that we underestimate these bycatch removals and

Two robustness trials were performed:
1) Over-estimation of dolphin estimates by a half
2) Underestimation if bycatch estimates by a factor of 3
These robustness trials are preliminary. Further trials need to be carried out. The values have been set to explore the impact of bias on the final result.

[6] See Chapter 2, Page 36 for information about SCANS and CODA and see Supplementary Chapter 7.4 on page 201 for all abundance estimates.

set inappropriate removal limit. To cover this scenario we set an underestimation ratio of bycaught individuals equal to 3. In that scenario, the estimated number of dolphins bycaught per year is three times lower than the actual number.

Each of the two robustness trials considered here is intended to illustrate the difference in the choice of quantiles at the end of the analysis. They need to be complemented by other robustness trials to cover several possible situations. The definition of robustness trials is the last part of the MSE framework. Figure 6.1 shows the MSE steps given the base case scenario but the same scheme is applicable for the bias scenarios. After running the simulations over 100 years, given several types of scenarios, we move on to the final stage of this study. The interest of having carried out an MSE approach is that a quantile value has been defined which is adapted to the achievement of the Management objective and which respects a precautionary principle without being totally conservative.

Application on common dolphins in the Bay of Biscay

The final step of the whole procedure is to apply the MSE approach using real historical abundance and bycatch data. The operating model is used once with the historical data. Then the control rule is applied to obtain the posterior distribution of possible removals. The performance statistic (quantile) selected from the tuning in MSE base case scenario and robustness trials is applied on the removals distributions to choose a bycatch threshold (see Real case Application on Figure 6.1).

The practical application is based on the use of real historical data in addition to the demographic data used previously. The data used are abundance estimates and bycatch estimates.

The abundance data that are used are related to the Bay of Biscay. This scale is not representative of the common dolphin management unit. We made this choice in order to start exploring the analyses and setting up the approach. We also made this choice on the basis of the available data for two reasons. First the demographic rates that were obtained in the Chapter 4 were more linked to individuals that are associated to the Bay of Biscay than to the whole North-East Atlantic. It seems to me more accurate to use a similar spatial scale. Secondly, bycatch estimates are obtained from the analysis of drifting trajectories of stranded individuals. Here again, the individuals are mainly associated with the Bay of Biscay area. Thirdly, the management and conservation issues for the common dolphin in the North-East Atlantic are mainly linked to bycatch pressure in the Bay of Biscay. It is for these reasons that I believe it is currently more appropriate to use the estimated abundances in relation to the Bay of Biscay only. The tolerable bycatch thresholds that will be obtained subsequently will therefore be related to the Bay of Biscay "population". The abundance estimates used for the applied case are obtained from three surveys that represent two time points of abundance assessment separated by about 10 years: SCANS II + CODA and SCANS III[7] . Abundances were estimated from observation by plane and boat. Where Scans III directly combines the two, SCANS II does not cover the whole area and the CODA ship survey was needed to complete the estimates. Abundance estimates were made depending on areas composed by "blocks" Figure 6.7.

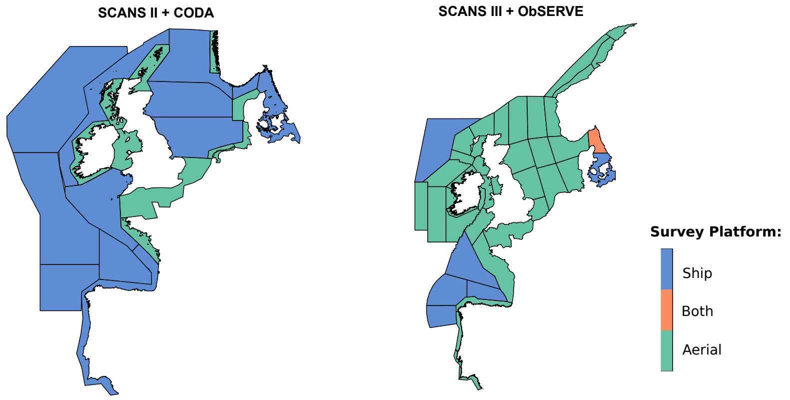

Figure 6.7: Survey platform and survey blocks of abundance surveys campaigns. SCANS I is not shown here as it was not used to obtain the abundances. Between campaigns, the blocks sampled are different. A recalculation of the abundances was necessary. This calculation was carried out within the ICES divisions. It took into account the density obtained in each block and the surface of the ICES division.

The blocks were not the same for the SCANS II + CODA and SCANS III campaigns. Abundance[8] data are provided by blocks. To allow for better cohesion we have recalculated the abundances taking into account the ICES divisions. We recalculated the abundances by multiplying the surface area of each ICES division by the estimated common dolphin density for the campaigns SCANS II + CODA and SCANS III (Figure 6.8).

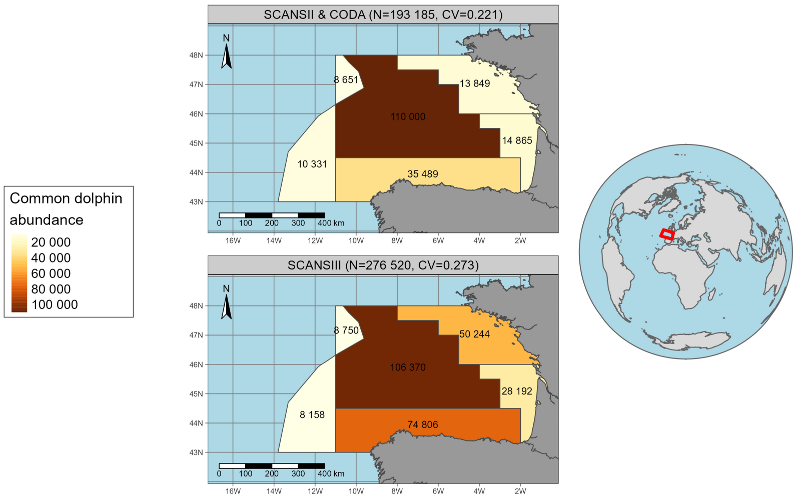

Figure 6.8: Common dolphin abundance used for this study depending on the ICES divisions. Abundances were recalculated using both ICES divisions specific surface and the estimated density in the SCANS II + CODA and SCANS III block.

The other historical data that was used to perform the Real case Application was the historical bycatch estimate made from the strandings between 1990 and 2020. Theoretically, it is possible to use French pair trawlers (PTM) estimates that were produced in

[7] ObSERVE is an aerial campaign conducted in the Ireland's EEZ whose abundance surveys are not useful for application in the Bay of Biscay. More information on ObSERVE on `https://www.gov.ie/en/publication/12374-observe-programme/`

[8] The abundance data used are not representative of the entire common dolphin management unit. The results obtained at the end will not be applicable to the management unit. This choice was made to facilitate the exploratory approach.

Chapter 5. But the estimation would be made according to one of all the fishing métiers operating in the Bay of Biscay. Other fishing *métiers* than PTM could have an impact on common dolphin in the Bay of Biscay. Within the French fishing fleet, gillnetters (GTR) and gillnetters (GTR) may be associated with common dolphin mortality in ICES divisions 8.a and 8.b. The approach used in Chapter 5 is currently only applicable to PTM. In the meantime, it is possible to use the estimates made from the strandings. To estimate bycatch, only common dolphins with evidences of contact with fishing nets were considered (Kuiken 1994) as well as the common dolphins found stranded during multiple or unusual mortality events related to fisheries. These multiple events are defined when a high number of strandings occur in a restricted area with a common cause of death. The threshold is defined at 30 cetaceans over 10 consecutive days recorded along a maximal distance of 200km in the Bay of Biscay and 10 individuals per 10 days per 200km of coastline along the coast of the western English Channel (Peltier et al. 2014). From the stranding location of the dolphin, a deterministic drift trajectory is inferred by a reverse drift model (developed by *Méteo France*) to determine its likely area of death at sea. The area of death is included in a grid cell. The number of dead dolphins in each cell is then corrected by the cell-specific probability that a carcass from that cell washes ashore (Peltier et al. 2013). The number of animals estimated dead at sea is available in supplementary material.

Theoretically it is possible to use the estimates made in Chapter 5. For the time being they only concern one fishing *métier* and are therefore unusable.

Baseline Management Strategy Evaluation assumptions

- The vital rates estimated in Chapter 4 are representative of those of the managed population.
- There is one closed and stationary population in the Bay of Biscay.
- The Conservation Objective produced by OMMEG is accepted by all parties and remains the same over the 100-year period considered.
- Abundance surveys are conducted every 6 years within 100 years.
- The Control rule used to produce the removals estimates remains the same over the 100-year period considered.

6.3 Results

Results are first presented for Management Strategy Evaluation comparing the depletion trajectories obtained under each quantile and each scenario. Then the population dynamic under the real case application and the removals threshold obtained are presented.

Management Strategy Evaluation

Demographic dynamics of the base case scenario

Figure 6.9 presents the simulated estimated abundance and associated applied bycatch (limit set by RLA + stochastic variation) along time-line for the base case scenario depending on each quantile. The value of depletion is estimated every year for 100 years. Results were averaged for all initial depletion levels. Only quantiles 0.6 to 0.8 are displayed because under 0.6 the CO is always reached. For each quantile the estimated abundance increases before reaching a plateau. The plateau is not reached after the same number of years depending on the quantile. All abundance estimation profiles are above the management objective (80% of K) except for the quantile at 0.8. The quantile whose profile is closest to the management objective is the one at 0.7.

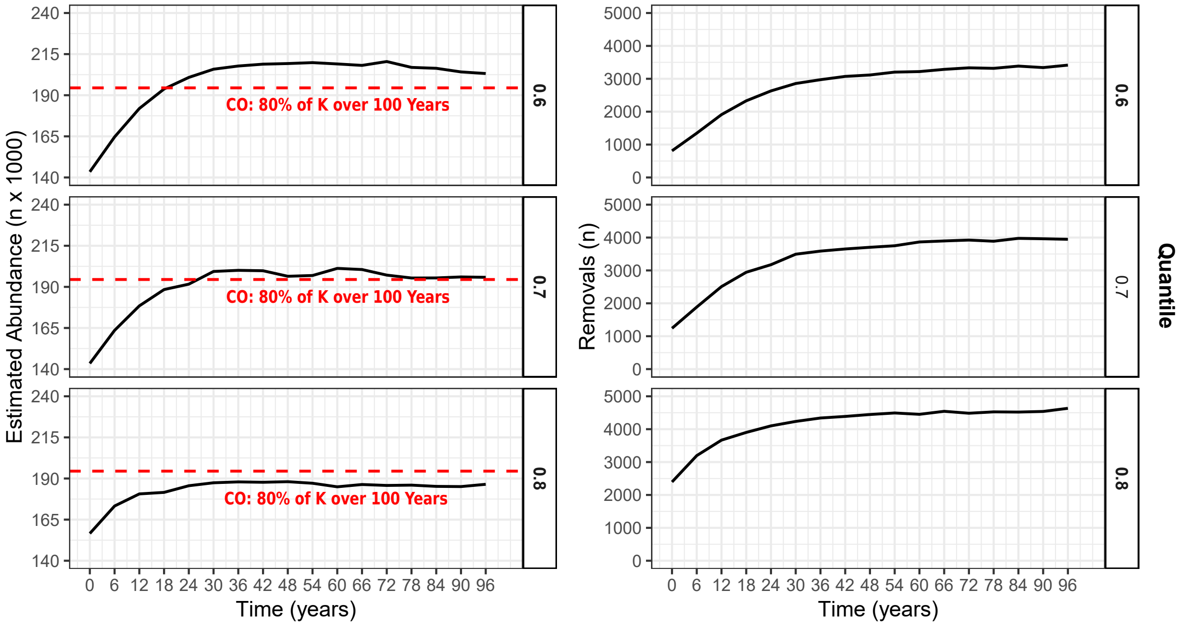

Figure 6.9: Base case scenario abundance and removals over years associated with quantiles. Only quantiles 0.6, 0.7, and 0.8 are depicted here. These are the most interesting to look at because it is at this point that the 80% threshold defined for K is reached. All quantiles below 0.6 meet the objective after 100 years. Here it is the quantile at 0.7 that should be retained. Because it is the one that best fits the conservation objective. It is associated with annual removals that fluctuate around 4100 at the end of the 100-year simulation.

Removals are also displayed. Their value increases as the quantile increases with for example a maximum value of 3500 at the 0.6 quantile and a maximum value of 4500 at the 0.8 quantile. Likewise for the simulated estimated abundance, the profile shows an increase and a plateau which is reached more quickly when the quantile is high. The estimated bycatch value is about 4000 dolphins with the quantile at 0.7 after 100 years.

Selection of the best quantile and associated removals

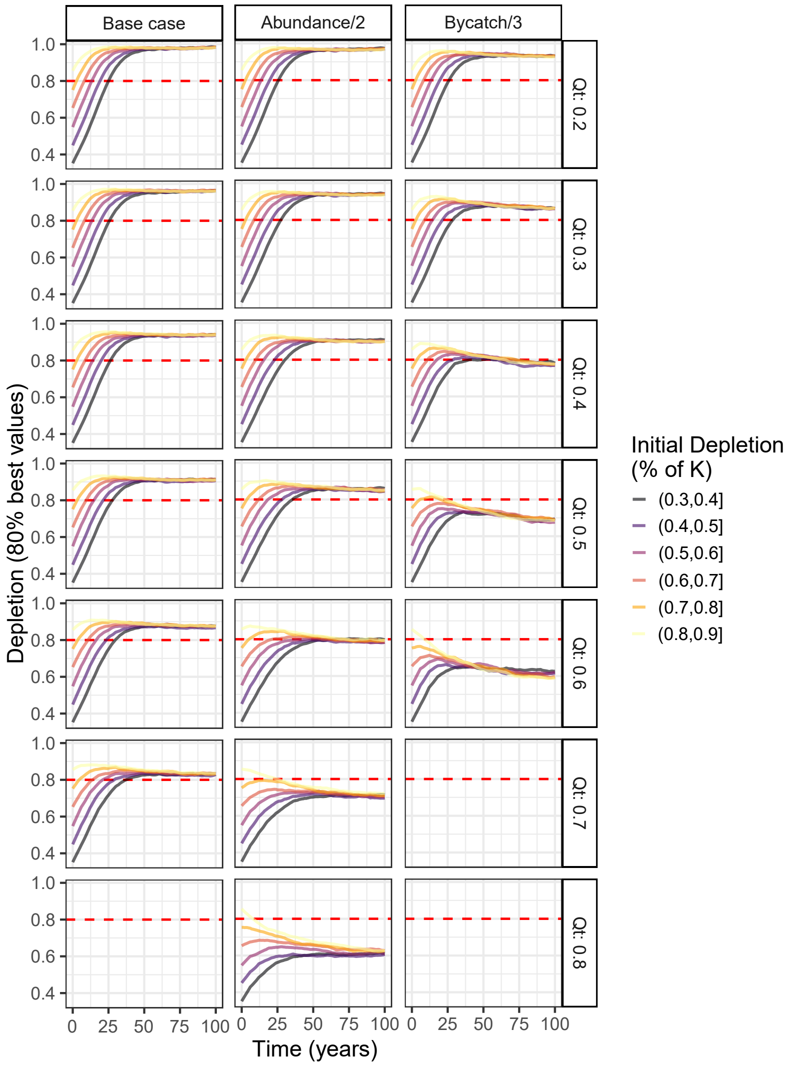

Figure 6.10: Robustness trials depletion levels for each quantile. When we start the simulation, we do not know the depletion state of the population with respect to K. To cover this uncertainty, 6 initial depletion levels are simulated for each scenario and quantile. In the base case, the quantile to be retained is 0.7. In the case of the underestimation of abundance by a factor of 2, the quantile to be retained is 0.5. In the case of an underestimation of the bycatch by a factor of 3, the quantile to be retained is 0.3.
The absence of curves for the last quantiles of the robustness trials is due to numerical problems.

As the initial depletion state of the population is not known, several initial depletion states were simulated. For each scenario (base case, underestimated abundance, underestimated bycatch), six initial depletion states (from [0.3, 0.4] to [0.8, 0.9]) were simulated under seven quantiles (from 0.2 to 0.8). At the end of the 100-year time series, the performance of each management strategy is assessed by comparing the value of each depletion curve to the 80% carrying capacity limit (Figure 6.10). The best 80% depletion values for each initial state are presented over a period of 1 to 100 years. For the baseline scenario, the best quantile to select based on the simulation is 0.7. This quantile value allows each depletion curve to meet the management objective of 80% K. For the underestimated abundance scenario, the best quantile to select is the quantile at 0.5. For the underestimated bycatch scenario, the best quantile to select is the 0.3 quantile.

For each combination of quantile and scenario, it is possible to calculate the value of removals as a percentage of K (Figure 6.11). The resulting distribution of removal for all time steps (independent of the initial simulated depletion state) is summarised. The higher the quantile, the higher the removal values. These removal values are purely indicative and do not constitute the final result of the approach.

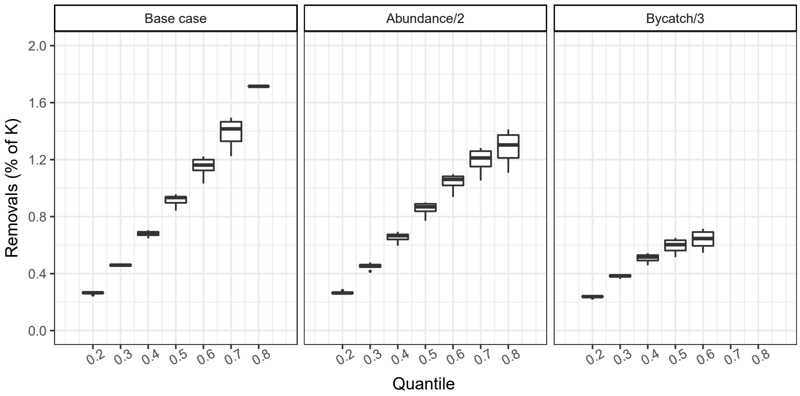

Figure 6.11: Removals to be applied in percentage of K. Each level of removals relatively to K are depicted for each scenario and quantile. Lower the quantile, lower the removals. The scenario with the highest removals is the base case. The scenario with the lowest removals is the one that includes a bycatch estimation bias.

Application on common dolphin population

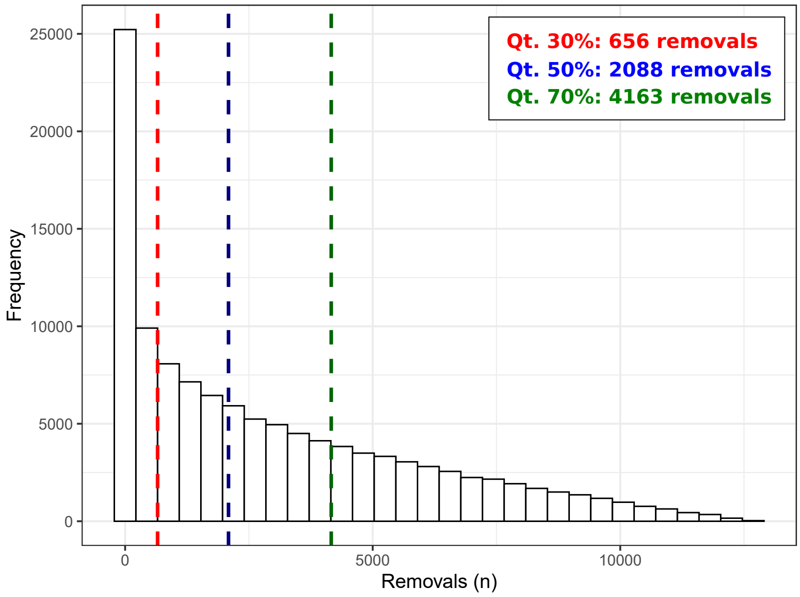

Figure 6.12: Final removals posterior distribution. The posterior distribution obtained in the Real Application case is depicted here. The maximum removal value is about 12500. The minimum is about 0. The quantiles that were obtained previously in the MSE approach involving the robustness trials allows to select removal value in the distribution.

The previous exercise (management strategy evaluation) aimed to obtain the quantile values for each scenario to achieve the CO. The application case aims to produce a distribution of removals using the actual data. The quantiles obtained previously are used to define the removals to be applied from this distribution (Figure 6.12). They range from 0 to approximately 13000 given the last abundance estimate. From this distribution (Figure 6.1 management application part to a representation of this step in the framework.) it is possible to choose values given the quantiles selected under the MSE. The quantiles obtained from the previous MSE approach are presented as dashed color lines (Figure 6.12) and associated removals are given in Table 6.1. The difference between quantile at 50% and 70% is about a factor of 2 (approximately 2000 and 4000). The quantile at 30% is associated to the lowest number of removals which is about 656 considering the last SCANS III abundance survey estimation of common dolphins in the Bay of Biscay.

Table 6.1: Removals to be applied. Here the removals that allows the population to reach the OMMEG CO are depicted. The higher removal value is the one for the base case with 4163 removals per year. The mid removal value is the one for the underestimated abundance with 2088 removals per year. The lower removal value is the one for the underestimated bycatch with 656 removals per year. In order to be conservative and to be cautious with the population viability, the lowest removal value should be kept. Here the yearly removals applied to the common dolphin population in the Bay of Biscay must not exceed 656 individuals per year in order to reach the CO set by OMMEG.

Quantile	**Removals**
30%	**656**
50%	2088
70%	4163

6.4 Discussion

The aim of the study is to define a tolerable removals (*i.e.* bycatch) threshold (management objective) to achieve the conservation objective defined by OMMEG based on the ASCOBANS recommendations : allow the population to reach or maintain an abundance level equal to 80% of its carrying capacity (*i.e.* K) over 100 years with a probability of 80%. The implementation of this management objective will then constitute the population management strategy until the next abundance surveys.

For this purpose, demographic data were used considering an adjustment on survival to obtain a stationary population. Then the MSE procedure was applied involving the selection of the CO, and the combined use of the operating model and the control rule over a period of 100 years to obtain the performance statistic. Actual abundance and bycatch estimates were then used to compute tolerable removal thresholds for the population given the latest abundance estimates. The choice between these thresholds then depends on the quantile selected from the MSE approach and the robustness trials associated with the base case scenario.

Conservation objective, operating model and control rule

The choice of an appropriate CO

The definition of a clear and justified CO conditions the subsequent MSE approach. The CO is relative to K, the carrying capacity of the environment for the population. In practice it is impossible to know the exact value of this carrying capacity. But knowing its exact value is not limiting. The order of magnitude of the carrying capacity, however, is much more important. In the case of the common dolphin population, it is more important to decide between a carrying capacity in the tens, hundreds of thousands or millions. It is at this level that the maximum abundance surveys inform the CO. Defining the percentage threshold of this carrying capacity to be achieved is a more general management consideration. This definition directly determines the number of annual tolerable bycatches in the population. The higher the percentage, the lower the number of removals and *vice versa*. If the percentage set is very high, *e.g.* 95% of K, then only the lowest quantile values will achieve this CO (Figure 6.10). In this case, the tolerable number of bycatches will be close to 0. It may be difficult to implement this threshold in view of the socio-economic stakes of fishing in the Bay of Biscay. If the percentage set is low, *e.g.* 50% of K, then the higher quantile values will also achieve the CO. In this case the number of bycatches may be very high. The management objective will do little to limit fishing but may be dangerous to the viability of the population. It is possible that the population will be too depleted before the next abundance survey (6-year cycle) to redefine the management objective. The population could also be subject to an Allee effect that would cause its extinction beyond a given abundance threshold. It could be interesting to implement an Allee effect in the operating model to take this into account. This Allee effect could be expressed as a probability of encounter between males and females as an example. The question of how to define an appropriate CO that takes into account the conservation of populations and the management of human activities is a key issue at the border of several disciplines.

The exact value of K has little influence on the final estimate. It is the order of magnitude of K that matters. The choice of an appropriate CB must take this order of magnitude into account.

Considerations on the Operating model

The MSE used here is based on multiple steps and fundamental assumptions. The operating model is based on the Leslie population matrix model with a Pella-Tomlinson density dependence for birth rates (Genu et al. 2021). The age-specific survival rates used to fuel this model are those obtain for the common dolphin population in the Chapter 4 adjusted to allow the population to be stationary. This construction makes it possible to obtain a population that does not decrease without the application of bycatch. This adjustment is a strong assumption that does not go hand in hand with what is obtained in terms of demography on this population. The Leslie matrix population model used here does not admit explicitly immigration. This assumption is very restrictive since the common dolphin population in the Bay of Biscay seems not closed as the abundance surveys and demography suggest.

Control rule and importance of data provision

The main interest of this work is that it is the first to be done with specific and locally determined demographic parameters on this population. This age-specific structured model allows the use of the RLA which is a possible control rule among others. Others control rules that can be used in the MSE are the PBR and the mPBR[9] . They did not require age-structured models but only the abundance of the population. The PBR can be calculated as it follows:

$$PBR = 0.5 \times R_{max} \times N_{min} \times F_r \quad (6.6)$$

Parameters of PBR: R_{max} as the maximum theoretical or estimated productivity rate of the population, N_{min} the minimum population estimate in number of animals and F_r the recovery factor.

From this control rule, a total of 4926 individuals per year were estimated as the limit of removals for the population in the whole North-East Atlantic area (ICES 2020b). The number of estimated bycaught dolphins for recent years is higher than this threshold. This thresholds is close to the one calculated here, in the base case scenario, using the RLA for the Bay of Biscay. The calculation of the PBR relies on the management objective of the population reaching 50% of carrying capacity. This CO is the one implemented by the MMPA. It does not corresponds to the CO proposed by the OMMEG group using the interim objective from ASCOBANS. The mPBR is suited for the ASCOBANS management objective and is associated to much lower bycatch thresholds with a removal limit around 900 individuals. This limit is closer to the estimation done using the RLA considering the scenario of a bycatch underestimation.

The use of RLA is less conservative when the accuracy of the data is higher and when there is more data. The removal limit determined when using the RLA on the Bay of Biscay population is close to that obtained from the PBR in the North East Atlantic. In this case, the use of population-specific demographic data allows for less conservatism. The use of the RLA in the framework of robustness trials also shows this particularly in the case of bycatch. In the base case scenario, bycatch estimates are assume to be accurate. This may look like transparent bycatch declarations from fisheries. In this case, the tolerable removals on the population

[9] mPBR is the modified PBR. It allows the estimation of tolerable removals thresholds taking into account the European conservation objective.

of the Bay of Biscay is 4163 dolphins per year. In the case where the number of catches is underestimated by 3, this limit is greatly reduced by a factor of almost 7 (656 tolerable removals each year in Bay of Biscay). Robustness trials in that case shows that knowledge of bycatches makes it possible to be less conservative. It is therefore in the interest of fisheries to communicate transparently on the number of bycatches made per year.

Application of the Management Strategy

In the case of the common dolphin in the Bay of Biscay, the most efficient management strategy to promote the sustainability of the population (without completely closing the fisheries) seems to be to set a limit of 656 bycatches per year. This threshold is associated with an underestimate of bycaught dolphins by a factor of 3. This scenario is extreme and other and less extreme robustness trials should be tested in the future. Within this study, this management objective seems to be the most precautionary given the scenarios tested and the current data. The base case scenario with a bycatch threshold of 4163 implies full confidence (*i.e.* unbiased) in the abundance estimates, bycatch estimates and in the demographic data in the operating model.
Bycatch estimates are currently made by modelling the reverse drift of carcasses (with bycatch evidence) found stranded on the seashore. It is difficult to be sure that these estimates are accurate. For example, they may be overestimated. The overestimation may be related to a possible misinterpretation of some bycatch evidence in favour of an over-representation of bycaughts individuals[10] . This hypothesis seems unlikely given that the evidence of incidental captures is well characterised for common dolphins (see Figure 2.19 in Chapter 2). In France, the examination protocol is well defined and applied by the members of the national stranding network. But the scenario of overestimation of catches will be tested. The scenario of underestimated catches foresees a maximum 656 catch limit. If a catch limit were to be applied, it would be 656 individuals per year. This is the lowest limit associated with the robustness trials. It is the most conservative value. Taking this threshold into account, the estimates we made in Chapter 5 are still below the threshold. Except if we take into account the 80% limit of the Bayesian uncertainty interval. But our estimates are for a single fishing *métiers* (Table 6.2).

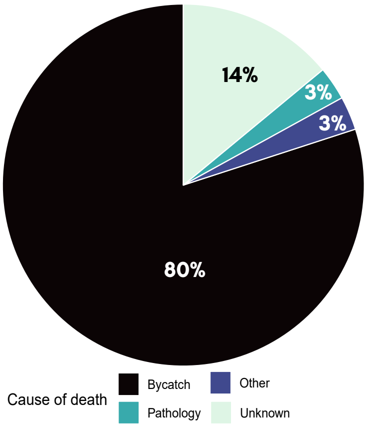

Figure 6.13: Cause of death for 2020.

Bycatch estimates are above this threshold in the Bay of Biscay, taking into account baseline stranding estimates. The current level of mortality reflects the current management strategy for the common dolphin population. This strategy involves the economics of the fishery, the viability of the common dolphin population, the

[10] As a reminder, 80% of individuals are considered dead due to capture in fishing nets on the basis of external examinations in 2020 and 82% on the basis of internal examinations.

Year	Model based (PTMs)		
2004	−656	−429	+478
2005	−656	−363	+761
2006	−656	−370	+647
2007	−640	−579	−437
2008	−644	−591	−466
2009	−473	−244	+164
2010	−652	−424	+338
2011	−647	−465	−21
2012	−633	−290	+534
2013	−643	−230	+890
2014	−656	−572	+272
2015	−654	−562	−210
2016	−601	−386	−273
2017	−500	−38	+759
2018	−655	−621	−493
2019	−597	−440	−215
2020	−652	−599	−466

Table 6.2: Difference between the threshold of 656 removals and estimated bycaught dolphins. Model based estimates corresponds to the Chapter 5 estimates with the 80 Bayesian Credibility Interval. Cells are depicted in red if the difference is in favour of an excess of the bycatch threshold. Model based estimates are made taking into account PTMs.

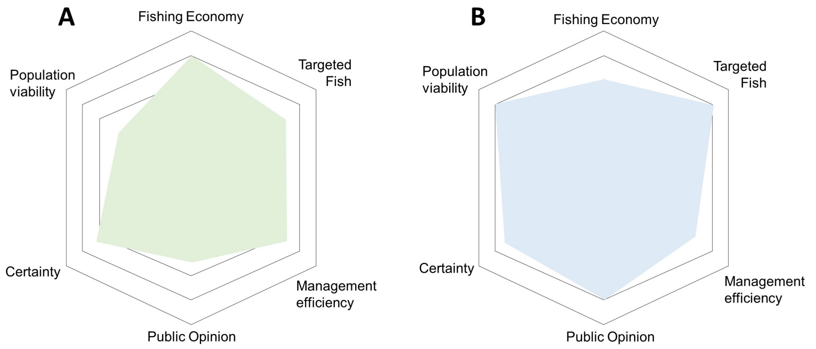

Figure 6.14: Diagram of qualitative management strategy. Rather than consider a quantitative management strategy, strategies may be defined taking into account several socio-economic variables. **A.** Strategy which is more concerned with the sustainability of the fishing economy. **B.** Strategy which is more concerned with the viability of dolphin and fish populations.

viability of the target fish species, public opinion and the certainty of estimates. In addition to these components, management effectiveness is also taken into account. A qualitative representation of the performance of these components for each management strategy can be imagined (Figure 6.14). This representation is adapted from (Punt et al. 2016). The current management strategy in the Bay of Biscay looks more like A. Despite ICES recommendations to implement time-area closures of fisheries, the government has chosen to favour the fishing economy. Public opinion is negatively influenced by the reports and the action of NGOs on the subject. If bycatch thresholds are defined and respected, then the management strategy could move from format A to format B. The sustainability of the dolphin population would be better taken into account, to the detriment of the fishing economy and in favour of public opinion.

This chapter closes the analytical part of the manuscript. At this stage we have explored different aspects:

- Chapter 2 on page 26 : Description of the common dolphin, its population in the North-East Atlantic, the associated conservation issues and the monitoring carried out on this population.
- Chapter 3 on page 43 : Development of a new survival analysis approach that takes into account covariate and random effects to estimate vital rates.
- Chapter 4 on page 70 : Estimation of vital rates for the common dolphin population, within the framework of the MSFD, which are estimated by taking into account various covariate and random effects.
- Chapter 5 on page 102 : Explanation and quantification of the bycatch phenomenon involving PTMs on a weekly, annual and ICES divisional basis.
- Chapter 6 on page 128 : Establishment of a tolerable bycatch threshold given the population's demographic viability, abundance, bycatch pressure and the CO set by OMMEG in European waters.

The following part is a discussion presenting three aspects related to this thesis. The first section deals with the general approach of the project. The second section deals with the North-East Atlantic common dolphin population. The third section deals with the cross-sectional monitoring.

DISCUSSION

General Discussion

7

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7.1 Project approaches

Aspects related to the demographic study

This thesis project was carried out using demographic approaches. The first approach was to develop a new methodology for estimating survival, based on the Reed model, from age-at-death data. This approach is a useful contribution to the literature. Its use implies the inclusion of an inter-individual frailty parameter. In addition to allowing the modelling of a bathtub shape hazard curve, the use of the frailty parameter allows heterogeneity within the study population to be taken into account. It is difficult to interpret this parameter on its own and it is more accurate to consider it as a statistical device for robust estimation. However it may be possible to strengthen its biological interpretation. It would be interesting to consider two inter-individual frailty parameters. One associated with the calf component of the life history, the other with the non-calf or juvenile-adult component. This would allow a better representation of survival and mortality in the population, taking into account the different frailties at different periods of life.
The survival estimation method is based on the use of age-at-death data and it is difficult to know whether the estimated vital rates (*e.g.* survivorship) are representative of those in the population. A possible solution would be to have both longitudinal monitoring data and age-at-death data for a population. Comparison of the longitudinal survivorship profile with that obtained through the cross-sectional survival approach would highlight the accuracy of the survival estimates. A limitation of this comparison is that, if there is a difference, the source of the difference cannot be defined. Is it a difference due to sampling or a difference due to the statistical approach or a combination of both? One way to compare would be to simulate longitudinal data as well as age-at-death data. Sampling and bias control would be provided by the simulation study. Any differences would be due solely to the statistical estimation of survival.

A possible improvement in the estimation of survival is to take into account two frailty parameters. One parameter specific to the calf component and the other specific to the non-calf component. Such an improvement could be made through a mixture modelling approach.

To check the plausibility of the survival rates estimated by the statistical approach, it would be interesting to simulate both longitudinal and age-at-death data and compare the survival estimates.

To control for sampling bias, stratified random sampling was useful. The use of this sampling framework allowed for greater confidence in the estimates of vital rates. When sampling in this way, the survival profiles estimated by the Siler and Reed models were almost identical. But this sampling scheme can only be used if there is a highly structured, centralised and coast-wide stranding Network. The French national stranding network is one of the most stable and unified stranding network in Europe. In Spain there is no single, centralised stranding network. Spain has many regional strandings networks along the mainland coast as well as separate networks for each of the Canary Islands. Germany has two stranding networks, while the Netherlands has four. Few European countries have a single stranding network. For those countries where this is the case, the network may not always be stable or long established (Figure 7.1. The French national stranding network has the advantage of being very reliable since the 1990s in recording all strandings on the Atlantic coast (Authier et al. 2014). Of the 25 stranding networks operating in North-Atlantic European waters, 11 routinely determine the reproductive status of females and 7 on *ad hoc* basis. With regard to age determination, data acquisition is variable since only 3 networks determine age ias part of a routine analysis, while 13 do so on an *ad hoc* basis (see Margin-Table 7.1). It may therefore be difficult to generalise this sampling approach to the whole of the European level.

Analysis	Routine	*Ad hoc*	Never	No reply	Total
Female reproductive status	11	7	1	6	25
Maturity state	10	7	1	7	25
Diet	9	10	0	6	25
Male reproductive status	7	10	1	7	25
Age determination	3	13	3	6	25

Table 7.1: Frequency of analysis from stranded animals performed by European stranding networks. Table from ICES (2021a).

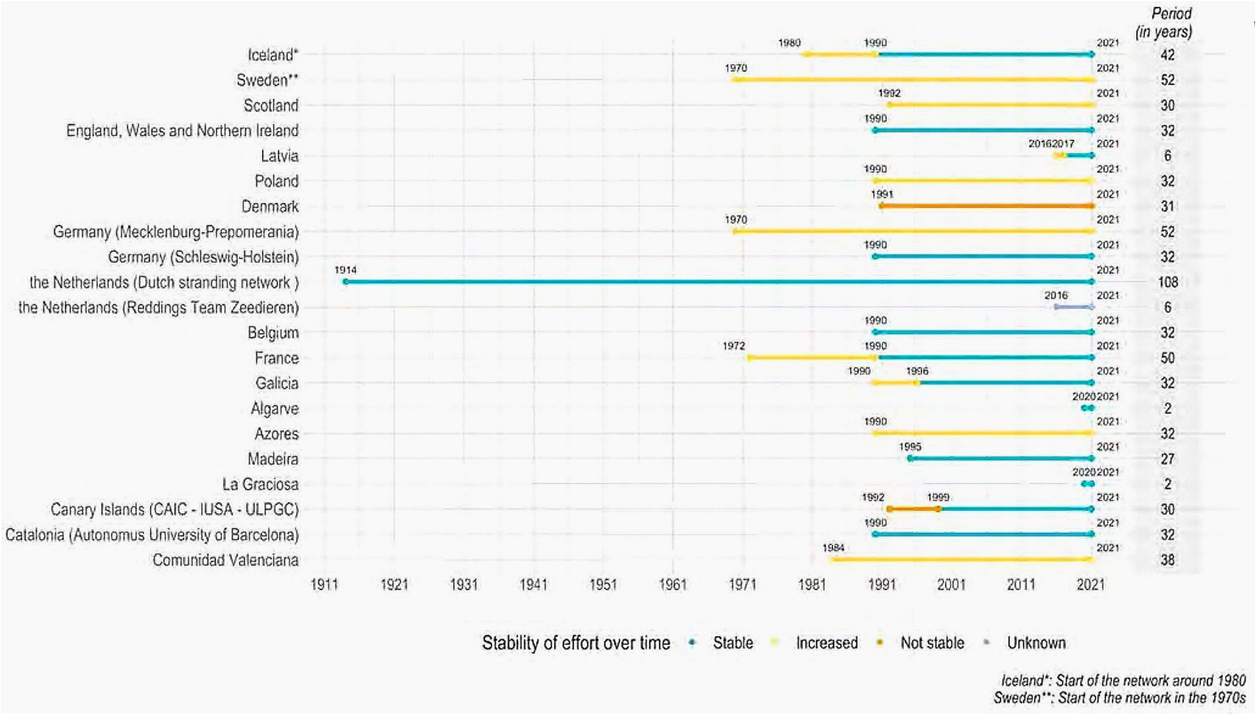

Figure 7.1: Period of activity of the networks that provided the starting date of their activity and the perceived stability of effort over time (as indicated by the respondents of the WGMME questionnaire). Very few European countries exhibit a unique and long-term stranding network. Island, United-Kingdom, Belgium and France have the most structured stranding networks.
Figure from ICES (2021a).

The possibility of including covariate and random effects in the analysis can provide a demographic indicator for the MSFD. At present, the criteria associated with obtaining demographic data for the MSFD descriptors are considered secondary. In other words, Member States' efforts to fulfil the descriptors should not focus on these criteria as a priority. Criteria associated with obtaining abundance data, for example, are considered primary criteria that can provide information on the viability of marine mammal populations (including the common dolphin). In Chapter 4, we have seen that the viability of the population seems to have deteriorated over the period of time considered (1997 to 2019). The use of random effects taking into account the cohort effect allowed us to identify possible differences in survivorship and age at sexual maturity for females. These differences could be used to develop an operational demographic indicator to immediately inform the demographic criteria of the MSFD descriptors. This indicator could take the form of a percentage difference in vital rates between cohorts (Figure 7.2). Differences from a baseline or mean profile could be reassessed every 6 years in each MSFD cycle.

Estimating vital rates taking into account random effects can be a new indicator of demographic status within the MSFD. This would help to identify the possibility of depletion before it occurs.

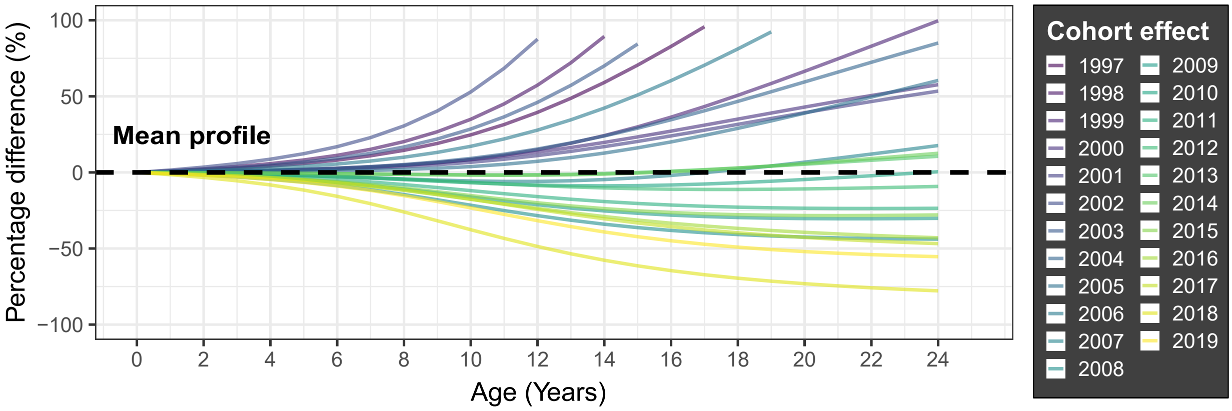

Figure 7.2: Relative percentage difference of cohort vital rates around the mean profile from 1997-2019. Relative percentage difference in survivorship. From 2012, the survivorship of adults seems reduced compared to the mean survivorship over the period.

The use of covariates also revealed a possible effect of bycatch on vital rates. This effect is quantifiable and could also be a pressure indicator for the demography of the common dolphin population to inform the MSFD. The effect of various anthropogenic pressures, such as pollutants, can be quantified at the demographic level for this population. For these reasons, I think that the criteria for assessing the "Good Environmental Status" of European Waters based on demography should not be considered secondary. Vital rates are important for knowing the viability of the population and it is now possible to quantify variations in the viability of the population. Vital rates provide earlier information on whether the viability of a population is impaired than abundance surveys. It is possible to identify a risk of depletion before it is observed. These criteria should be reviewed as primary criteria.

Demographic criteria are considered secondary. They should be reviewed as primary criteria. Demographic information for elusive marine mammal species can provide more detailed information on impacts and viability.

This demographic indicator could be used to fulfil the MSFD at the sub-regional scale. The MSFD considers the evaluation of water quality on a regional and sub-regional scale. For the common dolphin, the regional scale is the "North-East Atlantic", while the sub-regional scale is the "Bay of Biscay and Iberian Coast" and "Celtic Seas". Using the individuals stranded on the shores of these two sub-regions, an operational indicator could be produced to inform the demography of the common dolphin within the two sub-regions.

Aspects related to the conservation approach and management issues

This thesis project was carried out with the implementation of a management approach. The management approach is based in part on the use of bycatch estimates. The approach used in Chapter 5 to quantify bycatch from on-board observer data shows promise for using biased data. This approach can be used to add value to data that already exists but are considered biased. The ability to work with data that are considered biased should not prevent the collection of more representative data. Although promising for taking observation bias into account, the use of this approach is currently limited to PTMs. To extend its use, it would be necessary to be able to effectively calculate the fishing effort of passive *métiers* such as gillnetters. The use of this approach in the context of implementing management strategies currently seems to be limited since it cannot be generalised to all fishing *métiers*. On the other hand, it is interesting in terms of improving data that are considered to be of little use by the research community and providing information on the phenomenon of bycatch at a fine scale. The use of the joint model also makes it possible to highlight possible correlations or links between the various estimated variables (*e.g.* fishing duration and bycatch risk).

The estimation of the number of animals bycaught and associated variables makes it possible to valorise biased observer data. These data provide fine-scale spatio-temporal estimates. However, the use of this approach is limited by the availability of an accurate fishing effort dataset and sufficient bycatch observation data.

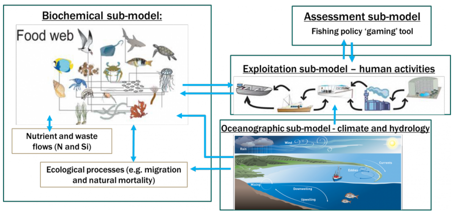

Figure 7.3: Diagram of Atlantis model. Models blocks are depicted such as relation between blocks. The model takes into account the whole ecosystem from the oceanography to the top of marine foodweb and human activities.
Figure from `https://niwa.co.nz/ecosystem-modelling-at-niwa/atlantis-ecosystem-model`.

The removal threshold produce through the MSE approach does not include any socio-economic index as it is done for some fisheries evaluation models such as the Atlantis model. The Atlantis model includes all the components of marine ecosystems from physics to human exploitation (Audzijonyte et al. 2019; Figure 7.3). The use of these complex models may be limited by their complexity. It can be difficult to define the links between all parts of the model and to understand how these parts interact. Analyses in the context of an MSE incorporating RLA are already a complex task involving many assumptions. For this reason, I think that the development of more complex models may be interesting from a theoretical point of view but not necessarily interesting from an applied point of view. Discussions between stakeholders (fisheries, scientists and decision-makers) are already difficult with regard to the bycatch and removal threshold. In my opinion, we need to keep it simple in order to facilitate understanding and decision making on the strategy to be adopted. From a scientific point of view, this should be reflected in the use of methodologies with limited complexity, rapid applicability and low dependence on computing time, as well as in the transparent availability of the methodologies used.

Methods for estimating tolerable bycatch rates should be kept simple, otherwise they may not be understood by all stakeholders and may therefore be difficult to apply.

The common dolphin, an elusive species

The notion of elusive species covers both demographic and management aspects. From a demographic point of view, these are species for which it is difficult to obtain data and vital rates. It is difficult to get an idea of the viability of the population on the basis of vital rates. It is also a species whose conservation is important in terms of the ecosystem balance (*i.e.* keystone) and therefore in terms of international legislation, especially in Europe. In Europe, the population is difficult to manage. Limited demographic knowledge is a contributing factor (Murphy et al. 2021). But difficult management discussions between fisheries, politicians, scientists and NGOs are also a contributing factor. Data on bycatch of this species in French waters are also very limited. The European Commission has set up an Infringement Procedure against France in July 2020:

> "*The Commission is asking France, Spain and Sweden to implement the measures required under the Habitats Directive (Council Directive 92/43/EEC) and Common Fisheries Policy to avoid unsustainable by-catches of dolphin and porpoise species by fishing vessels.* [...] *Despite well-documented evidence of these species being caught in fishing gear, the problem persists. France, Spain and Sweden have not taken sufficient action to monitor by-catches in their waters and by their fleets, nor made full use of the possibilities that the Common Fisheries Policy provides to comply with their obligation under the Habitats Directive and protect these species.* [...] *As France, Spain and Sweden have not taken the necessary steps to address these deficiencies, the Commission is sending letters of formal notice to the three countries, which will have three months to address the shortcomings raised. Otherwise, the Commission may decide to send a reasoned opinion*"[1] .

One of the difficulties in monitoring this population is that it is difficult to define and relate it to the OSPAR Management Unit. The next section is a discussion of the definition of this population.

[1] Follow this link to see the full procedure of the European Commission: `https://ec.europa.eu/commission/presscorner/detail/en/INF_20_1212`

7.2 Definition of the North-East Atlantic common dolphin population

Population migration and possible distributional changes

Exchanges between stocks and management units

Animal populations can exchange individuals through the phenomenon of migration which may occur between different stocks in the case of the common dolphin. Migration is composed of immigration which is the arrival of new individuals, including breeders, into the population, and emigration which is the final departure of individuals from the population. Sometimes the flow of individuals between two populations is not reciprocal. In this case, we speak of a source population that provides individuals to a sink population that receives them. This migration flux implies that the ecological conditions are met. Firstly, there must be a high production of individuals in the source population. Secondly, the sink population must suffer a high loss of individuals (*e.g.* through high extrinsic mortality) leaving vacant places to occupy the trophic niche of the species. Thirdly, there must be a migration corridor between the two populations with no geographical barrier.

Stocks can exchange individuals through dynamic source (donor) and sink (receiver) migration processes.

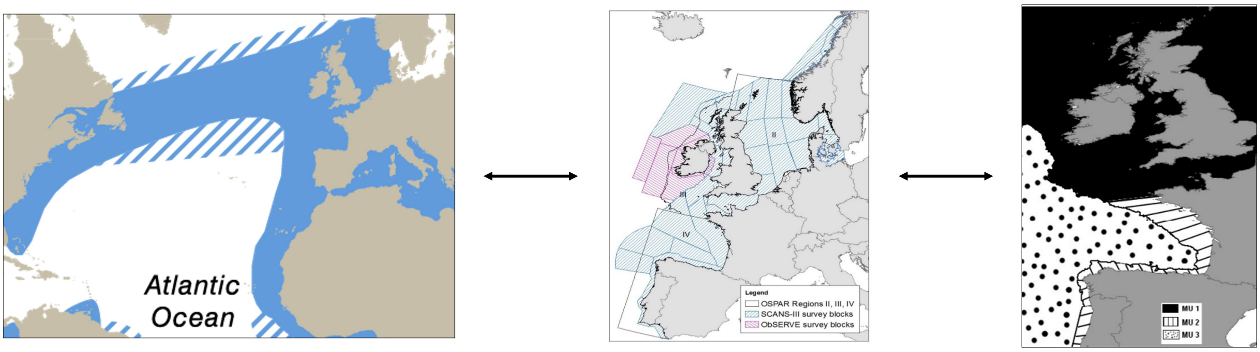

Figure 7.4: Possible management units for the North-East Atlantic common dolphin. The current management unit recognises a panmictic population by taking into account the Bay of Biscay, Iberian coast, Celtic seas and North sea. This management unit could be divided into three separate units. It could also be extended to a larger scale, including much of the North Atlantic.
Figures from Perrin (2018), ICES (2021a) and Caurant et al. (2009).

The vital rates obtained in this project are not consistent with the abundance estimates, which raises the question of the definition of the management unit. The vital rates are associated with a large majority of dolphins presumed dead on the Bay of Biscay continental shelf. Population projections show extinction in 50 years, as do the projections made by Mannocci et al. (2012). The population status also appears to have deteriorated since 1997, with an increasingly low growth rate. But these estimates are not consistent with the observed trend in abundance. The population

There is an inconsistency between the population projections and the observed trend in abundance in the Bay of Biscay and in the Management Unit.

does not appear to be declining at the scale of the Bay of Biscay and the management unit covering the Bay of Biscay, Iberian coast, Celtic seas and North Sea. It is possible that the Bay of Biscay shelf is associated with a sink population that receives individuals from other continental shelves (*e.g.* Iberia and Portugal) and Celtic seas. In this case, it is possible that the currently recognised management unit is too large and needs to be redrawn according to the classification proposed by Caurant et al. (2009).

The management unit may not be fragmented enough. Several sub-units should be defined as there may be sink-source exchanges between continental shelf stocks.

Another possibility is that the resulting vital rates are representative of the management unit recognised by OSPAR but that this management unit receives external individual inputs allowing it to be stationary. It is assumed that the population is not viable given current estimates of bycatch numbers across the management unit (ICES 2019). But the population abundance seems to be stationary at the scale of the management unit (Hammond et al. 2017). The currently recognised management unit may not include the majority of the common dolphin population. Migratory flows between the currently recognised management unit and other stocks could explain the stationarity of abundance. This hypothesis is difficult to verify. But it is possible that the currently recognised management unit is not the most appropriate one (Figure 7.4). On the one hand, by omitting external migrations. On the other hand, by not being sufficiently fragmented.

The management unit may not include the majority of the common dolphin population. In this case, it may not be large enough and should be expanded to the North Atlantic scale.

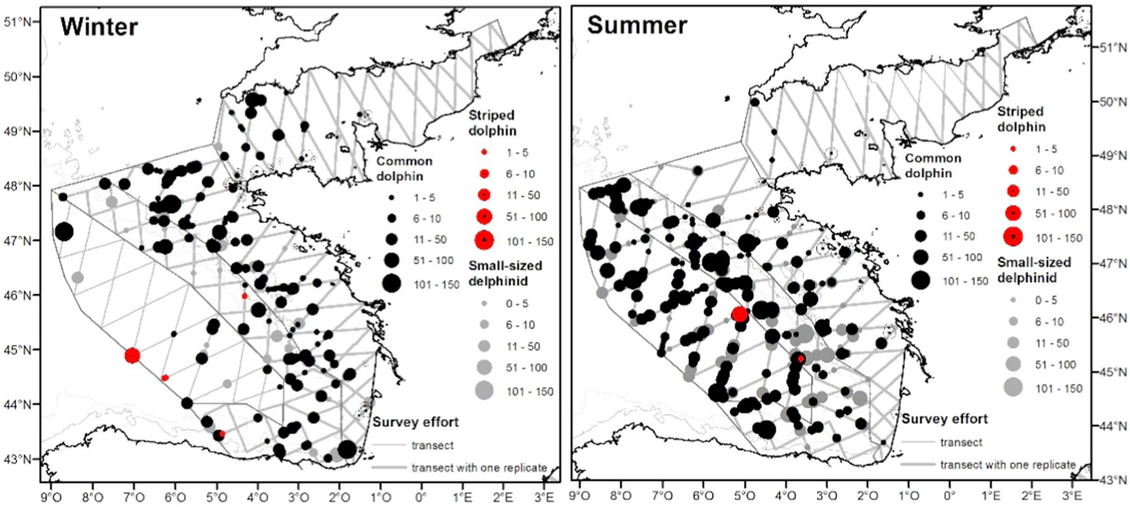

Figure 7.5: Common dolphin sightings from the SAMM surveys. SAMM surveys were conducted in Winter (November 17th 2011 to February 12th 2012) and Summer (May 16th to August 8th 2012). There were more common dolphins observed in summer on the oceanic part of the Bay of Biscay than in winter.
Figure from (Laran et al. 2017)

It is difficult to have a precise idea of the distribution of the common dolphin within the management unit but it is possible that seasonal variations in abundance in the Bay of Biscay are linked to source-sink dynamics. Abundance between summer and winter on the slope and the oceanic part of the Bay of Biscay appears to be different (Figure 7.5). The influx of individuals in summer may be linked to the breeding season (Murphy et al. 2021, 2009; Murphy, Collet, and Rogan 2005). These seasonal changes have been identified by the Seasonal Abundance of Marine Mammals (SAMM) surveys (Laran et al. 2017). Common dolphin sightings are from winter (17 November 2011 to 12 February 2012) and summer (16 May to 8 August 2012). The winter period sampled mixes months of very low density (November-December) and months of very high density (February) (unpublished data). In my opinion, one main highlight of these surveys is that the oceanic part of the Bay of Biscay may be subject to immigration during Summer (reproduction period). The abundance of small-sized delphinids (common dolphins and striped dolphins) in the Bay of Biscay in Summer 2012 was estimated at 493,591 individuals (95% CI: 342,000 - 719,000) whereas in winter 2011 it was estimated at 284,894 (95% CI: 174,000 - 481,000). It is possible that the difference in abundance of individuals is due to the contribution of non-resident individuals in the Bay of Biscay that come to breed in summer. It is difficult to say whether some of these individuals then remain in the Bay of Biscay to live there. It is also difficult to know the sex and age of the individuals that might move.

There seems to be a difference in dolphin abundance between summer and winter in the Bay of Biscay. This difference mainly concerns the continental slope and the oceanic part of the Bay of Biscay.

Overall change in distribution

These seasonal movements could be nested within larger spatio-temporal phenomena. Oceanographic processes are known to be structured in space and time. One way to represent this structure is the Stommel diagram generally involves two dimensions (space and time) but may involve a third (*e.g.* biomass). These representations are initially used to characterise the spatio-temporal phenomena of marine ecosystems (Haury, McGowan, and Wiebe 1978; Margin-Figure 7.6). These diagrams are useful for gaining a better understanding of the spatio-temporal phenomena structuring a system and their scales. They have also been applied to characterise the development of the biosphere (Holling 1992) and also the socio-ecological systems (Holling, Gunderson, and Ludwig 2002). I here provide a rough example of diagram that can be used as an approximate representation (Figure 7.7). The advantage of such a representation is that it allows the linking of different potentially related phenomena that do not take place at the same spatiotemporal scales. Here, it allows us to move from changes in the life history of a resident population, which may be driven by migration (when allocating resources for breeding or feeding), to larger scale phenomena such as distributional changes.

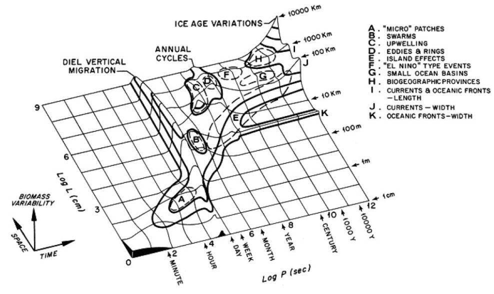

Figure 7.6: Marine biology Stommel Diagram. Emphasizes factors in marine biology, with an emphasis on biological productivity, here labeled "biomass variability".
Figure from Haury, McGowan, and Wiebe (1978)

The presence and residence of top predators is strongly influenced by the presence of their prey. Low prey availability can

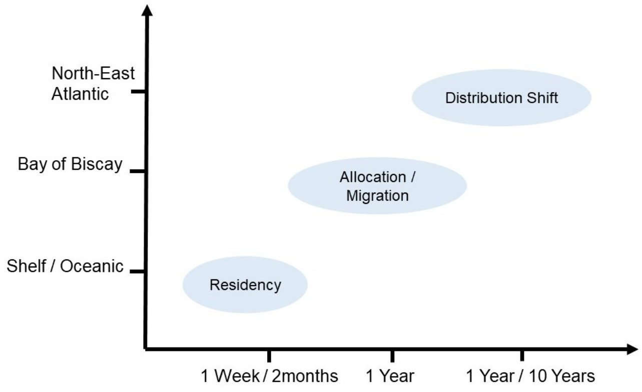

Figure 7.7: Rough Stommel diagram for common dolphin. This raw diagram presents processes associated with the population at three spatio-temporal scales. The population can be resident of the Oceanic or Shelf parts for about two months. Individuals may migrate within the Bay of Biscay each year. The population may change its distribution on a larger spatial and temporal scale later. This diagram is only a rough and conceptual view and should not be considered as completed.

influence the energy budget of the predator and ultimately influence its demography (MacLeod et al. 2007). The harbour porpoise (*Phocoena phocoena*, Linnaeus 1758) is the smallest odontocete in Europe with a length of about 1.5m and a weight of 50kg; it is also found in the North-East Atlantic ocean. This species has a shorter lifespan, a younger age at first reproduction and a shorter calving interval. Because of its small size, the harbour porpoise cannot survive long periods without feeding and almost dies after 3 days without food (Kastelein et al. 1995). The harbour porpoise was widespread in the North Sea and fed mainly on sandeels (genus *Hyperoplus*). These fish species are essential to the ecosystems of the North Sea (Greenstreet 1996). They are also essential for the survival of harbour porpoises in spring. This season is associated with the coldest water temperatures in the North Sea, which requires a high energy intake to maintain a stable internal body temperature (Watts, Hansen, and Lavigne 1993). The presence of sandeels is also crucial for the survival of weanlings that are about to take their first food intakes.

The viability of the predator population depends partly on its prey. The harbour porpoise, for example, is heavily dependent on sandeels in the North Sea.

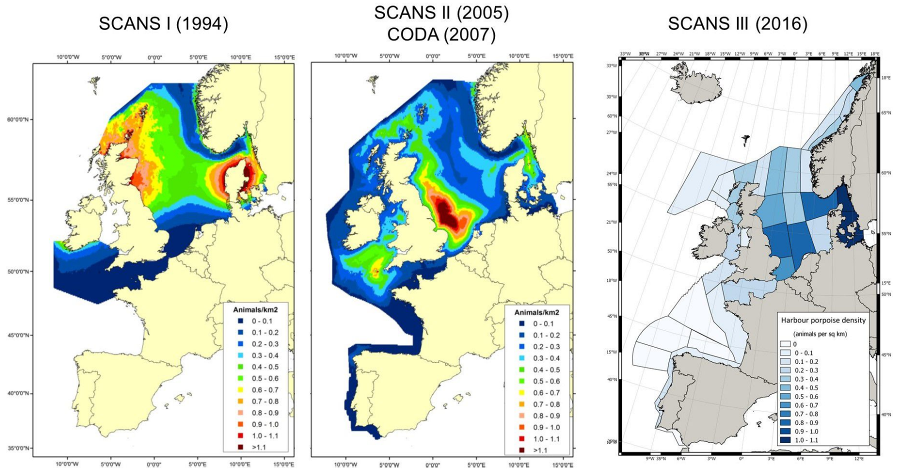

Figure 7.8: Density of Harbour porpoise estimated from the SCANS and CODA campaigns. The time period under consideration ranges from 1994 to 2016 with 3 main estimates. The density of harbour porpoises in the North-East Atlantic appears to have possibly changed over the period. The population now seems to be denser in the Western Channel, Celtic seas and Bay of Biscay than before.
Figures from Hammond et al. (2017, 2013).

This type of ecological control is called "bottom-up" control. Sandeels may induce bottom-up control on harbour porpoises. The large fishing industry that developed during the 1980s contributed to the decline of the sandeel stock in the North Sea (Furness 1999). Furthermore, the recruitment of sandeels in the North Sea has decreased since the 2000s, with a possible combined influence of fishing and climate change (ICES 2006) through an impact on plankton communities (Beaugrand et al. 2002, 2003; Frederiksen et al. 2006). The decrease in sandeel stocks and quality has had an impact on harbour porpoises, with greater starvation and lower survival rates in the North Sea (MacLeod et al. 2007). It is possible that this limited access to the resource has led to a migration of harbour porpoise from the North Sea to adjacent waters (Hammond et al. 2017, 2002, 1995).

The bottom-up of sandeels over harbour porpoises, combined with a decline in the sandeels stock, may have caused a change in the distribution of harbour porpoises in the North-East Atlantic.

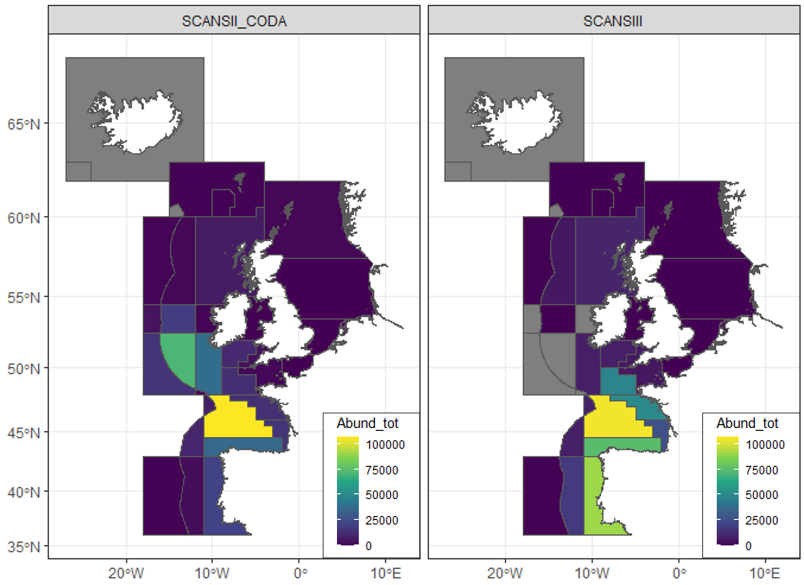

Figure 7.9: Abundance estimates of common dolphin by ICES divisions. The abundance estimates seems to be slightly higher for SCANS III than for SCANS II + CODA. Estimates from Hammond et al. (2017).

It is possible that the common dolphin population is at a stationary abundance throughout the Northeast Atlantic and that the demographic rates estimated in this project are related to part of the population sampled in the Bay of Biscay. There may be more prey of interest available in the Bay of Biscay than in the past. Fishing mortality pressure in the Bay of Biscay would be higher than in other parts of the North-East Atlantic, but population abundance would be essentially stationary on a large scale. Abundance surveys in the North-East Atlantic of SCANS II + CODA and SCANS III seem to show that the abundance of the population is almost stationary or perhaps increasing very slightly. Recent works by Evans and Waggitt (2020) also supports an increasing trend in abundance observed in the North-East Atlantic using Waggitt et al. (2020). Recently, Astarloa et al. (2021) also highlighted a trend of increasing abundance of common dolphin in the Bay of Biscay and the correlation of this trend with environmental and biological

The demographic rates obtained in the Bay of Biscay may not be representative of the whole North-East Atlantic. It is possible that bycatch pressure is responsible for the observed values.

variables using the Vector-Autoregressive Spatio-Temporal (VAST) model (Thorson 2019). The authors point out that the increase in estimated abundance is not necessarily a sign of a growing population but may reflect migration from unsampled areas. The correlation between common dolphin abundance and the North Atlantic Oscillation Index, prey abundance and chlorophyll is studied (Figure 7.10). Some correlations are highlighted but it is difficult to attribute the possible change in distribution of common dolphins to these variables. It is difficult to link variations in abundance or changes in distribution of common dolphins to environmental and prey data. This is mainly due to the scarcity of data and the rare co-occurrence of the two predator-prey system data in the large scales of the phenomena of interest (Gilbert et al. 2021; Astarloa et al. 2021).

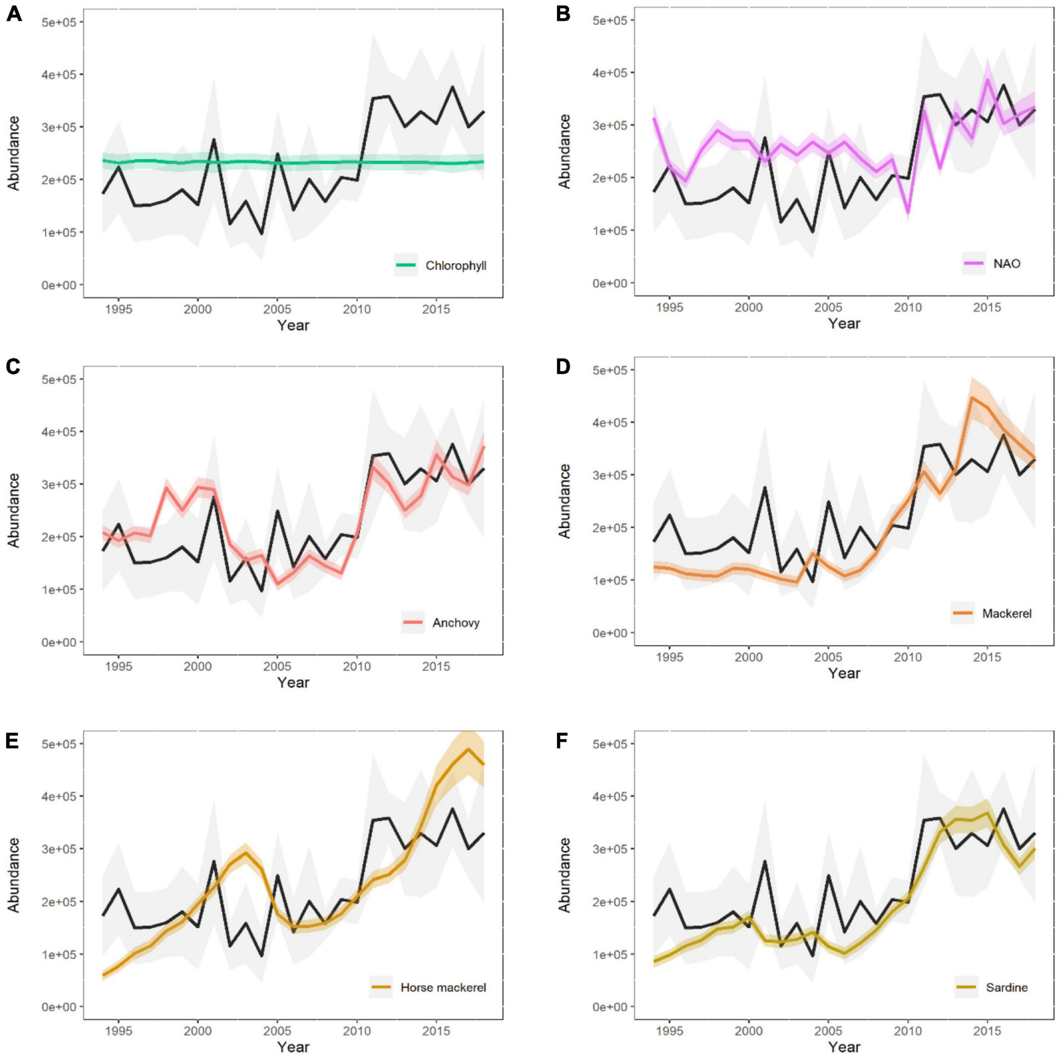

Figure 7.10: Correlation between common dolphin abundance and ecosystem variables. Abundance estimates predicted by the baseline spatio-temporal model (black line) and by the covariates-based model (with no random effects, colored line) so that the contribution made by each variable (A–F) can be visualized.
Figure from Astarloa et al. (2021).

Abundance estimates: an incomplete indicator

Abundance is an indicator of interest to assess the "Good Environmental Status" of marine European waters (European Parliament 2008) but it may be incomplete to assess the viability of megafauna populations. This indicator is considered to fulfil Descriptor 1 (D1[2]) and Descriptor 4 (D4[3]). Abundance assessment at the scale of a particular population is very instructive since it provides an initial assessment of the population's state (Laran et al. 2017). At the scale of a community (*e.g.* cetaceans in the Bay of Biscay) it can also inform the biodiversity state of the cetaceans community which is an important aspect of the D4 criterion (Azzellino et al. 2014; Lauriano et al. 2014).

[2] `https://mcc.jrc.ec.europa.eu/main/dev.py?N=19&O=118&titre_chap=D1%20Biological%20diversity`

[3] `https://mcc.jrc.ec.europa.eu/main/dev.py?N=22&O=133&titre_page=&titre_chap=D4%20Food%20webs`

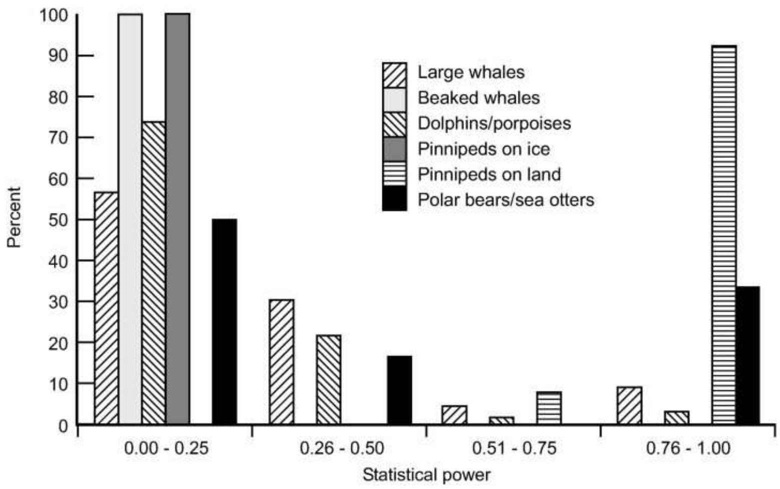

Figure 7.11: Percent of stocks within four ranges of statistical power. Statistical power is the probability of correctly rejecting the null hypothesis that a population is not declining (*i.e.*, one-tailed t-test) when the stock is experiencing a precipitous decline (50% over 15 yr). Results are summarized for six categories of marine mammals: large whales, beaked whales, dolphins and porpoises, pinnipeds on ice, pinnipeds on land, and polar bears and sea otters.
Figure from (B. L. Taylor et al. 2007).

The ability to detect population declines in abundance below a critical threshold remains poor for many marine mammal species. Abundance trend cannot be effective in identifying populations at risk because the statistical power to resolve abundance trends is sometimes very low if the time series is sparse (B. L. Taylor et al. 2000). The statistical power to detect a precipitous decline through abundance studies was calculated by B. L. Taylor et al. (2007) (Figure 7.11). A precipitous decline is defined by the authors as a "decline of 50% over a 15-yr monitoring period". They justify this choice by the fact that such a decline would lead to the classification of a stock as "depleted" under the MMPA and as "vulnerable" or "endangered" under the IUCN Red List guidelines (B. L. Taylor et al. 2007). In Figure 7.11, we can see that the statistical power (probability of correctly rejecting the null hypothesis that a population is not declining) is very low for dolphins and porpoises population (the common dolphin was not included in their analyses). These results indicate that the use of abundance estimates to detect precipitous declines is not appropriate for small cetacean populations.

Using abundance trends alone to define the status of small cetacean populations can be dangerous due to low statistical power.

Examples of delays between the onset of extrinsic mortality and the implementation of management measures

Uncertainty in abundance indicators may limit the conservation of small cetaceans affected by bycatch (B. L. Taylor et al. 2000). There may be a delay between the onset of pressure and the implementation of management measures. This delay may be detrimental to the viability of populations. Two examples will follow to support this point.

Harbour porpoise in California

The first example concerns the harbour porpoise in California. In the mid-1980s, an increasing number of porpoises were found stranded on the shoreline, as well as an expansion of coastal gillnet fishing in central California. These two observations led to the assumption that the population was threatened by fishing. To monitor this population, mortality was assessed by an observer program and porpoise abundance was estimated by surveys and back-calculation from fishing effort and mortality rates (B. L. Taylor et al. 2000). Uncertainty in the parameters tended to make it impossible to determine the level of depletion and the MNPL. The MMPA was not able to conserve this species and its preservation was achieved indirectly through fishery closures associated with the capture of sea otters (B. L. Taylor et al. 2000). This example shows that the mere availability of some abundance and bycatch data does not allow the implementation of conservation measures at the right time.

The harbour porpoise in California and the Tuna-Dolphin problem are two representative examples of the delay between the onset of depletion, its recognition and the implementation of management measures.

Tuna-Dolphin problem

The second example involves many steps over 60 years, encompassing many areas of expertise (biology, conservation policy, legislation), media coverage and the creation of a label for consumers (Supplementary-Figure 1). It is known as the "Tuna-Dolphin Problem" and has recently been the subject of a review made by Ballance et al. (2021). The history of this problem is extensive and is provided in Appendix 7.4. In the East Pacific Ocean, large-bodied yellowfin tuna (*Thunnus albacares*, Bonnaterre 1788) associate with several species of dolphins such as the pantropical spotted (*Stenella attenuata*, Gray 1846), the spinner (*Stenella longirostris*, Gray 1828) and the short-beaked common dolphin. These dolphins interact together with birds in a beneficial way (Scott et al. 2012; Ballance, Pitman, and Reilly 1997). These associations are readily visible at the surface and provide some indication to purse seine fisheries targeting tuna. Purse-seine are deployed near dolphin schools,

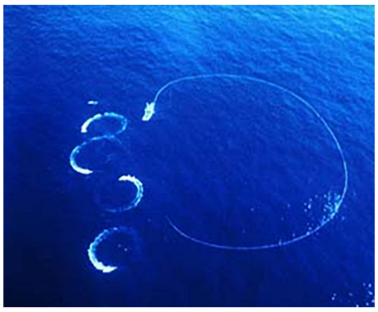

Figure 7.12: Aerial photograph of a purse-seine set on a school of tuna and dolphins. The purse-seine vessel is deploying the net in a large circle around the entire school while a skiff holds the end of the net in place. In this photograph the net is not yet closed; four speedboats are driving in tight circles near the opening to prevent the dolphins (and tuna) from escaping.
Photo from Ballance et al. (2021).

resulting in high levels of bycatch (Figure 7.12). All three dolphin species were recognised as bycaught in the purse-seine Tuna fishery (Perrin 1969; Figure 7.13). Catches were in the hundreds of thousands between 1960 and 1995. Between 1995 and 2020, they fell to around a thousand.

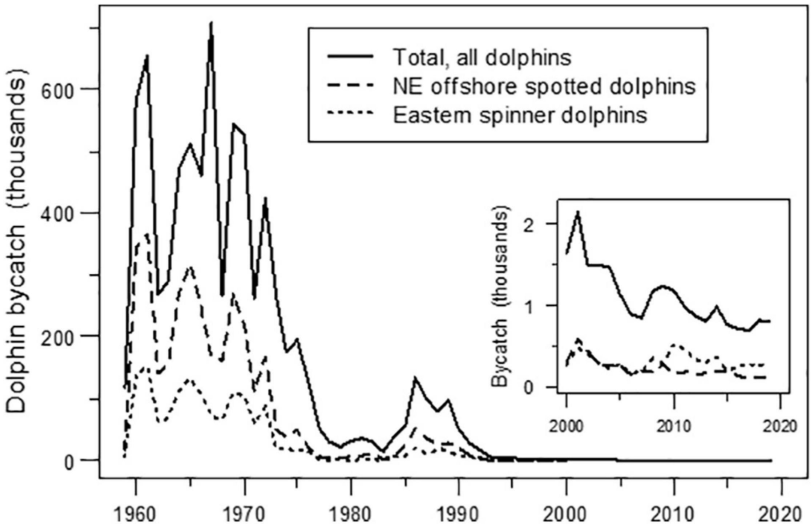

Figure 7.13: Estimated number of dolphins killed annually in the eastern tropical Pacific tuna purse-seine fishery. Total for all dolphins and separately for the stocks of the two dolphin species with the highest number killed. The inset graph has an expanded vertical scale to show details from 2000 to 2019 (change of scale on the Y-axis).
Figure from Ballance et al. (2021).

The observation of bycatch numbers from 1960 to 1970, and in particular the outcry over the magnitude of dolphin mortality, prompted the establishment of the MMPA in 1972, which aims to reduce bycatch mortality to a level close to zero. Given the degree of uncertainty regarding the status of the population, numerous data acquisition efforts have been made to justify its depleted status. In total, "nine abundance surveys over 12 years, 17 years of relative trend indices from data collected on the tuna vessels, 25 years of observer data on dolphin mortality rates in the fishery, and 34 years of data on fishing effort" have been required. From the first abundance estimate to the recognition of the depleted status of the population, 23 years of inaction were reported (Wade 1994). By the late 1970s, it was clear that the dolphin mortality was too high relatively to the populations abundances estimates. However, it was only after sufficient data had been collected and analytical methods developed, *i.e.* until 1993, that it was possible to prove that the dolphin populations were reduced to 44% of its total abundance (Wade 1993a,b). At this time, the populations were declared depleted under the MMPA (depletion being defined as stock abundance below 60% of carrying capacity; Ballance et al. 2021).

This example is similar to the case of the common dolphin in the North-East Atlantic. There is currently uncertainty about the true status of the population, given the abundance estimates and the poor usability of on-board observer data. EAlthough we have developed new methods and provided new bycatch estimates from a biased observer scheme, it is not possible to estimate the total bycatch mortality of the population due to the lack of adequate data (and not because of a lack of methodology, *e.g.* see Chapter 5). Using only abundance estimates, observer programmes and stranding mortality monitoring, it is possible that the mismatch between the actual time of depletion and the recognised time of depletion is dangerous for the viability of the population.

7.3 Population dynamics of elusive species

Life-history traits variations

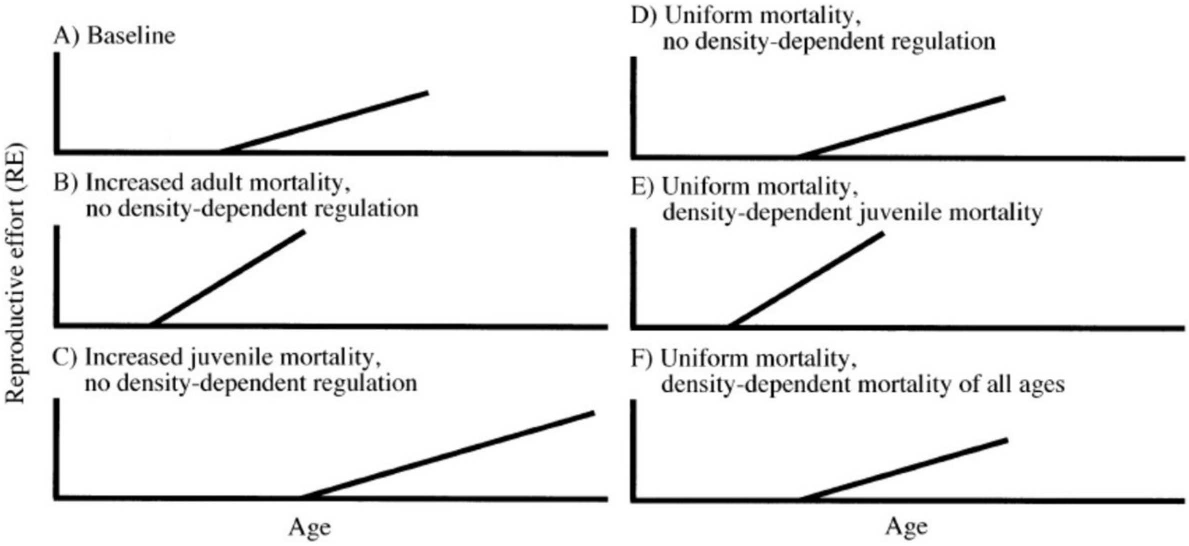

Figure 7.14: raphical representation of predicted changes in optimal reproductive effort (RE) of a generalized life history. RE is defined as the proportion of resources allocated to reproduction as opposed to investment in growth or survival. The age at which RE increases from zero indicates age at maturity. The linearly increasing depiction of RE with age is arbitrary, and plot A is the baseline iteroparous life history. Plots B–D give predictions for unregulated populations growing exponentially after: **(B)** mortality increases only for older age classes (earlier age at maturity and higher RE at each age), **(C)** mortality increases only for younger age classes (later age at maturity and lower RE at each age), and **(D)** mortality increases uniformly across all ages (no change from baseline). Plots E and F give predictions for regulated populations subjected to density dependence: the effect of a uniform increase in mortality when density dependence affects **(E)** only juveniles (note the increase in RE over baseline and earlier age at maturity) vs. **(F)** all ages (no change from baseline).
Figure from Reznick, Bryant, and Bashey (2002).

We found a possible decrease in the age at sexual maturity of females compared to the methodology commonly used in the literature. The age at sexual maturity of females decreases by about one year according to these results (8 to 7 years). Using the joint model and random effects approach, it appeared that the age at sexual maturity of females also appeared to decrease over the period considered. It can be assumed that this possible change is part of a life history optimisation (Ferriére and J. Clobert 1992). Age at sexual maturity should respond differently depending on the mortality experienced by the population and on the presence of density-dependent mortality (Reznick, Bryant, and Bashey 2002;

Figure 7.14). It is possible that increased adult mortality in the population favours genotypes that reproduce earlier. This assumption has also been made by Perrin, J. R. Henderson, et al.; Barlow; Chivers and Myrick Jr for the North-East Pacific dolphins (Perrin, J. R. Henderson, et al. 1979; Barlow 1989; Chivers and Myrick Jr 1993). The survivorship also seemed to decrease according to the results of the joint modelling approach. There may be a link between age at sexual maturity of females and survivorship of adults. This link could depend on the extrinsic mortality rate (Ricklefs 2010). It is possible that the extrinsic mortality experienced by adults decreases their maximum potential longevity and thus their age at sexual maturity.

The population may undergo a process of variation in vital rates with a shorter life history than before (shorter life expectancy and advanced reproduction).

Loss of interest in cross-sectional monitoring

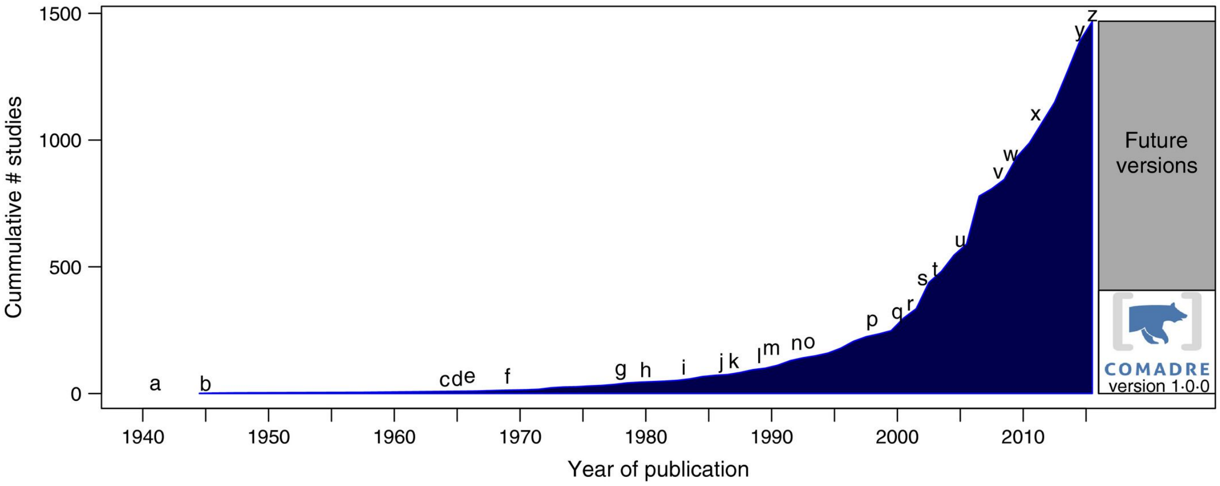

Figure 7.15: Cumulative number of studies published prior to 27.07.2015 containing animal matrix population models (MPMs). Some Important events in the development of animal MPMs: **(a, b)** applications of matrix population models in demography, **(f)** nonlinear, density-dependent MPMs for animals, **(g)** sensitivity analysis for stage-classified MPMs and calculation of selection gradients for animals, **(i)** calculation of the stochastic growth rate from an animal MPM, **(k)** application of elasticity analysis to conservation biology and Life Table Response Experiment analysis, **(n)** presentation of multistate mark–recapture methods for estimating stage-structured MPMs in animals, **(o)** development of MPM from photograph identification data.
Figure from Salguero-Gómez et al. (2016).

Longitudinal monitoring is now favoured to study the demography of long-lived megafauna species. Monitoring of these species traditionaly used age-at-death data or hunting bags to obtain vital rates (cross-sectional monitoring). The most important assumption regarding these data is that the population must have a stationary age-distribution (Caughley 1966). In the wild, this assumption is rarely met (McCullough et al. 1994; Menkens and Boyce 1993) and it is even more difficult to achieve it with the large marine mammals whose strandings are used (Barlow and Hohn 1984; Stolen and Barlow 2003). Demographic rates estimated by cross-sectional monitoring may not be reliable in these cases.

Longitudinal monitoring (when feasible) and the associated analyses,have therefore been favoured and have undergone significant development. Since the Cormack-Jolly-Seber (Seber 1965; Cormack 1964; Jolly 1965) approach, numerous developments in modelling and sampling protocols have taken place (Lebreton et al. 1992). The 1990s saw many developments in the use of CMR and radio telemetry protocols to estimate survival rates (Lebreton, Pradel, and J. Clobert 1993; Gaillard, Festa-Bianchet, and Yoccoz 1998). Survival analyses based on longitudinal monitoring is now an entire well developed scientific field in its own with a firm statistic basis (Gaillard, Festa-Bianchet, and Yoccoz 1998) and can be used to feed demographic databases such as COMADRE (Salguero-Gómez et al. 2016; Figure 7.15).

Longitudinal monitoring has been favoured for the study of long-lived megafauna species for which such monitoring is feasible. The associated survival analyses have developed strongly since the 1990s and longitudinal analysis is now a field of statistical analysis in its own right.

Cross-sectional monitoring remains the most suitable approach for some marine megafauna species that may be elusive. It is also the only possible approach for fish populations and exploited stocks. For some species of marine megafauna, there is a lack of demographic information (Heppell, Caswell, and Crowder 2000; Moore and A. J. Read 2008) and it may be necessary to conduct population viability analyses (W. F. Morris et al. 2002). For marine mammals associated with bycatch, population managers are tasked to make decision (*e.g.* fisheries closures) despite a large amount of uncertainty (Thompson et al. 2000; Harwood 2000). Since the development of Siler (1979) and Heligman and Pollard (1980) approaches, there has been few methodological development associated with cross-sectional monitoring. A recent improvement has been the development of the package strandCet (Saavedra 2018) which is interesting for taking into account additional mortality and the treatment of sampling biased age classes (*e.g.* due to bycatch). A question arises: why is the community so reluctant to produce vital rates from cross-sectional monitoring?

Cross-sectional monitoring has not received the same attention from the community. Despite the fact that it is the only feasible monitoring for elusive species and fish stocks.

The contribution of this project to cross-sectional approaches

Obtaining vital rates from cross-sectional monitoring of long-lived megafauna species is limited by the lack of sampling control and the limited possibility to measure variability in vital rates (Gaillard, Festa-Bianchet, and Yoccoz 1998). One of the points of this work was to partially address these limitations.

With regard to the first item, the use of stratified random sampling is intended to allow for better control of the sampling. This control takes place prior to the analysis of the data and aims to avoid introducing additional uncontrolled bias.

The use of post-stratification to quantify human pressures (*e.g.* bycatch) is also a type of correction. Here, it is carried out during the analysis, in order to take into account possible biases in the representativeness of the data.This is of interest for elusive species, such as the common dolphin, whose bycatch is not well informed. The inclusion of covariates and random effects in the joint model to quantify vital rates is also an improvement in approaches. With this development it is possible to quantify the effect of different factors on vital rates and to highlight variations at the population level.

Application of the demographic approach to other megafauna species

When available, age-at-death data should be used to their fullest potential (Ferguson 2002). Here I propose an analytical and a conceptual framework which incorporates important elements of this thesis project (Figure 7.16). This diagram incorporates both elements of the literature and elements developed within the framework of the project for illustrative purpose.

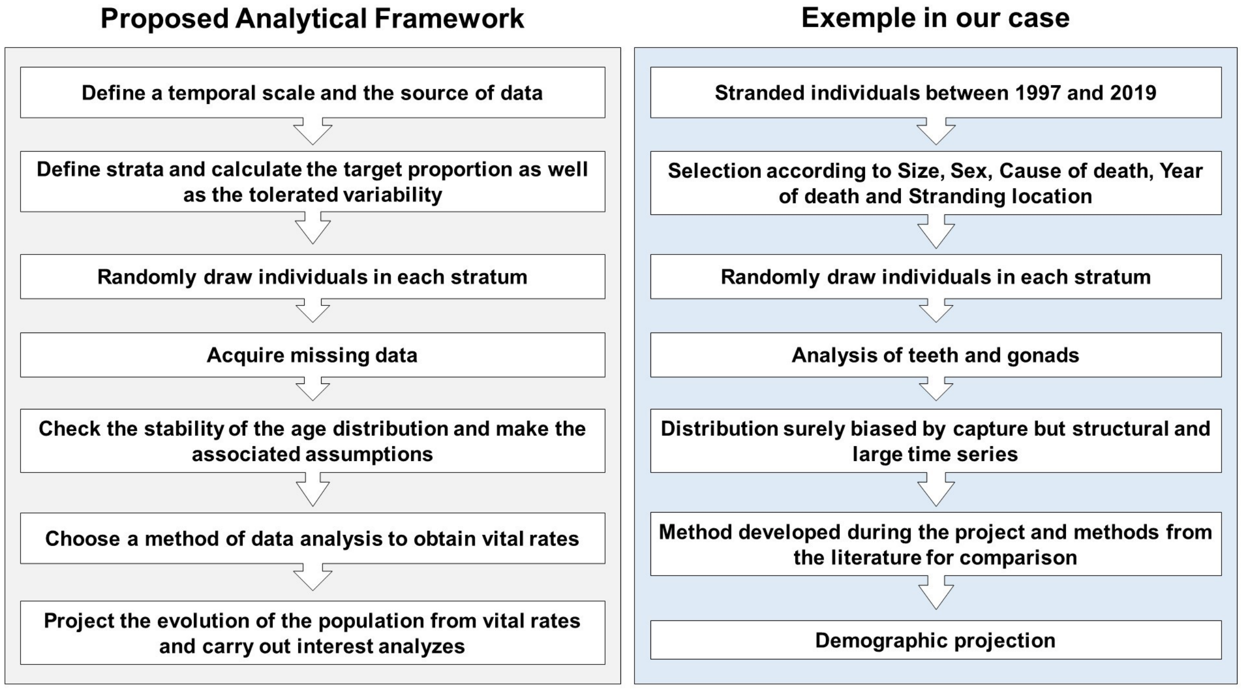

Figure 7.16: Diagram of the proposed framework along with the example in our case. The steps are defined to allow for a better consideration of representativeness bias. This framework is primarily a point of discussion and not definitive.

Odontocete species

This framework is transposable to other odontocete species and can serve different purposes depending on the problems associated with the population. It is preferable that data be collected by a stable and centralised stranding network. The more stable the stranding network is over time and centralised, the longer and more representative the period covered can be. This reduces the bias associated with collecting stranded individuals.

Harbour porpoise in North-East Atlantic

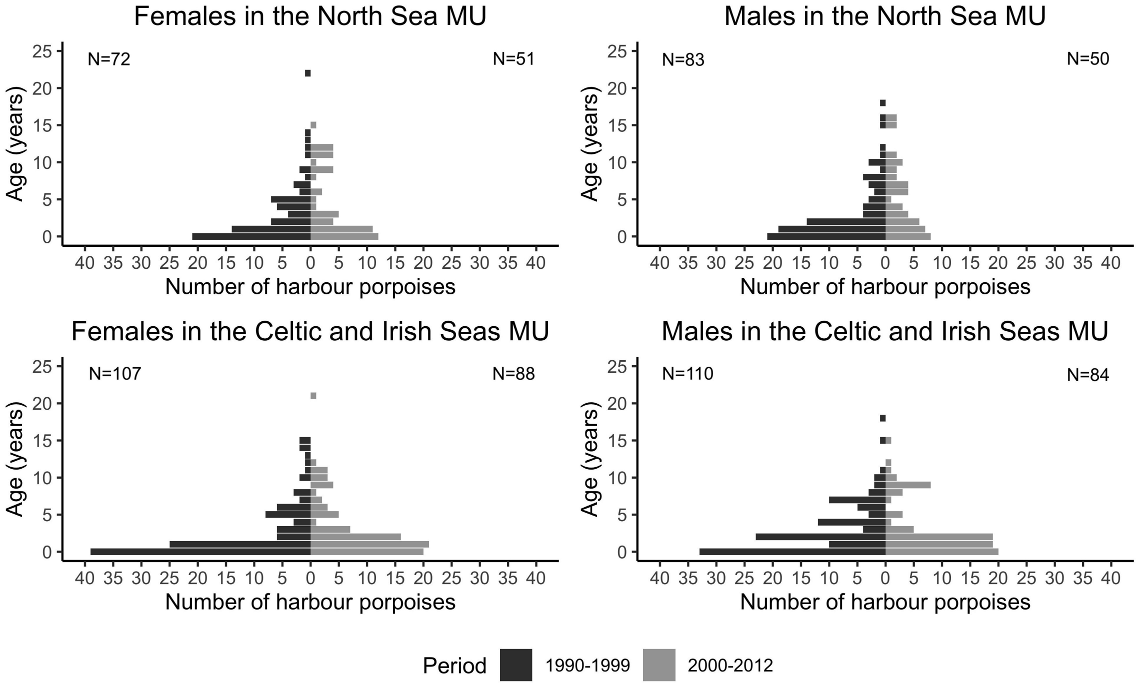

Figure 7.17: Age-frequency distribution and sample sizes of female and male harbor porpoises sampled within the North Sea MU and Celtic and Irish seas MU during the two time periods, 1990–1999 and 2000–2012. These data could be analysed with our joint modelling approach. This would highlight possible differences in vital rates values depending on area and/or sex.
Figure from Murphy et al. (2020)

The harbour porpoise is also a species for which there are strong conservation issues in European waters (ICES 2020b). The Baltic Sea population is now listed as critically endangered (Benke et al. 2014). In the North-East Atlantic the Harbour population is distributed from Norway to southern Spain. Two genetically distinct stocks are recognised, the first in Spain, the second between France and Norway (Fontaine et al. 2007). The population has been divided into several management units based on genetic differentiation but also on morphological differences (Evans and Teilmann 2009; JNCC 2015; Margin-Figure 7.18). However, it appears that the overall population is subject to all types of pressure (Murphy et al. 2020), notably primary (bycatch) (ICES 2020b), secondary (pollution disruption) (Murphy et al. 2015) and tertiary (noise disturbance) (Brandt et al. 2011). It is also supposed that climate change influences the physical condition of harbour porpoises (Heide-Jørgensen et al. 2011). With regard to population trends, declining trends have been observed in the Celtic and Irish Seas (NAMMCO, IMR 2019).

Some biological parameters are well know for the overall population and the different stocks (*e.g.* age-at-death in Figure 7.17) but there are still uncertainties about the population dynamics of these stocks (Murphy et al. 2020). It could be of interest to apply the framework used here to produce stock-specific population rates (via covariates). This will also allow the identification of possible changes in life history traits over time as a function of stock to explore possible exchanges between sinks and sources. his would help to refine and prioritise the management interest of the different units recognised by the MSFD.

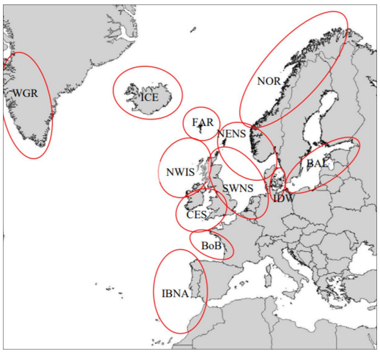

Figure 7.18: Map showing Recommended Management Units for Harbour Porpoise in the ASCOBANS Agreement Area and Environs. Figure from Evans and Teilmann (2009).

Hector's dolphin

Dolphins of the genus *Cephalorhynchus* are distributed in the Southern hemisphere in South-America, South Africa and New Zealand. The Hectors'dolphin (*Cephalorhynchus hectori*, van Beneden 1881) is the only species of this genus tto occur in New Zealand waters (A. N. Baker 1978) has recently been estimated to be around 15,000 individuals (Annex D 2017). The biological parameters of this species were determined with an average lifespan of 20 years and an age at sexual maturity between 6 and 9 years for females (Slooten 1991). From the age distribution of the dolphins obtained from standings, the survivorship of the population and its growth rate were determined using the Siler model and a Leslie matrix approach (Slooten and Lad 1991). The population appears to have a low growth rate and entanglement in gillnet fisheries is suspected to be an important source of additional mortality for this population, as is predation by sharks (Dawson and Slooten 1993; Slooten, Fletcher, and B. L. Taylor 2000). A sub-species of Hector's dolphin, the Maui's dolphin (*Cephalorhynchus hectori maui*, Baker 2002) lives in the north of New Zealand (Margin-Figure 7.19). The population of this subspecies has fallen to about 60 individuals (C. S. Baker et al. 2016). It might be interesting to use a similar methodology to that employed in this project on the Hectors dolphin population. The population size of 15,000 individuals could provide enough strandings to achieve vital rates. The advantage could be to use the long age-at-death data time serie (without using only females samples) and discriminate the impact of predation and bycatch on the value of survival rates as covariate effect. The use of the year of stranding could be of interest to identify a possible shift in life history-traits.

Figure 7.19: Hector's dolphin draw and distribution. Hector's dolphins are found along the east coast of the South Island. They are found down the West Coast to Jackson Bay and Fiordland. On the south coast, two bays east and west of Invercargill have Hector's dolphins.
Draw from `https://www.fisheries.noaa.gov/species/hectors-dolphin`.
Distribution from `https://teara.govt.nz/en/map/4675/distribution-of-hectors-and-mauis-dolphins`.

River dolphins

River and coastal dolphin populations can be monitored both on the basis of individuals found stranded and from capture-recapture programmes. It is the case for the population of Irrawaddy dolphins (*Orcaella brevirostris*, Owen 1866) that lives in the Mekong river (Cambodia) and is currently classified as Critically Endangered by the IUCN (Beasley et al. 2013). It was possible to conduct the two surveys and compare their results. Survival rates were both estimated by a carcass recovery programme and a capture-recapture programme. The authors concluded that the comparison was interesting and provided more information on the bias that could impact the survival estimate for the two monitoring (Beasley et al. 2013). Coastal dolphins species can be followed through capture-recapture studies such as the Guiana dolphins (*Sotalia guianensis*, van Beneden 1864) (Cantor et al. 2012). It could be of interest to use age-at-death data to compare between the estimates made through CMR monitorings and carcass recoveries for similar species.

Pink dolphin in colombia ©Jaime Rojo.

Mammal and/or megafauna species

The current challenges in terms of the biodiversity crisis linked to direct anthropogenic impact or indirectly through climate change, require a global cooperative effort to acquire biological data (Urban et al. 2016). Vital rates are an important source of information for understanding and predicting the effects of anthropogenic impacts and climate change (Paniw et al. 2021). Demographic databases are particularly interesting given the issues outlined above and allow both sharing and a global effort to produce demographic indicators (Salguero-Gómez et al. 2016). These databases also provide good sources of information for generating life history knowledge and are important today in a context of digitisation of ecology that requires good and reproducible research practices.

The European wild boar (*Sus scrofa*, Linnaeus 1758) is studied using several forms of monitoring (hunting bags, CMR monitoring, age or stage matrix models): (Sáaez-Royuela and Telleriia 1986; Keuling et al. 2013; Massei et al. 2015). For this species, it might be interesting to compare age-at-death estimates and individual long-term monitoring.
The Arctic fox (*Vulpes lagopus*, Linnaeus 1758) is a mammalian species for which little demographic information exists (Tannerfeldt and Angerbjörn 1996; Meijer, Norén, and Angerbjörn 2011). The analysis of the teeth of this species allows the determination of variations in their feeding ecology in addition to age (Ungar et al. 2021). With the approach of this thesis, it would be possible

to link ecological variations and vital rates of threatened Arctic fox populations.

Crocodilians are an order of sauropsids for which little information is available on population trends. They may be sensitive to pressures such as mercury contamination. The few demographic studies focus mainly on the Mississippi alligator (*Alligator mississippiensis*, Daudin 1802; D. Taylor and Neal 1984). Age is approximated by body size (Hutton 1986; Eaton and Link 2011). Although it appears that age-based matrix models do not necessarily capture the effect of factors on populations for crocodilians, it may be of interest to provide baseline estimates of survival rates.

Some species are important to indigenous human populations. The S'ami people depended on the presence of reindeer (*Rangifer tarandus*, Linnaeus 1758), which they partially domesticated. This is no longer the case, but there is still a strong link between this people and the presence of reindeer in the Arctic. Other peoples such as the Inuit still hunt reindeer. This species seems to be impacted by climate change: (Heggberget, Gaare, and Ball 2002; Moen 2008). Recent progress has made it possible to determine the age at death of this species (Van den Berg, Loonen, and Çakırlar 2021). It could be interesting to link the survival of this species to variations in the environment and food resources in order to better understand its dynamics and to favour the conservation of the culture of certain indigenous peoples.

Arctic fox © Marco Gaiotti.

7.4 Conclusion and perspectives

This thesis project has provided a new and more flexible approach to survival modelling based on linear regression. This approach allowed the inclusion of covariates and random effects. It seems appropriate to model the survival of elusive species taking into account covariates and random effects. This project allowed a new assessment of the common dolphin population in the Bay of Biscay to be conducted. The stratified random sampling developed in the demographic study allowed a better representation of the stranded population and avoided potential selection biases that could affect the survival estimate. The survival modelling approach developed in the project allowed the variation in vital rates over time to be modelled. It also highlighted the effect of bycatch or sex. The associated population projections showed that the viability of the population has potentially deteriorated over the time period considered. The viability of the population appears to be strongly threatened by bycatch as an external mortality force. The multilevel regression with post-stratification approach adapted to estimate bycatches allowed for the first time to use an on-board observer dataset despite its known biases. It also provided an estimate of bycatch and associated parameters at a spatial and temporal scale never achieved before for common dolphins in the Bay of Biscay. Ultimately, the management strategy evaluation approach allows the combination of demographic and bycatch estimates to define sustainable removal limits for the Bay of Biscay common dolphin population. This is primarily a feasibility exercise as the study area considered does not take into account the entire management unit currently recognised for the common dolphin. This approach is the first to take into account several types of data specific to this population in order to define management strategies with regard to the conservation objective proposed by OMMEG in European waters.

This work is important from both a fundamental and an applied point of view. Elusive species are defined in this project as species that may have one or more of the following characteristics: difficult to monitor individually, sparsely distributed, difficult to estimate anthropogenic mortality and difficult to implement management policies. The demographic approach developed in this project is an interesting contribution to the literature on these species. It addresses some of the issues inherent to cross-sectional monitoring and analyses. It shows that the sampling of individuals is important to minimise bias in the estimation of vital rates. It provides a method for estimating vital rates that allows the effect of different variables on vital rates to be estimated. It could be very interesting to apply this modelling approach to other elusive species such as the harbour porpoises in the North-East Atlantic. This population presents major conservation challenges. The number of strandings seems to be sufficient for stratified random sampling. We also have long time series that would allow us to test for variation in vital rates over time. The covariates to be tested are also multiple. We have data on contamination by pollutants. We also have strandings in several management units, which would allow us to highlight differences in viability between populations.

The work carried out in this project is mainly associated with the Bay of Biscay. However, the current management unit of the common dolphin is much larger and includes a large part of European Atlantic waters. It is difficult to generalise the demographic results and removal thresholds obtained in this project to the whole management unit. It might be interesting to apply the project's approach using further data covering more of the European coastline. But for the time being, the demographic estimates produced can directly feed into the MSFD. It would even be possible and interesting to revise the classification of demographic indicators within the framework of the MSFD. The work carried out could provide an operational indicator that would make it possible to highlight an alteration in viability before it is translated into a depletion that could be detected by abundance surveys.

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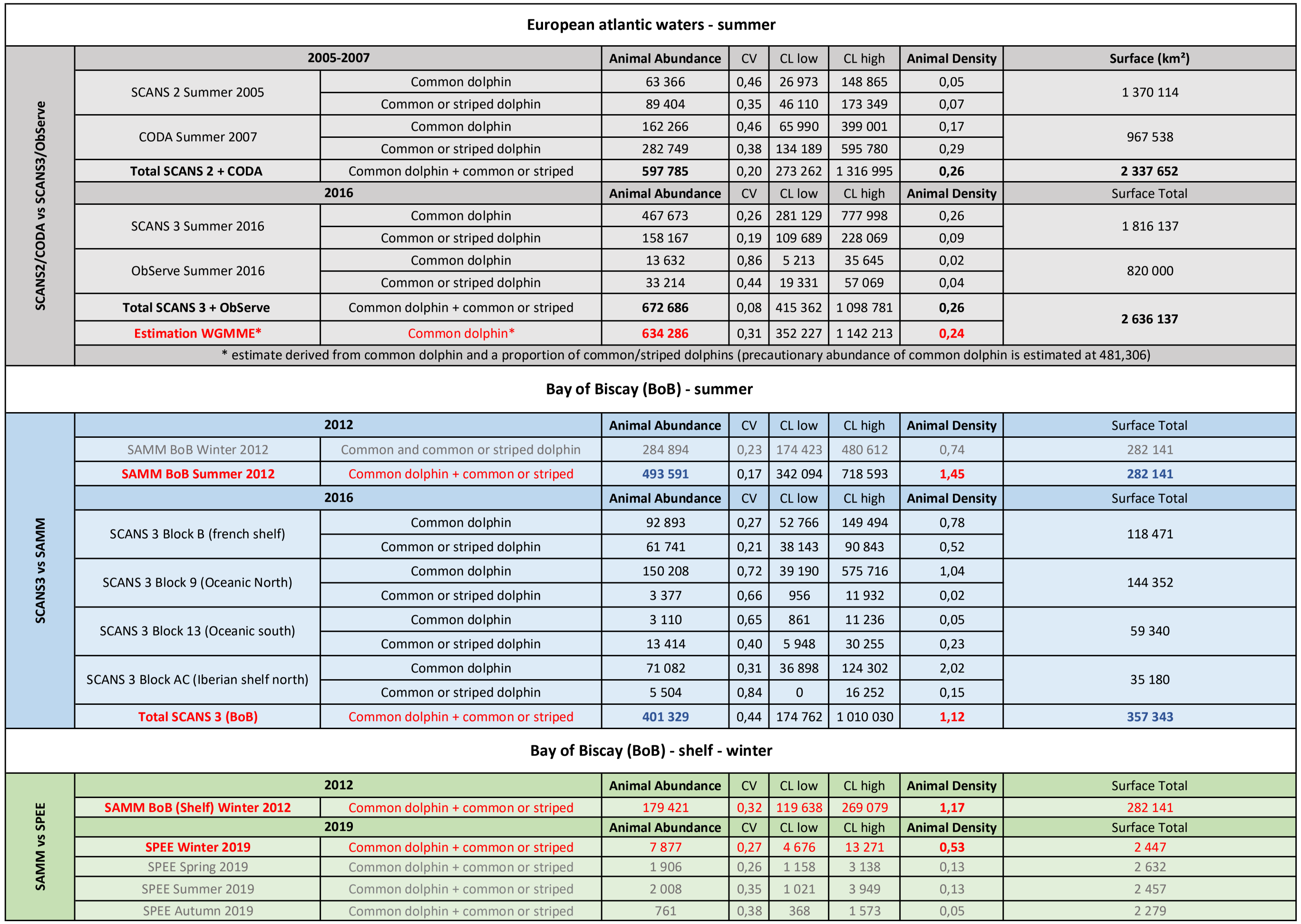
APPENDIX

Appendix 1: Abundance estimates and MSFD Marine regions



European atlantic waters - summer								
SCANS2/CODA vs SCANS3/ObServe	2005-2007		Animal Abundance	CV	CL low	CL high	Animal Density	Surface (km²)
	SCANS 2 Summer 2005	Common dolphin	63 366	0,46	26 973	148 865	0,05	1 370 114
		Common or striped dolphin	89 404	0,35	46 110	173 349	0,07	
	CODA Summer 2007	Common dolphin	162 266	0,46	65 990	399 001	0,17	967 538
		Common or striped dolphin	282 749	0,38	134 189	595 780	0,29	
	Total SCANS 2 + CODA	Common dolphin + common or striped	**597 785**	0,20	273 262	1 316 995	**0,26**	**2 337 652**
	2016		Animal Abundance	CV	CL low	CL high	Animal Density	Surface Total
	SCANS 3 Summer 2016	Common dolphin	467 673	0,26	281 129	777 998	0,26	1 816 137
		Common or striped dolphin	158 167	0,19	109 689	228 069	0,09	
	ObServe Summer 2016	Common dolphin	13 632	0,86	5 213	35 645	0,02	820 000
		Common or striped dolphin	33 214	0,44	19 331	57 069	0,04	
	Total SCANS 3 + ObServe	Common dolphin + common or striped	**672 686**	0,08	415 362	1 098 781	**0,26**	**2 636 137**
	Estimation WGMME*	Common dolphin*	**634 286**	0,31	352 227	1 142 213	**0,24**	
	* estimate derived from common dolphin and a proportion of common/striped dolphins (precautionary abundance of common dolphin is estimated at 481,306)							
Bay of Biscay (BoB) - summer								
SCANS3 vs SAMM	2012		Animal Abundance	CV	CL low	CL high	Animal Density	Surface Total
	SAMM BoB Winter 2012	Common and common or striped dolphin	284 894	0,23	174 423	480 612	0,74	282 141
	SAMM BoB Summer 2012	Common dolphin + common or striped	**493 591**	0,17	342 094	718 593	**1,45**	**282 141**
	2016		Animal Abundance	CV	CL low	CL high	Animal Density	Surface Total
	SCANS 3 Block B (french shelf)	Common dolphin	92 893	0,27	52 766	149 494	0,78	118 471
		Common or striped dolphin	61 741	0,21	38 143	90 843	0,52	
	SCANS 3 Block 9 (Oceanic North)	Common dolphin	150 208	0,72	39 190	575 716	1,04	144 352
		Common or striped dolphin	3 377	0,66	956	11 932	0,02	
	SCANS 3 Block 13 (Oceanic south)	Common dolphin	3 110	0,65	861	11 236	0,05	59 340
		Common or striped dolphin	13 414	0,40	5 948	30 255	0,23	
	SCANS 3 Block AC (Iberian shelf north)	Common dolphin	71 082	0,31	36 898	124 302	2,02	35 180
		Common or striped dolphin	5 504	0,84	0	16 252	0,15	
	Total SCANS 3 (BoB)	Common dolphin + common or striped	**401 329**	0,44	174 762	1 010 030	**1,12**	**357 343**
Bay of Biscay (BoB) - shelf - winter								
SAMM vs SPEE	2012		Animal Abundance	CV	CL low	CL high	Animal Density	Surface Total
	SAMM BoB (Shelf) Winter 2012	Common dolphin + common or striped	179 421	0,32	119 638	269 079	**1,17**	282 141
	2019		Animal Abundance	CV	CL low	CL high	Animal Density	Surface Total
	SPEE Winter 2019	Common dolphin + common or striped	7 877	0,27	4 676	13 271	**0,53**	2 447
	SPEE Spring 2019	Common dolphin + common or striped	1 906	0,26	1 158	3 138	0,13	2 632
	SPEE Summer 2019	Common dolphin + common or striped	2 008	0,35	1 021	3 949	0,13	2 457
	SPEE Autumn 2019	Common dolphin + common or striped	761	0,38	368	1 573	0,05	2 279

Figure 1: Estimated abundances of common dolphin and stripped dolphin for the SCANS II, CODA, SAMM and SCANS III surveys. Abundances are provided by survey cruise, by block and by species. Table formatted by Olivier Van Canneyt, Observatoire Pelagis.

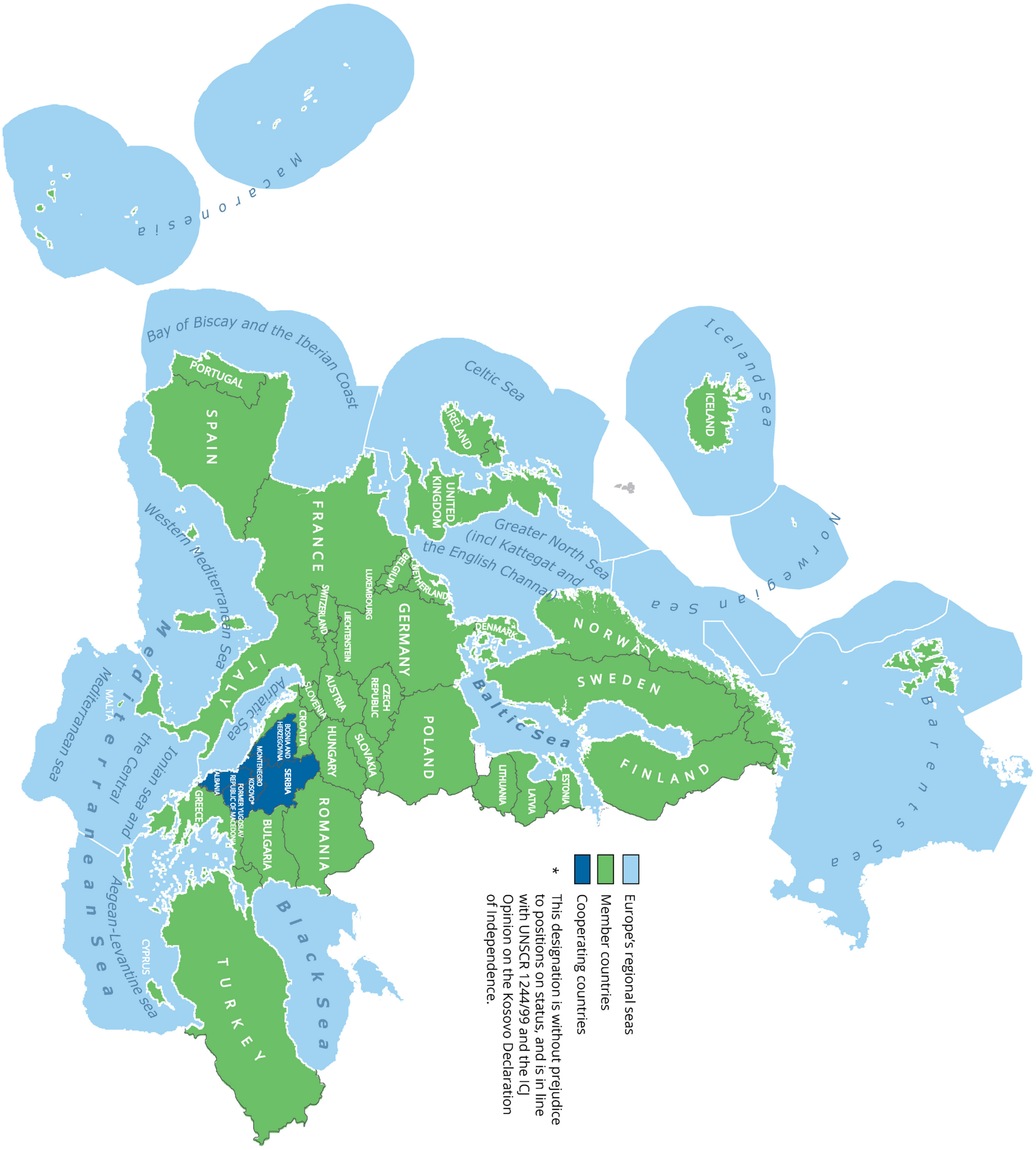


Figure 2: Marine regions as identified by the European Marine Strategy Framework Directive. Figure from `http://www.eea.europa.eu/about-us/countries-and-eionet/marine-regions`.

Appendix 2: Flexible regression approach simulation study

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ORIGINAL ARTICLE

Flexible parametric modeling of survival from age at death data: A mixed linear regression framework

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Abstract

Many long-lived vertebrate species are under threat in the Anthropocene, but their conservation is hampered by a lack of demographic information to assess population long-term viability. When longitudinal studies (e.g., Capture-Mark-Recapture design) are not feasible, the only available data may be cross-sectional, for example, stranding for marine mammals. Survival analysis deals with age at death (i.e., time to event) data and allows to estimate survivorship and hazard rates assuming that the cross-sectional sample is representative. Accommodating a bathtub-shaped hazard, as expected in wild populations, was historically difficult and required specific models. We identified a simple linear regression model with individual frailty that can fit a bathtub-shaped hazard, take into account covariates, allow goodness-of-fit assessments and give accurate estimates of survivorship in realistic settings. We first conducted a Monte Carlo study and simulated age at death data to assess the accuracy of estimates with respect to sample size. Secondly, we applied this framework on a handful of case studies from published studies on marine mammals, a group with many threatened and data-deficient species. We found that our framework is flexible and accurate to estimate survivorship with a sample size of 300. This approach is promising for obtaining important demographic information on data-poor species.

KEYWORDS

age at death, Monte Carlo study, regression, survival analysis, survivorship

1 | INTRODUCTION

The protection and conservation of wildlife is a salient challenge in the Anthropocene, where human-induced pressures are both far-reaching in their geographic and temporal scope, and acute in their impact on biodiversity (Bongaarts, 2019). Long-lived species are particularly sensitive to these pressures: they can act as sentinel species for whole ecosystems (Heithaus, Frid, Wirsing, & Worm, 2008). Their demographic trajectory (e.g., extinction) can also affect the functioning of ecosystems, especially in the case of top predators (Beschta & Ripple, 2009; Ritchie et al., 2012). Assessing the demographic viability of long-lived species in the face of current and future pressures is required for their proactive conservation; but such an endeavor may be hampered in practice because of logistical challenges in monitoring and collecting relevant data at the relevant spatiotemporal scales.

The classical way to assess a populations viability is to first construct a static life-table where mortality and fecundity rates for a cohort of individuals are tallied at each age/stage of their life cycle (Caughley, 1966). Knowledge of mortality at each age/stage allows to investigate the associated hazards, estimate vital rates, such as (cumulative) survival; and to project the population trajectory forward in time using matrix models (Caswell, 2001; Leslie, 1945). Historically, the age at death data used to construct life-tables were cross-sectional (e.g., Gompertz, 1825): a sample of the population is taken at a specific time and the observed age structure is assumed similar to that of a cohort of individuals had we been able to monitor them from birth to death. This cross-sectional design allows for a rapid demographic assessment (Boyd, Bowen, & Iverson, 2010; Margules & Austin, 1990, pp. 126–127.) whose accuracy however hinges on the assumption that the cross-sectional design approximates well a longitudinal one.

Longitudinal designs, whereby an individual is monitored from birth to death are, in wildlife ecology, a byproduct of capture-recapture studies. The initial motivation for the latter was the accurate estimation of abundance in open populations when detectability is less than perfect (Cormack, 1964; Jolly, 1965; Seber, 1965). Models (e.g., the Cormack-Jolly-Seber model) tailored for these life history data can provide accurate estimates of survival that can be fed into matrix population models (e.g., Fujiwara & Caswell, 2001). Since the 1980s, the emphasis of capture-recapture studies in wildlife ecology shifted from abundance to survival estimation (Lebreton, Burnham, Clobert, & Anderson, 1992) and the inclusion of individual-level covariates, which paved the way for a better understanding of evolution and natural selection in the wild (Cam, 2009). Concomitant with this change in focus was the less frequent reporting of life-tables in publications, an omission partly mitigated by the rise of open online databases such as COMADRE/COMPADRE (Salguero-Gómez et al., 2015; Salguero-Gómez et al., 2016). From an applied perspective in conservation, the obvious drawback of capture-recapture studies is the time and manpower required to collect data, especially for long-lived species. White, Nagy, and Gruber (2014) recently proposed a new development that aims to avoid birth to death monitor. From both juvenile mortality and fecundity, it is possible to infer adult mortality. However, it requires monitoring the juvenile part of the whole population in order to model the overall population dynamics. The mismatch between the necessary delay in data acquisition and the urgency of mitigation on conservation decisions can be acute, suggesting interest for cross-sectional data that have the additional benefit of being applicable on species where the identification of individuals is difficult (Williams, Nichols, & Conroy, 2002). One alternative to species identification, for vital rates estimation, is the use of count data. This approach may involves the building of an N-mixture model relying on the individual-state knowledge. Zipkin et al. (2014) proposed a development that allows taking into account data even if the individual stage is unknown. Another way to obtain vital rates with count data, as time-series, is to conduct an inverse modeling approach: this method also presents the advantage to consider individual-level state data (González, Martorell, & Bolker, 2016). Even if these approaches are promising for hard to monitor species, they remain difficult to apply on some species, especially very mobile ones.

Assuming that cross-sectional data on age at death are available and representative, conservationists now face some further choices, such as non-parametric (e.g., Kaplan–Meier survivorship curves; Clark, Bradburn, Love, & Altman, 2003; Kaplan & Meier, 1958) versus parametric modeling. The latter presents the advantage to provide smoothing and to summarize the data in a handful of parameters. This is small sample attractive: non-parametric approaches such as the Kaplan–Meier estimators (also known as Product Limit Estimators) for survivorship is piecewise constant with discontinuities at the time of death of individuals in the sample. While assumption-lean, this estimator may yield from small samples rough survivorship curves shaped like staircases that can be difficult to compare. Even with little sample size (i.e., few age at death data regarding the overall time series length), parametric modeling aims to estimate smooth survivorship and allow the statistical comparison of parameters values (Kleinbaum & Klein, 2010). It is important to notice that the estimation hinges on the correct specification of the underlying model. More realistically, the challenge is to find a parsimonious model that will nevertheless accommodate the available data without shoehorning the analysis into a convenient, but not necessarily realistic, template. For long-lived animal species, a realistic model should provide the so-called bathtub-shaped curve whereby there is a high juvenile mortality, followed by a lower and rather constant adult mortality and, finally, a late increase due to senescence (Choquet, Viallefont, Rouan, Gaanoun, & Gaillard, 2011; Siler, 1979). Although there are models to accommodate this bathtub pattern (Heligman & Pollard, 1980; Siler, 1979), they can be difficult to fit (but see Saavedra, 2018), their goodness of fit can be hard to measure; and they usually do not allow for the inclusion of individual-level covariates such as sex.

Our aims are to investigate a parametric approach for the construction of life-tables in a data-poor context, with long-lived vertebrate species in mind. We will first present a simple regression modeling framework for the analysis of age at death data (with or without right-censoring) that can accommodate mortality patterns such as constant, increasing/decreasing, unimodal or bathtub-shaped. Importantly, this framework allows the seamless inclusion of individual-level covariates. We then conduct a Monte Carlo simulation study with five biological scenarios to assess our framework, focusing on the accurate estimation of survivorship and mortality. Finally, we illustrate our methodology on a handful of real case studies, with a focus on marine mammals. This group includes many elusive and long-lived species that are threatened (Avila, Kaschner, & Dormann, 2018), data-deficient (Parsons, 2016) and difficult to study with a longitudinal approach. The most common age at death data for marine mammals are obtained from strandings (i.e., cross-sectional monitoring) which may be associated to selection biases. However, stranding samples are a source of age data from which it is possible to obtain vital rates.

2 | MATERIALS AND METHODS

2.1 | Definitions

Survival analysis deals with the analysis of the timing of death (Clark et al., 2003; Kaplan & Meier, 1958; Lesaffre & Lawson, 2012; Tanner & Wong, 1984). We assume data $y \geq 0$ to be time-to-event data, for example longevity, survival time or age at death data. Such data can be collected from stranding of animals (that is marine animals that are washed ashore), or any recovery of dead specimens (e.g., *Lepus europaeus*, Pallas 1778; *Ovis dalli*, Nelson 1884) when aging is possible (e.g., from teeth growth layers). Let the index i denotes the i^{th} individual, and N the sample size. The equation $y_i \sim \mathcal{D}(\theta)$ reads as datum y_i follows statistical distribution $\mathcal{D}$ of parameters θ and with probability density function $f(y;\theta)$ and cumulative density function $F(y;\theta) = \Pr(y \leq t) = \int_0^t f(y;\theta)\mathrm{d}y$.

The survival function $S(t;\theta)$ gives the probability of being alive at time t, that is $\Pr(y > t) = 1 - \Pr(y \leq t) = 1 - F(y;\theta)$. At the population level, this quantity correspond to the fraction of the population that is still alive at age t, that is cumulative survival or simply survivorship. The hazard rate, or age-specific mortality rate, is the instantaneous probability of dying at time $t + \mathrm{d}t$ given that and individual i has survived until time t.

$$h(t) = \lim_{\mathrm{d}t \to 0} \frac{\Pr(t \leq y_i < t + \mathrm{d}t; y_i > t)}{\mathrm{d}t} \tag{1}$$

With parametric models, the hazard rate can be expressed in terms of the probability density and survivorship functions:

$$h(t;\theta) = \frac{f(t;\theta)}{S(t;\theta)}, \text{with } S(t;\theta) > 0 \tag{2}$$

Estimation of the hazard rate function is the goal of parametric survival analysis (Lesaffre & Lawson, 2012).

2.2 | Data simulation scenarios

We considered five biological scenarios corresponding to different patterns in survivorship and the underlying hazard (Figure 1, see Text S1):

1. A unimodal distribution of age at death corresponding to a unimodal hazard, whereby mortality risk increases in early ages, peaks and decreases in late life.
2. A mixture of two hazards corresponding to either a unimodal (a) or bimodal (b) distribution of age at death.
3. A bathtub-shaped hazard due to individual frailty, that is individual-specific risk of mortality.
4. A bathtub-shaped hazard with an additional bump in early life due, for example, to an additional source of mortality.

Each scenario is associated to survivorship and hazard functions (Figure 1).

2.3 | Statistical analysis of age at death data

We used parametric models $\mathcal{M}$ of age at death data y to estimate hazard and survivorship rates (see Data S1 for model code): the latter are especially of interest to conservationists. We assumed that the exact timing of death is available, but our framework can easily accommodate censoring (that is cases when death is known to have occurred before or after measurement). Our framework consists in modeling the logarithmic transform of y_i in a regression framework (location-scale model):

$$\log y_i = \mu + \sigma \times \varepsilon_i - \frac{Z_i}{\beta} \tag{3}$$

where μ is a location parameter; σ and $\frac{1}{\beta}$ are (positive) scale parameters; and Z_i are independent standard exponential deviates. The parameter $\frac{1}{\beta}$ quantifies individual frailty (Kannisto, 1991; Reed, 2011) or persistent demographic heterogeneity sensu Cam, Aubry, and Authier (2016). The choice of the statistical distribution for the residuals ε_i determines the shape of the underlying hazard rate. We considered three different choices, each corresponding to a model (see Text S2 for the associated survivorship and hazard functions).

- $\mathcal{M}_1$: $\varepsilon_i \sim \mathcal{N}(0,1)$ and $\frac{1}{\beta} = 0$ ($\beta = +\infty$)

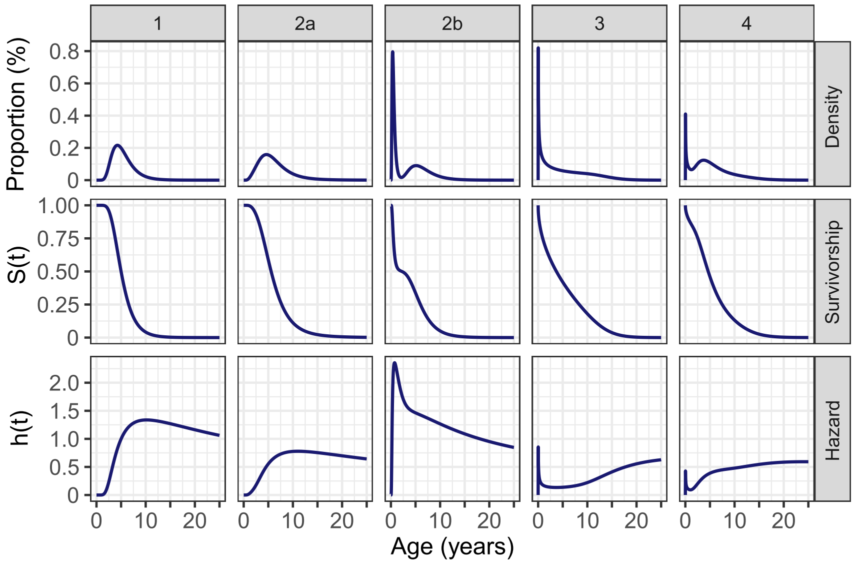

FIGURE 1 The five biological scenarios considered in the Monte Carlo simulation study. Scenario 1 corresponds to a low juvenile mortality, a high adult mortality and no senescence. Scenario 2a corresponds to a low juvenile mortality and a higher adult mortality plateau. Scenario 2b corresponds to a high juvenile mortality and a lower adult mortality that decreases in a linear fashion. Scenario 3 corresponds to a high juvenile mortality, a lower adult mortality and senescence (bathtub shaped hazard). Finally, Scenario 4 corresponds to a high juvenile mortality and a high adult mortality, with a transient dip in mortality risk between these two life-stages

This model assumes a log-normal distribution for y_i, which corresponds to a unimodal hazard curve.

- $\mathcal{M}_2$: $\varepsilon_i \sim \mathcal{G}(0,1)$ and $\frac{1}{\beta} = 0$ ($\beta = +\infty$)

This model assumes a Gumbel distribution for the residuals ε_i, which corresponds to a Weibull distribution for y_i. It is known as the Accelerated Failure Model. The hazard rate is monotonic: it can be constant, increasing or decreasing depending on the value of σ.

- $\mathcal{M}_3$: $\varepsilon_i \sim \mathcal{N}(0,1)$ and $\frac{1}{\beta} > 0$

This choice leads to assume a normal-Laplace distribution for $\log y_i$, which induces a flexible hazard curve depending on the value of β (Reed, 2011). In particular, the hazard can be a bathtub-shaped, as expected for example for long-lived species of vertebrates in the wild (Choquet et al., 2011).

Our framework given by Equation (3) is a flexible location-scale model and boils down to a generalized linear mixed model (GLMM; Bolker et al., 2009) with a handful of parameters $\theta = (\mu, \sigma, \beta)$ to accommodate a large diversity of survivorship and hazard curves (see Text S2 for equations). One attractive feature of this framework is the seamless incorporation of p individual-level covariates x_{ip} in Equation (3) (Reed, 2011):

$$\log y_i = \mu + \sum_{j=1}^{p} \gamma_p x_{ip} + \sigma \times \varepsilon_i - \frac{Z_i}{\beta} \tag{4}$$

An important restriction of our approach is that only time-invariant individual-level covariates can be included. This covers however interesting cases such as sex-differences in survival or differences due to geography (that is comparing different populations of the same species).

2.4 | Monte Carlo study

Our aim is to carry a Monte Carlo study (e.g., Morris, White, & Crowther, 2019) to investigate whether our modeling framework can provide accurate survivorship estimates from age at death data. We considered five biological scenarios to cover a diversity of realistic mortality patterns. For each scenario, we simulated 100 data sets of sample size 100, 200, 300, 400, 500 and 1000 to provide recommendations on the minimum sample size required for accurate estimation. Data simulation was carried out in `R` version 3.6.0 (R Core Team, 2019) using base

TABLE 1 Design of the Monte Carlo study: model $\mathcal{M}_2$ acts as a negative control as it was never used to simulate data, hence it should not be selected as the best model as it is misspecified

Model/scenario	1	2a	2b	3	4
$\mathcal{M}_1$	+	–	–	–	–
$\mathcal{M}_2$	–	–	–	–	–
$\mathcal{M}_3$	–	–	–	+	–

Note: Likewise, scenarios 2a, 2b and 4 corresponds to data generated from mixture models not included in the set: they serve as tests of the performance of our framework to obtain accurate estimates with mispecified models. Finally, scenarios 1 and 3 act as positive control as they correspond to data simulated under models $\mathcal{M}_1$ and $\mathcal{M}_3$, respectively.

functions such as `rnorm` and `rexp`. Each simulated data set was then analyzed with our framework that considered three parametric models. Crucially, we considered scenarios for which the true model was not among the set (Table 1). In other words, we assessed the performance of our framework under the possibility that none of the candidate models is correctly specified with respect to the data at hand. For example $\mathcal{M}_2$ is a Weibull model, which is widely used in survival analysis (Kleinbaum & Klein, 2010) it is biologically unreasonable for marine megafauna and top predators as a model over their entirely lifetime because it cannot accommodate the expected bathtub-shape hazard. Model fitting was done with software Stan version 2.18 (Carpenter et al., 2017) called from `R` via the library `rstan` (Stan Development Team, 2018). Three chains were run with a warm-up of 500 iterations, followed by an additional 1000 iterations. No thinning was performed but the delta parameter of the NUTS algorithm was increased from 0.80 to 0.95 to avoid divergent transitions and the maximum tree depth increased to 15. Parameter convergence was assumed when its $\hat{R}$ statistics was lower than 1.10. Upon convergence, the three chains were pooled to obtain a sample of ≈1000 values from the posterior distribution.

Model fit was assessed with the widely applicable information criterion (WAIC, Gelman, Hwang, & Vehtari, 2014), computed with `R` package `loo` (Vehtari, Gelman, & Gabry, 2017). Survivorship estimates from each model were computed from the posterior distribution of parameters, and visually compared to the true survivorship curve and a non-parametric (Kaplan–Meier) estimate. Because we carried out a simulation study, the true survivorship curve was known and could have been used to compute the root-mean-squared error (RMSE). However, in practice, this is not the case and we chose instead to compute RMSE with respect to the non-parametric Kaplan–Meier survivorship estimates. The latter were thus assumed to represent the best estimates available to researchers, and the aim was to assess whether a parametric model could provide a fit as good as that from a non-parametric approach.

$$\mathrm{RMSE}_{\mathcal{M}} = \sqrt{\mathbb{E}\left[\left(\hat{S}_{KS}(t) - \hat{S}_{\mathcal{M}}(t)\right)^2\right]} \tag{5}$$

where $\hat{S}_{KS}(t)$ is the Kaplan–Meier estimate of survivorship at age t, $\hat{S}_{\mathcal{M}}(t)$ is the corresponding estimate from parametric model $\mathcal{M}$, and the expectation is taken over a sequence of values of t.

In order to assess model selection and model check, it is necessary to determine if the models represent well the data. Conn, Johnson, Williams, Melin, and Hooten (2018) recently reviewed some ways to proceed. We choose to do a prior predictive check to test for adequacy between models and time to event data (Text S3 and Figure S1). We also did a posterior predictive check (Text S3 and Figure S2) to see whereas data simulated through the fitted models are similar to that observed from the Barlow and Hohn (1984) data set. The comparison is done with both the true Kaplan–Meier survivorship curve and the ones from posterior simulated data sets (Text S3).

Our focus was on accurate estimation of survivorship, and thus we assessed goodness-of-fit by comparing the expected mean survivorship under each model to the observed Kaplan–Meier estimates. This focus was in line with downstream use of such estimates in matrix population models: here the salient statistics we want our model to reproduce (Gelman, 2003) is the survivorship function.

Our study design is summarized in Table 1 and Figure 2. It consisted in a comprehensive factorial design crossing (a) sample size (100, 200, 300, 400, 500 and

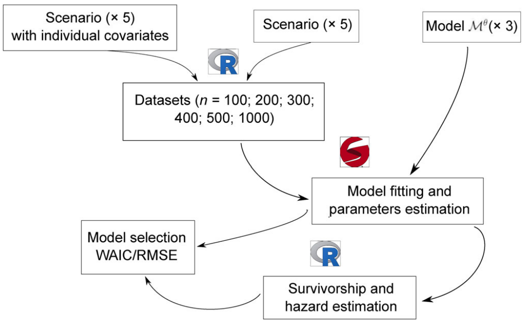

FIGURE 2 Monte Carlo study flowchart. We considered five biological scenarios, six different sample sizes for data, and three models for analysis. For each combination, we assessed model fit and the accuracy of parameter estimates. Model selection is done with Watanabe-Akaike information criterion (WAIC) and root-mean-square error (RMSE) [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Case studies

Data set	Taxon	Species	Sample size	Covariate
Murphy et al. (2012)	Pinniped	Monk seal (*Monachus monachus*, Hermann 1779)	28	Sex
Slooten (1991)	Cetacean	Hector's dolphin (*Cephalorhynchus hectori*, Van Beneden 1881)	60	None
Rodríguez-Caro et al. (2019)	Chelonian	Spur-thighed tortoise	154	None
Murphy et al. (2009)	Cetacean	Common dolphin (*Delphinus delphis*, Linnaeus 1758)	515	None
Kesselring, Viquerat, Brehm, and Siebert (2018)	Cetacean	Harbor porpoise (*Phocoena phocoena*, Linnaeus 1758)	561	Area
Saavedra (2018)	Cetacean	Delphinidae	579	None
Barlow and Hohn (1984)	Cetacean	Pantropical spotted dolphin (*Stenella attenuata*, Gray 1846)	1892	Sex

Note: Data sets were selected based on the availability of published (raw) data, species and sample size.

1000), (b) mortality patterns (five scenarios), (c) parametric models (three models) and (d) individual covariate inclusion. Two covariates (x_1, x_2) were generated by sampling from a Bernoulli distribution with probability 0.5. These covariates could represent for example sex or two sub-populations in different geographic areas.

2.5 | Applications

We analyzed real data sets from published case studies (Table 2) within our framework, and compared the estimated parametric survivorship curves with the nonparametric Kaplan–Meier one. All species in Table 2 are marine mammals except the spur-thighed tortoise (*Testudo graeca*, Mertens 1946) which was included to compare our approach with that of Rodríguez-Caro et al. (2019) in a data-poor context for conservation. It is important to precise that data from Rodríguez-Caro et al. (2019) were obtained from live animals, still alive at the time of measurement (Rodríguez-Caro, Graciá, Anadón, & Gimenez, 2013; Sanz-Aguilar et al., 2011). However, we used these data as if they were age at death data and ignored right-censoring.

3 | RESULTS

Across all scenarios and sample size, parameter convergence (assessed with $\hat{R}$) was not equivalently reached depending on the model and scenario (see Figures S3 and S4a). $\mathcal{M}_1$ always converged very easily. In contrast, $\mathcal{M}_2$ and $\mathcal{M}_3$ were not as good as $\mathcal{M}_1$ to converge with 1000 iterations (500 as warm up). More precisely, convergence for $\mathcal{M}_3$ was difficult for β given this configuration (see Figures S5 to S10). An increased in the number of iterations per chains (here from 1,000 to 2000) solved the problem (Figure 3).

3.1 | Hazard rate estimation

Estimated hazard curves are shown in Figure 4 for each combination of scenario, model and sample size. Models $\mathcal{M}_1$ and $\mathcal{M}_3$ were the best fitting ones in the first and third scenarios respectively (i.e., positive control, Table 1): estimates were accurate and precision increased with sample size. For scenarios 2a, 2b and 4, all estimates were biased, and precision increased with sample size (Figure 3). In contrast, model $\mathcal{M}_2$ never provided accurate hazard estimates (i.e., negative control). The same results were obtained when covariates were included (not shown).

3.2 | Survivorship estimation

Estimated cumulative survival curves are shown in Figure 5 for each combination of scenario, model and sample size. Across all scenarios and sample sizes, estimates from model $\mathcal{M}_3$ were the most accurate (Figure 5, see Text S4 and Figure S11 for RMSE results). Precision increased with sample size. In particular, survivorship rates estimated with $\mathcal{M}_3$ were very close to Kaplan–Meier estimates for sample size $\geq$300. This sampling size also provided a good confidence interval precision with a maximum width of 0.04% while estimating survivorship (Figure S12). Predictive ability, as measured with WAIC, was the greatest for model $\mathcal{M}_3$: it was consistently ranked first across each combination of scenario and sample size,

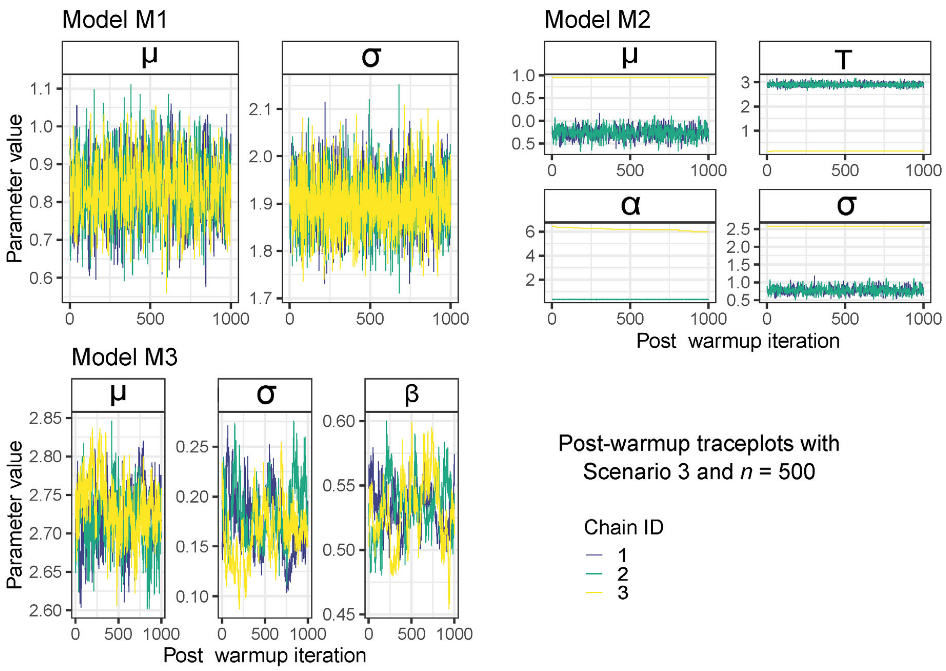

FIGURE 3 Models parameters convergence assessment for each sampling size with n(warm-up) = 1000 iterations and a total of N = 2000 iterations [Color figure can be viewed at wileyonlinelibrary.com]

even for scenario 1 where model $\mathcal{M}_1$ was the true data-generating mechanism (see Text S4 and Figure S13).

3.3 | Covariate effects

Covariate effect estimation is summarized on Figure 6 as a difference between survivorship rates. Model $\mathcal{M}_2$ could not estimate difference in survivorship. Model $\mathcal{M}_1$ is only effective for both scenario 1 and 2a. $\mathcal{M}_3$ could estimate accurately covariate effects when the difference is expressed as an unimodal pattern (i.e., scenario 1, 2a and 3). The precision of the estimated effect increased with sample size for models $\mathcal{M}_1$ and $\mathcal{M}_3$. With small sample size, sign errors on the effect of covariate was possible but disappeared with sample size ≥300.

3.4 | Case studies

Estimated survivorship curves from published data sets are plotted against the Kaplan–Meier curves in Figure 7 for each model. Model $\mathcal{M}_3$ was the most flexible: it provided the most accurate estimates for each data set. Uncertainty, as measured with 80% credible intervals were narrower with model $\mathcal{M}_3$, and overlapped most with Kaplan–Meier estimates. Model $\mathcal{M}_3$ consistently had the lowest WAIC.

In the handful of case studies where covariates were available (Table 2), a similar pattern arose. Including covariate can be expected to account for more variation in the data, and a lower WAIC. For both $\mathcal{M}_1$ and $\mathcal{M}_2$, this was indeed the case. For $\mathcal{M}_3$ it was only true with the Murphy et al., 2012 data set (see Text S4 and Table S1). The estimated covariate effect for both Barlow and Hohn (1984) and Kesselring et al. (2018) case studies is summarized on Figure 8 (see also Text 5). Models $\mathcal{M}_1$ and $\mathcal{M}_3$ both estimated a survivorship difference between each covariate. As it is the case without covariates (Figure 7), the $\mathcal{M}_3$ curve fits the Kaplan–Meier estimate better. However, there is a discrepancy between both, for each covariate. $\mathcal{M}_3$ is able to spot a difference depending on covariate, but is not able to perfectly fit the Kaplan–Meier estimate.

4 | DISCUSSION

We assessed the ability of a simple linear mixed model to estimate hazard and survivorship rates with

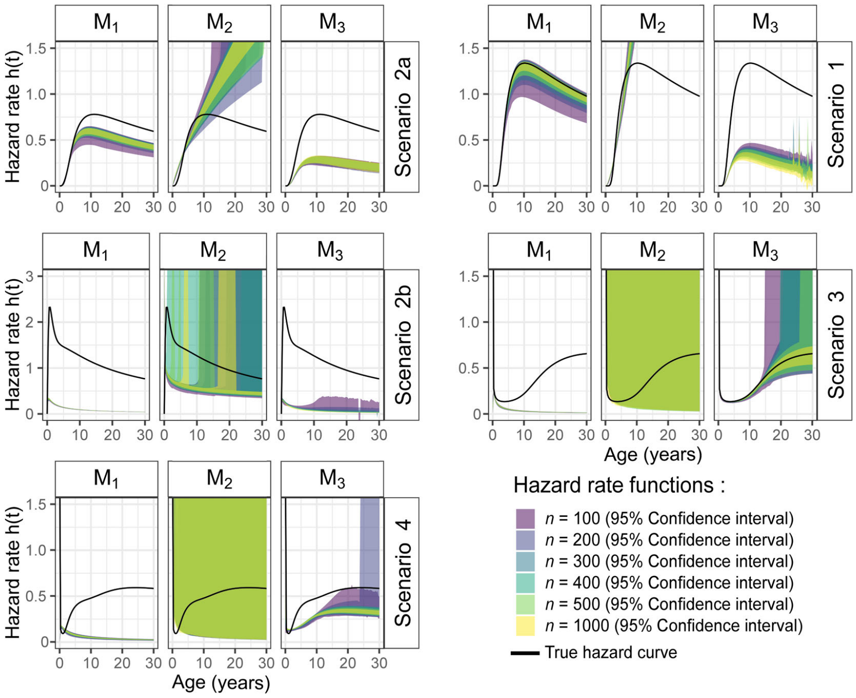

FIGURE 4 Estimated hazard curves confidence intervals for each combination of scenarios (rows), models (columns), and sample size (facets). Estimated confidence intervals are depicted in each panel and compared to the true hazard curves (in black). Even-numbered scenarios (2a, 2b and 4) are on the left, and odd-numbered ones (1 and 3) on the right [Color figure can be viewed at wileyonlinelibrary.com]

cross-sectional age at death data. We used Monte Carlo simulations to investigate the accuracy and precision of estimates across a diversity of mortality patterns and several sample sizes. We contrasted the performance of three different models and found one model, the model $\mathcal{M}_3$; that was consistently better with respect to prediction of survivorship, even when it was misspecified.

4.1 | Age at death data and sampling bias

A crucial but implicit assumption of the cross-sectional approach to survival analysis is that the sample is representative of the larger population, especially with respect to age structure (Caughley, 1966). This assumption is on the data set, not on the modeling. The way of collecting age at death data is therefore determinant to support this assumption. Transerval designs involving, for example, recording of dead carcasses, hunting bags or population census must match the representativity premise. However, it is possible that an implicit process (e.g., bycatch) shapes the observed age frequency (e.g., from stranded animals). In this case, it is necessary to explore some potentials age-dependent selection biases in the population (Barlow & Hohn, 1984). With stranding data, the stationary age distribution assumption needs to be substantiated with auxiliary data, but ultimately, it is likely to remain a working hypothesis on which any cross-sectional method will lean on. In the case of cetaceans, many species are not amenable to study with a longitudinal design, and strandings remain an important source of information (e.g., Murphy et al., 2009), and demographic information in particular (Ferguson, Stirling, & McLoughlin, 2006; Saavedra, 2018). When longitudinal studies are not possible, there are very limited options to obtain demographic information. In some cases, a comparative approach may be possible where information on species with similar life histories can be leveraged (Caswell, Brault, Read, & Smith, 1998; Hashimoto, Shirakihara, Shirakihara, & Hiramatsu, 2013). This choice relies crucially on the assumption of between-species similarity. Even if comparative data are available,

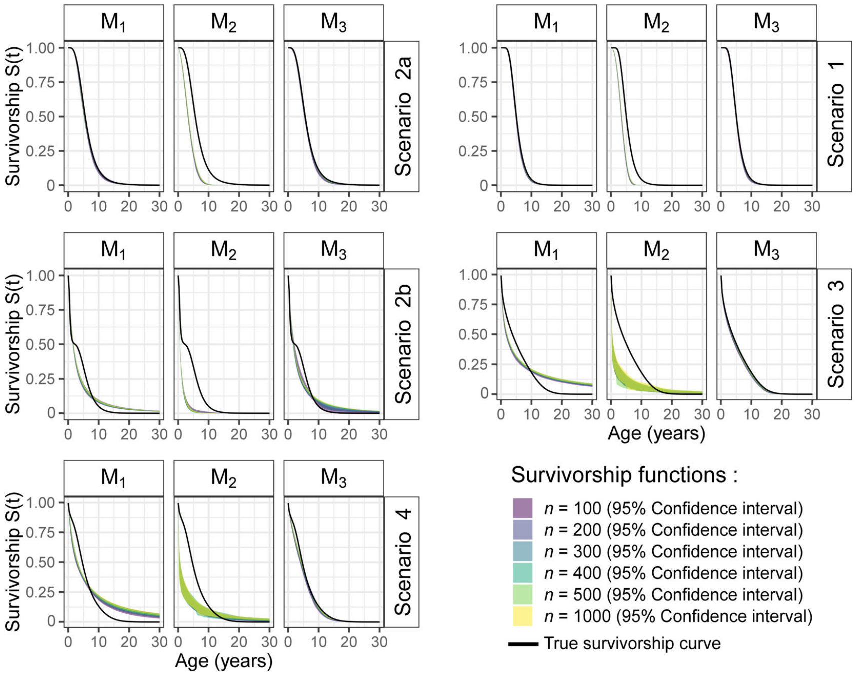

FIGURE 5 Estimated survivorship confidence intervals for each combination of scenarios (rows), models (columns) and sample size (facets). Estimated confidence intervals are depicted in each panel and compared to the truth (in black). Even-numbered scenarios (2a, 2b and 4) are on the left, and odd-numbered ones (1 and 3) on the right [Color figure can be viewed at wileyonlinelibrary.com]

the ecological context may be too different to justify this approach in some instances. Strandings may be the only available source of data, and even if they are suspected to suffer from some selection bias, a pragmatic approach to conservation requires to use them (Boyd et al., 2010), keeping in mind the inherent limitations of these data.

Many conservation instruments specifically requires to use the best available science (e.g., the Marine Strategy Framework Directive EC 2008/56 in Europe). The operative expression "the best available science" may be understood broadly as what lies at the intersection of state-of-the-art methods, good data and accurate knowledge. In practice, there may be a hiatus between the canonical approach that should be, and the pragmatic one that can be pursued at the time conservation actions need to be decided. A conclusion of a species being data-deficient often leads to the doldrums with respect to conservation decisions (Parsons, 2016). Likewise, the many uncertainties that can affect any scientific studies can easily lead to inactions (Ascher, 2004). It is because we are starkly aware of these limitations that we carried out this study to identify a pragmatic approach to estimate survivorship rates from age at death data. Crucially, all the models we used are conditional of the underlying sample being representative of the population it is taken from. Granting this assumption, we identified a simple model from Reed (2011) to obtain accurate estimates.

4.2 | Prediction accuracy and models' goodness of fit

Traditionally, estimating survivorship rates of marine mammals with cross-sectional data was done with parametric models such as the Siler or Heligman-Pollard models (Heligman & Pollard, 1980; Siler, 1979). These models aim at reproducing a bathtub-shaped hazard curve, but need several parameters to do so. Furthermore, they can be difficult to fit although new tools have been developed to use these models (Saavedra, 2018). A remaining challenge with these models is to assess goodness of fit, to incorporate individual-level covariates and perform model selection. The simple parametric form of Reed (2011) for analyzing the logarithm of age at death data provides a bathtub-shaped hazard with a linear mixed model, the current workhorse of ecologists (Bolker

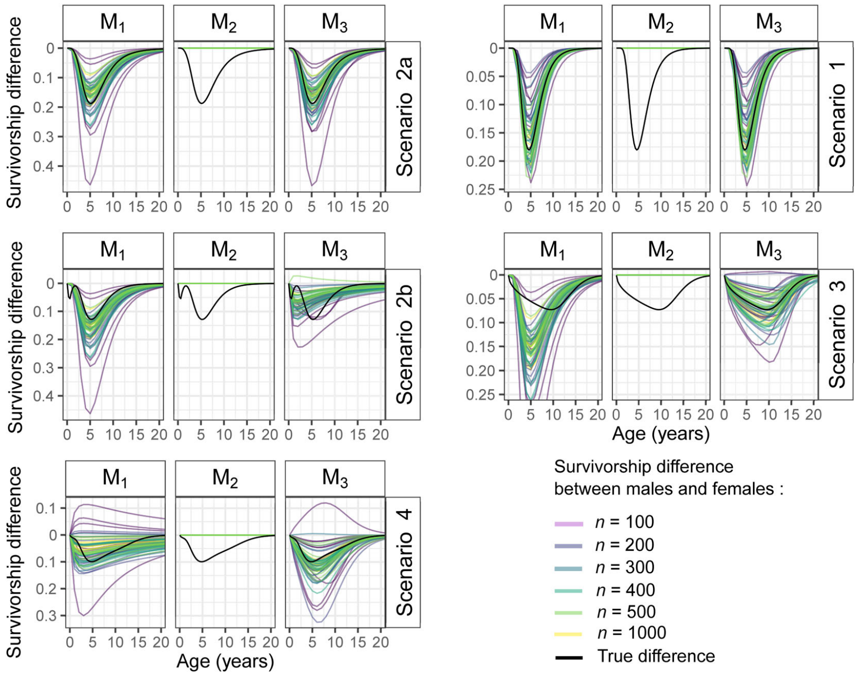

FIGURE 6 Estimated survivorship difference ($(\hat{S}_{\mathcal{M}}(t)|x=1)-(\hat{S}_{\mathcal{M}}(t)|x=0)$) under each scenario. The covariate effect could correspond to that of sex (e.g., $x=1$ for females and $x=0$ for males). Ten estimated difference curves are depicted in each panel and compared with the truth [Color figure can be viewed at wileyonlinelibrary.com]

et al., 2009). This linear mixed modeling framework allows for a seamless incorporation of covariates, and to use standard tools for model selection and goodness-of-fit assessments. In other words, model $\mathcal{M}_3$ brings back survival analysis within the comfort zone of ecologists. We harnessed the simplicity of Reed (2011) to conduct our Monte Carlo study, and found that the model suggested by Reed (2011), our model $\mathcal{M}_3$, was very accurate in predicting survivorship (i.e., it consistently had the lowest RMSE), even in cases when it was not the true model behind the data (see Text S6 to have details about priors). This result is important as it suggests to start building model of increasing complexity from $\mathcal{M}_3$ and use tools such as WAIC (Gelman et al., 2014) to balance model complexity with prediction accuracy.

From our simulations, we can recommend a sample size of at least 300 individuals to obtain accurate and precise estimates of survivorship, from which age-specific survival estimates can be derived (see Figure S14 for parameters estimates). This sample size recommendation is practical and realistic (e.g.. Kesselring et al., 2018; Mannocci et al., 2012; Murphy et al., 2009). This recommendation is mostly to obtain precise estimates, but may be relaxed in some cases where only sparse data may be available (data-poor context hereafter). Estimates from a simple linear model with an individual frailty term, were accurate, if imprecise, with a sample size as small as 100. The possibility to use sparse data is critical as it can help conservation of marine mammals, many of which being classified as data-deficient (Parsons, 2016; Schipper et al., 2008). Some of the cases studies presented in this paper support this statement, although, with so few data, including covariates in the model will be difficult or will require great care (see, e.g., Cox, Authier, Orgeret, Weimerskirch, and Guinet (2020)). Rodríguez-Caro et al. (2019) recently provided an approach to estimate survival in data-poor settings using inverse modeling, also to obtain accurate estimates of demographic rates. With the latter, population matrix models can then be used to assess population dynamics and the fate of populations over time (Caswell, 2001).

5 | HAZARD AND FRAILTY

A linear mixed model can fit age at death data very well: this ability comes for the individual frailty term, which

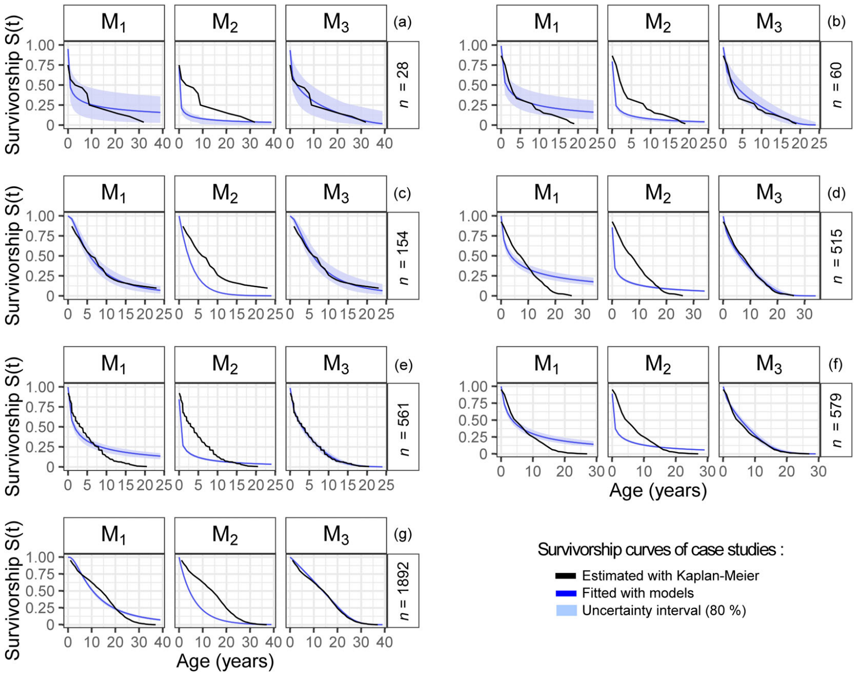

FIGURE 7 Survivorship curves estimated from published data sets. Each subpanel corresponds to a case studies in Table 2. Data set size is represented horizontally. Panels are associated to the following data sets: (a) Murphy et al., (2012); (b) Slooten, (1991); (c) Rodriguez-Caro et al., (2019); (d) Murphy et al., (2009); (e) Kesserling et al., (2018); (f) Saavedra, (2018); (g) Barlow and Hohn, (1984) [Color figure can be viewed at wileyonlinelibrary.com]

corresponds to an individual random effect in the mixed modeling framework. Individual frailty in statistical models translate the empirical observation that two similar individuals (with respect to observable features of their phenotypes) can nevertheless differ markedly in their longevity (Cam et al., 2016; Kannisto, 1991). The parametric form (i.e., exponential) for individual frailty gives extra flexibility to the model, and can accommodate a bathtub-shaped hazard curve (Reed, 2011). However, in our simulations, we found that estimating hazard rates was more difficult than estimating survivorship rates (Figures 3 and 4). Thus, even though we identified a model ($\mathcal{M}_3$) for reliable and accurate estimation of survivorship, the same model was less reliable with respect to hazard. In other words, the individual frailty term in our model $\mathcal{M}_3$ should not be over-interpreted, and is probably best seen as a statistical device for robust estimation. Hazard estimation is a difficult statistical problem (Watson & Leadbetter, 1964), for which there are better tools available, especially non-parametric ones (see, e.g., Hanson & Jara, 2013), than the simple parametric approach we considered in this study. Non-parametric approaches to infer the shape of the hazard curve are data-hungry: Hanson and Jara (2013) using Bayesian non-parametric, which is better described as a model with a massive number of parameters (Hoff, 2013). The traditional Kaplan–Meier approach is truly a non-parametric approach but it does not give access to the underlying hazard, and give rough (i.e., non-smooth; Figure 5) survivorship rates with small sample size. In data-poor settings, parametric modeling remains attractive because it has interpretable parameters (e.g., individual frailty) and because these parameters can smooth out noise in data, yielding more precise estimates if the model is at least approximately correct, or more pragmatically, if it is grounded in theory (e.g., bathtub-shaped hazard for natural populations) and cannot be rejected from a goodness-of-fit test. It is precisely in this data-poor setting that we envision our parametric modeling approach to be most useful. Because the approach boils down to linear mixed effects modeling, great flexibility in model specification of additional random effects (e.g., year effects, sex-specific frailties) is possible provided there are enough data to offset the increase in complexity.

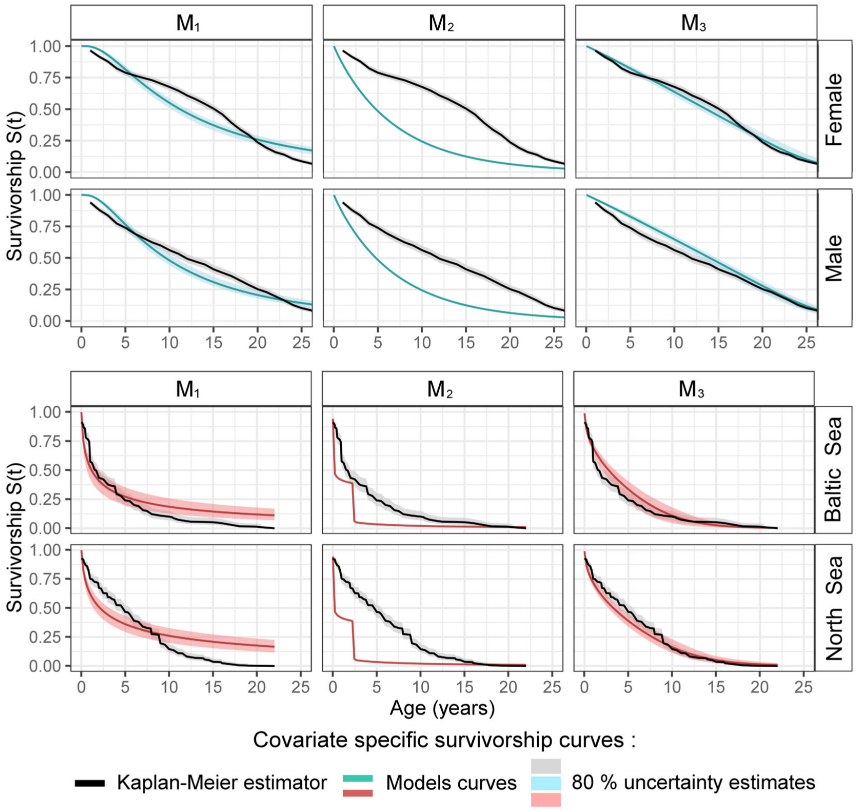

FIGURE 8 Estimated survivorship difference $((\hat{S}_{\mathcal{M}}(t)|x=1)-(\hat{S}_{\mathcal{M}}(t)|x=0))$ for both case studies [Color figure can be viewed at wileyonlinelibrary.com]

6 | BENEFITS AND LIMITS

We believe our approach is very valuable to estimate survivorship from sparse data but may be inadequate for bimodal age at death data distribution. A bimodal distribution of age at death data may be a sign of selection in data collection Barlow & Hohn, 1984. Rather than consider the sampling as biased, our approach can accommodate the selection phenomenon through two ways. Firstly, it is possible to consider the selection bias as a covariate in the study if one such covariate is available (e.g., Bycatch index). If no such covariate is available, it may be possible to build a mixture of two models (e.g., $\mathcal{M}_1$ and $\mathcal{M}_3$) in order to take into account an additional mortality on some age classes. However, such a development requires to conduct its own simulation study which is beyond the scope of this study. Since our approach is based on linear regression, it is straightforward to expand the model (e.g., random year effects, mixtures) while using familiar and well-established methods for model selection (e.g., WAIC) and assessment of model fit (e.g., posterior predictive checks, R^2 statistics). These features are assets, and suggest that our approach is complementary to existing ones (e.g., Heligman & Pollard, 1980; Saavedra, 2018; Siler, 1979) to estimate vital rates in some data-poor species.

7 | CONCLUSION

Survivorship and hazard estimation are the goals of survival analysis but they remain difficult to achieve, even for some long-lived and charismatic vertebrate species such as cetaceans. User-friendly modeling methods are of primary interest to leverage the demographic information available in sparse, but previous, data that field ecologists have collected. We think that our framework can facilitate the difficult statistical problem of survival analysis in data-poor context by providing ecologists with a flexible method to obtain accurate survivorship estimates from age at death data. A simple linear mixed-model can accommodate various mortality patterns without drastically increasing the number of estimated model parameters. All the methods developed to assess fit quality within models can be applied since our framework is based on a mixed linear regression approach. This framework is also very convenient to deal with small sample size. With as few as 100 data points, survivorship may be estimated to conduct exploratory analysis. With 300 data points, survivorship estimates can be precise enough to build life-tables and project populations trajectories taking into account covariates. Covariate inclusion can allow to distinguish different causes of mortality (e.g., pathology, bycatch, collision and so on) and to quantify their respective influence on survival. This is valuable when the studied population is under various pressures as it may allow to identify the most threatening ones, and to design efficient and relevant conservation policies accordingly.

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AUTHOR CONTRIBUTIONS

Matthieu Authier, Vincent Ridoux and Etienne Rouby conceived the ideas; Matthieu Authier and Etienne Rouby chose the methodology; Etienne Rouby carried out the analyses; Etienne Rouby and Matthieu Authier led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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Appendix 3: Insights of the demographic approach

Histology

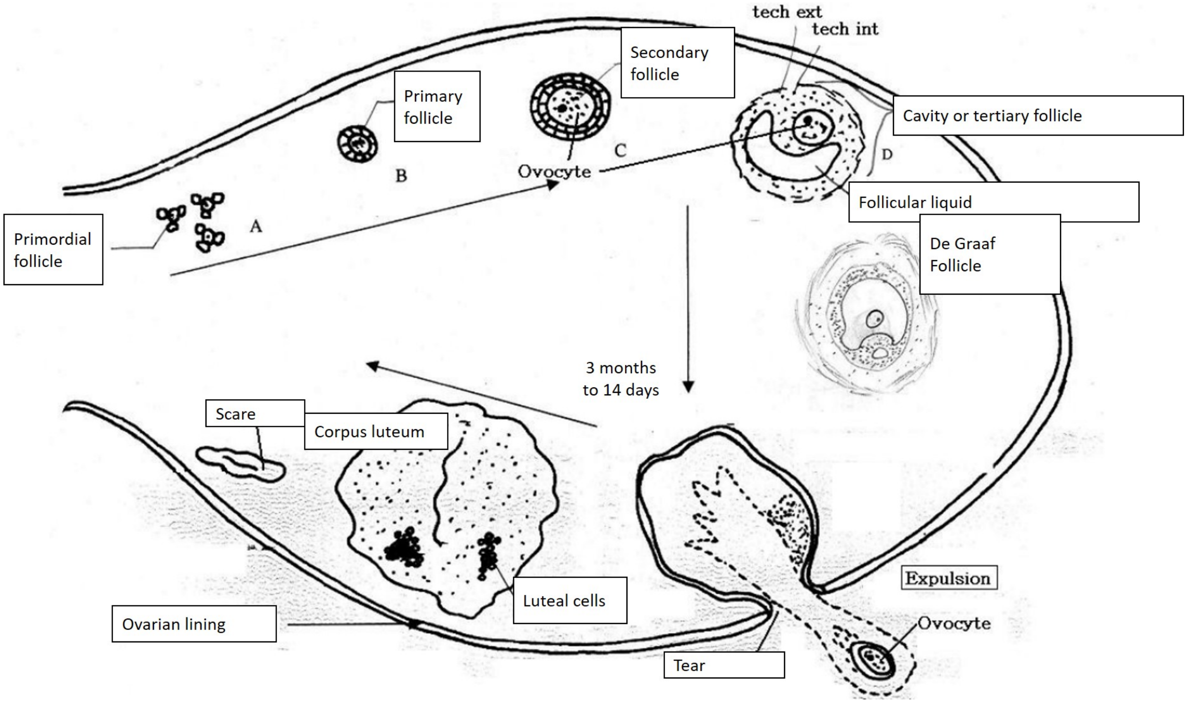

Figure 1: Diagram of the ovulation process with the important stages of the corpuses.

Convergence

To estimate vital rates from from previously acquired data, we built 8 models combining both a survival and a reproduction part. The survival part was built from (Rouby, Ridoux, and Authier 2021) framework and the reproduction component was built from an Accelerated failure time framework. The two components may share a part of the overall variance. Estimation was carried out in a Bayesian framework using programming language `Stan` (Carpenter et al. 2017b) called from `R` v.4.0.1 (R Core Team 2020) with library `Rstan` (Stan Development Team 2020). `Stan` uses Hamiltonian dynamics in Markov chain Monte Carlo (MCMC) to sample values from the joint posterior distribution (Carpenter et al. 2017b). Four chains were initialised from diffuse random starting points and run for a total of $20,000$ iterations, discarding the first $10,000$ as warm-up. Default settings for the No-U-Turn Sampler (NUTS) were changed to 0.90 for `adapt delta` and 15 for `max treedepth` (Hoffman and Gelman 2014).

Siler and Heligman-Pollard

Complementary to the use of this model, we also used the models of Siler (Siler 1979) and Heligman-Pollard (Heligman and Pollard 1980) which are the conventional methods in cross-sectional survival analysis on delphinids (Mannocci et al. 2012; Barlow and Hohn 1984; Stolen and Barlow 2003; Barlow and Boveng 1991; Secchi and Fletcher 2004). The Siler model is a five-parameter model (a_1, b_1, a_2, a_3 and b_3). Siler parameter estimations are realised using the Nelder & Mead optimization function (Nelder and Mead 1965) method and `optim` function of the package `stats` in `R` as detailed in the `strandCet` package (Saavedra 2018). The survivorship $l(x)$ and the total mortality $q(x)$ are expressed as the product of the three competing risks processes:

$$l(x) = l_j(x) \times l_c(x) \times l_s(x) \tag{1}$$

$$q(x) = q_j(x) + q_c(x) + q_s(x) \tag{2}$$

with the exponential decreasing risk due to the juveniles:

$$l_j(x) = exp\left(\left(\frac{-a_1}{b_1}\right) \times \left(1 - exp\left(-b_1 \times x\right)\right)\right) \tag{3}$$

$$q_j(x) = a_1 \times exp(-b_1 \times x) \tag{4}$$

with the constant risk experienced by each age-class:

$$l_c(x) = exp(-a_2 \times x) \tag{5}$$

$$q_c(x) = a_2 \tag{6}$$

with the exponential risk due to senescent ages:

$$l_j(x) = exp\left(\left(\frac{a_3}{b_3}\right) \times \left(1 - exp\left(b_3 \times x\right)\right)\right) \tag{7}$$

$$q_j(x) = a_3 \times exp(b_3 \times x) \tag{8}$$

The Heligman-Pollard model used here is suited to admit cetacean bycatch at age 0 as it is explained in (Saavedra 2018). The mortality function at age x is expressed as it follows:

$$q(x) = A^{(x+B)^c} + \left(I + D \times exp\left(-E\left(ln\left(\frac{x}{F}\right)\right)^2\right)\right) + \frac{GH^x}{(1 + GH^x)} \tag{9}$$

It considers three mortality components: the young mortality curve $A^{(x+B)^c}$, the "accident hump" in adult life (for exemple due to bycatch) $D \times exp\left(-E\left(ln\left(\frac{x}{F}\right)\right)^2\right)$ and the adult mortality curve $\frac{GH^x}{(1+GH^x)}$. The parameter I allows to control the starting point of the mortality curve, making possible to represent bycatch at age 0.

Both Siler and Heligman-Pollard models were computed using the `strandCet` `R` package and are used for comparison with the Reed survival model (Reed 2011). The use of Siler and Heligman-Pollard is more consistent with the literature and acts here as a sensibility analysis on the survival estimation for the common dolphin population.

We applied the Heligman-Pollard model on the dataset used in this study to compute mortality depending on the three life-components detailed in (Heligman and Pollard 1980). By using the methodology developed by (Saavedra 2018), it was possible to take into account a bycatch effect on 0 age-class. The overall mortality curve showed an increasing mortality from 0 to 21 years (figure 2) with a "plateau" from 5 to 8 years. The hump from 0 to 6 is associated to the additional mortality model component whereas the increasing along the lifetime is due to the senescent component of the model.

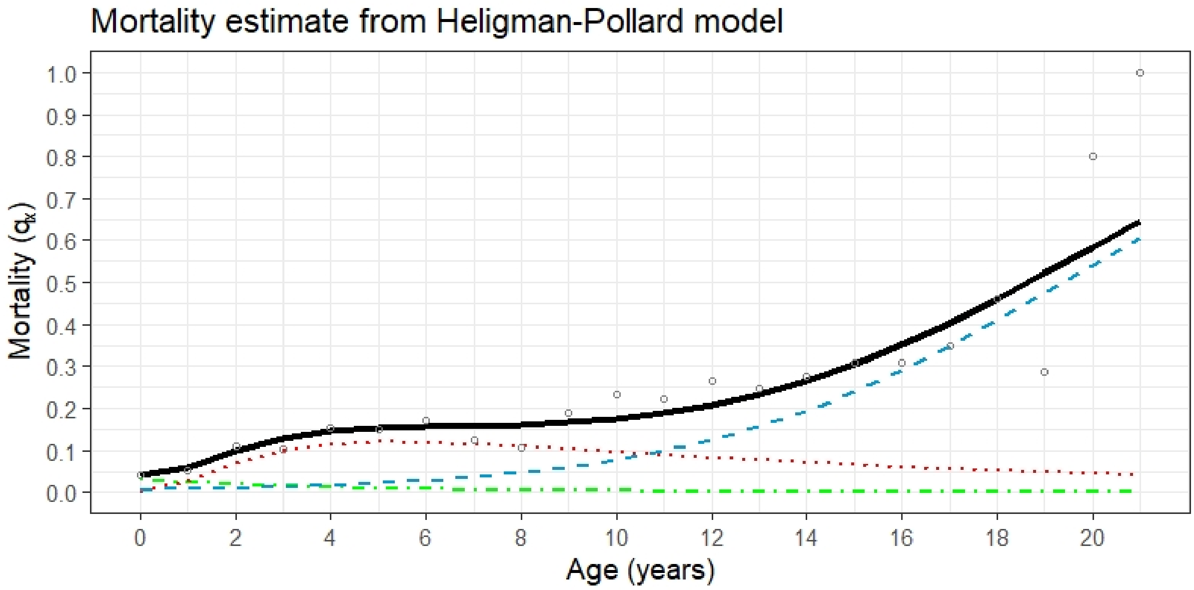

Figure 2: Mortality estimation for each age-class realised with the Heligman-Pollard adaptation from the `StrandCet` package that allows to take into account a bycatch effect on 0 age-class. The black solid line represents overall mortality. The blue dashed line is the mortality part associated with senescent individuals. The green dashed line is the mortality part due to juveniles. The red dotted line corresponds to the additional mortality part on the natural mortality. The white circles corresponds to the observed mortality rates computed with the data.

Logistic regression for Age at Sexual Maturity

To be consistent with the literature, we also used a logistic regression approach to compute the proportion of mature females and the age at sexual maturity (ASM) along the ages (Mannocci et al. 2012; Murphy et al. 2009; Danil and Chivers 2007). The logistic regression was fitted using a generalized linear model approach with the `glm()` function of the package `stats` on `R`. It is also possible to use the `dose.p()` function of the package `MASS` on `R` to determine the ASM using the previously fitted GLM.

Leslie Matrixes

Both Leslie matrixes and elasticities were computed using the `demogR` package on `R`. To compute the matrix, we assumed a female population taking into account the age-specific cumulative survival $l(x)$ (as it is detailed in the package options) and the age-specific fertility rates $f(x)$. The multiplier for fertility equals 1 (since all age-class are of length one) and the `infant.class` parameter is equal to `TRUE` since there are three infant age-class.

Life-tables building

Life-tables are useful tools to explore the demographical strategy of a particular species or of a population during its lifetime. We created North-East common dolphin life-tables on a period-based approach (i.e. vertical life-tables). We built life-tables depending on each modelling approach (*i.e.* simple; with covariate; with year effect). Here we present the basic structure of our life-table approach.

For each age x, several rates are computed. The first rate to be computed is Q_x which is the probability of dying between age x to $x+1$: $Q_x = 1 - (\frac{l_{x+1}}{l_x})$ with l_x as the survivorship rate to age x (probability to reach the age x). From Q_x it is possible to compute D_x which is the number dying in the interval x to $x+1$: $D_x = N_x \times Q_x$ with N_x the number of individuals alive in the middle of the age class x. The number surviving to at least age x, L_x, can be deducted as: $L_x = N_x - D_x$. From L_x we can compute the total number of person-years lived by the cohort from age x until all members of the cohort have died T_x (i.e. the sum of L_x from x onwards): $T_x = \sum_{a=x}^{\infty} L_x$. Finally, it is possible to derive the life expectancy at age x: e_x as $e_x = \frac{T_x}{L_x}$. It is possible to add the age-specific fertility rates obtained with pubescents $f_P(x)$ which are used to build the Leslie-Matrix.

WAIC and LOOIC of models

Table 1: Model selection. Models are ordered in increasing order of **WAIC** (the smaller, the better the fit). se stands for 'standard error'.

Model	Specification	Joint modelling	**WAIC**$_{se}$	**LOOIC**$_{se}$
8	cov + years + trend + cor	Yes	733_{13}	1169_{16}
7	cov + years + trend	Yes	730_{13}	1150_{16}
6	cov + years + cor	Yes	782_{13}	1195_{16}
5	cov + years	Yes	780_{13}	1194_{16}
4	years + cor	Yes	781_{13}	1192_{16}
3	years	Yes	777_{13}	1190_{16}
2	cov	No	922_{14}	1307_{17}
1	simple	No	925_{14}	1318_{17}

Appendix 4: Explain and quantify the incidental captures of common dolphins

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Spatiotemporal models highlight influence of oceanographic conditions on common dolphin bycatch risk in the Bay of Biscay

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ABSTRACT: The population of short-beaked common dolphins *Delphinus delphis* of the Bay of Biscay (northeast Atlantic) has been subjected to potentially dangerous levels of bycatch since the 1990s. As the phenomenon intensifies, it represents a potent threat to the population. Here, we investigated the relationship between bycatch mortality and oceanographic processes. We assumed that oceanographic processes spatiotemporally structure the availability and aggregation of prey, creating areas prone to attract both common dolphins and fish targeted by fisheries. We used 2 datasets from 2012 to 2019: oceanographic data resulting from a circulation model and mortality data inferred from strandings. The latter allows location of mortality areas and quantification of the intensity of mortality events at sea. We fitted a series of spatiotemporal hierarchical Bayesian models using integrated nested Laplace approximations (INLA). Results provided first insights on how bycatch of common dolphins in the Bay of Biscay might be related to key seasonal and dynamic oceanographic features. We showed that from a statistical predictive point of view, the monthly trend of 2019 bycatch mortality could be predicted with few oceanographic covariates. This study highlights how gaining knowledge about environmental influences on interactions between short-beaked common dolphins and fisheries could have great conservation and management value. Identified relationships with oceanographic covariates were complex, as expected given the dynamic aspects of oceanographic processes, dolphins and fisheries distributions. Further research focusing on smaller time scales is needed to elucidate proximal drivers of common dolphin bycatch in the Bay of Biscay.

KEY WORDS: Spatiotemporal modelling · Reverse drift modelling · Prey−predator relationship · Sea surface temperature · Thermal fronts · Eddies

1. INTRODUCTION

Incidental catch, or bycatch (i.e. the undesired catch of nontargeted species in fishing gear), represents the most potent and well-identified threat to small cetaceans' populations (Reeves et al. 2005). Because they are long-lived species, cetaceans cannot sustain high rates of depletion (Lewison et al. 2004, Mannocci et al. 2012). Bycatch has already led populations or species to serious reduction (Reeves et al. 2005, Brownell et al. 2019) or even extinction (Turvey et al. 2007, Brownell et al. 2019), the vaquita porpoise *Phocoena sinus* Norris and MacFarland, 1958 (Norris & MacFarland 1958) being a potentially immi-

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nent example of the latter outcome (D'Agrosa et al. 2000, Jaramillo-Legorreta et al. 2007, 2019).

Short-beaked common dolphins *Delphinus delphis* Linné, 1758 in the Bay of Biscay (northeast Atlantic) have been subjected to potentially dangerous levels of bycatch since the 1990s (see Murphy et al. 2019 for a review). In France, the magnitude of bycatch is evidenced by high numbers of strandings of bycaught dolphin carcasses on the Atlantic seaboard. Mannocci et al. (2012) estimated that with 1000 bycaught individuals per year, the northeast Atlantic population could be reduced by 20% in 30 yr and could become extinct in a hundred. Still, the phenomenon has become more intense in the past decade. Since 2016, the number of strandings has increased every year (http://seamap.env.duke.edu). Bycatch estimates from strandings that occurred solely in the Bay of Biscay have been above what the population of common dolphins of the whole northeast Atlantic can theoretically sustain (Mannocci et al. 2012, Peltier et al. 2016, ICES 2020). From January to April 2019 alone, strandings suggested bycatch levels as high as 9500 individuals (95%CI: [6890; 14 200]) (Dars et al. 2019).

Stranding data can be complementary to data from European observer programs and can provide relevant information on cetacean bycatch (Peltier et al. 2016, IJsseldijk et al. 2020). In France, they have been instrumental to estimate the magnitude of common dolphin bycatch in the Bay of Biscay (Peltier et al. 2016) and to reveal a strong seasonality, with increased mortality in winter months (January to March) (Peltier et al. 2016, 2019, 2020, Dars et al. 2019). From 2016 onward, strandings of animals showing bycatch evidence have risen in summer (July and August), although to a lesser extent than in winter (Dars et al. 2019). Stranding data further made it possible to identify spatiotemporally varying mortality areas (as areas where carcasses of bycaught dolphins were released from fishing boats) through reverse drift modelling of carcasses trajectories (Peltier & Ridoux 2015, Peltier et al. 2016, 2021). In winter months, most bycatch events likely occur in the southern part of the continental shelf and slope (Peltier et al. 2016, 2020), resulting in strandings all along the shore from the south of the Finistère region to the border to Spain, whereas in summer most carcasses strand in southern Finistère (Fig. 1). Finally, the bycatch pattern displays high interannual variability, with different stranding levels and associated bycatch level estimates from year to year (Peltier et al. 2016).

Stranding data further revealed possible association between bycatch events and common dolphin preys. The reverse drift modelling of carcasses allowed the identification of some potentially high-risk fisheries and their caught fish species (Peltier et al. 2020, 2021). The analysis of stomach content of bycaught stranded animals suggested that most dolphins were feeding when death occurred. Moreover, some fish species targeted by common dolphins (e.g. mackerel or sardine) are also included in the diet of predatory fish species of fisheries interest (e.g. hake or seabass) (Spitz et al. 2013). Hence, changes in the local distribution and abundance of prey species might be a substantial driver of the co-occurrence of common dolphins, commercial fish species and fisheries in localized areas.

As marine mobile predators, cetaceans have a dynamic distribution integrating ecological processes across all levels of the trophic web (Croll et al. 1998, Barlow et al. 2020). The proximal relationship between prey and predator could drive the spatiotemporal variability of the bycatch pattern: fish distribution is notoriously variable in both space and time (Hyrenbach et al. 2000) and is governed by many factors ranging from dynamic oceanographic conditions to each species' annual cycle. In this study, we aimed at assessing the influence of oceanographic

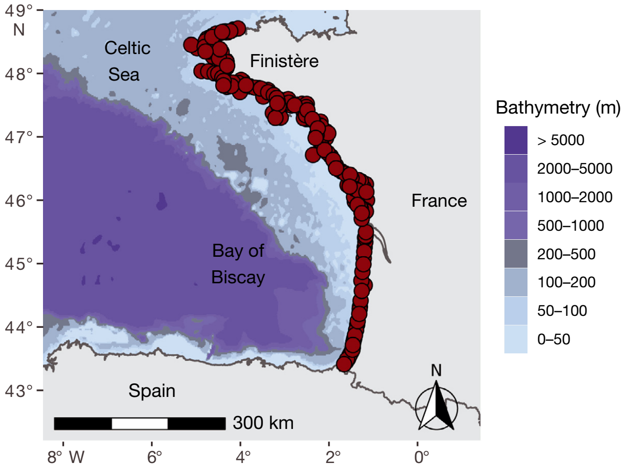

Fig. 1. Study area showing bathymetry and geographic references mentioned in the text, and location of common dolphin stranded carcasses used for the study (red dots)

processes on bycatch of common dolphins in fishing gear. We thus focused on the distal relationship between marine predators and oceanographic processes. We assumed oceanographic processes spatiotemporally structure the availability and aggregation of prey, creating areas prone to attract common dolphins and predatory fish targeted by fisheries and consequently increase the bycatch risk. For instance, meso and submesoscale processes such as fronts (where 2 joined water masses differ by their density), upwelling or eddies enhance the enrichment, concentration and retention of nutrients (Bakun 1996). These processes facilitate the development of trophic networks, from phytoplankton to zooplankton, to fish and finally, to apex predators (Bakun 1996, 2006).

Knowledge of oceanographic conditions is readily available from either remote sensing or modelling. This information is therefore commonly used to make inferences about prey availability and species distribution (Forney 2000, Becker et al. 2010, Best et al. 2012, Stephenson et al. 2020). Oceanographic data have been previously used in the context of bycatch studies, either to identify high risk areas through the association of species distribution modelling and distribution of fishing effort (Žydelis et al. 2011, Murray & Orphanides 2013, Di Tullio et al. 2015, Díaz López et al. 2019) or to identify possible drivers of bycatch events (Gardner et al. 2008, Cosandey-Godin et al. 2015, Hahlbeck et al. 2017, Scales et al. 2018). Cosandey-Godin et al. (2015) suggested the forecasting of high bycatch risk areas to identify mitigation measures. We investigated relations between mortality of common dolphins in fishing gear and oceanographic processes in the Bay of Biscay. Predicting high bycatch areas was beyond the scope of this paper, although it constitutes a promising venue for further investigations.

This work capitalized on 2 sources of data: the bycatch–mortality index inferred from strandings and fine-scaled essential oceanographic variables (EOVs) (García-Barón et al. 2020, Tew-Kai et al. 2020). We selected physical variables significantly contributing to the characterization of the ocean realm (Tew-Kai et al. 2020). We used hierarchical Bayesian models to account for spatiotemporal processes: bycatch mortality areas, oceanographic processes, and common dolphin and fisherie distributions are dynamic in both space and time. The area of study was limited to waters of the Bay of Biscay, with a small part of the Celtic Sea (Fig. 1). After model fitting, we used out-of-sample, 1-step-ahead prediction to predict bycatch mortality in 2019 from oceanographic processes.

2. MATERIALS AND METHODS

2.1. Dolphin mortality index from stranding data

2.1.1. Mortality index

For most bycatch events, no data or location at sea is available. However, some bycatch events are detectable from the stranding of common dolphins presenting bycatch evidence (Kuiken 1994). To determine the origin of carcasses, a reverse drift trajectory can be computed with the drift prediction model MOTHY (Modèle Océanique de Transport d'Hydrocarbure, developed by Météo France; Daniel et al. 2002), integrating drift conditions and characteristics of dolphins' carcasses (see Peltier & Ridoux 2015, Peltier et al. 2012). Reverse drift trajectories of bycaught animals were used to compute a mortality index (MI) to identify probable mortality areas and to quantify the intensity of mortality events at sea in space and time (Fig. 2).

From 2012 to 2019 stranding data, only carcasses presenting bycatch evidence or which stranded during an intense mortality event were selected. Intense mortality events are when more than 30 dolphins strand on 200 km of coastline within 10 d (Peltier et al. 2016). We further selected carcasses with estimated mortality windows up to 15 d (2384 out of 4544, i.e. 52 %). For each carcass, a reverse drift trajectory was calculated with MOTHY, with one point every 10 h. Drift tracks were limited from 0 to 5 or from

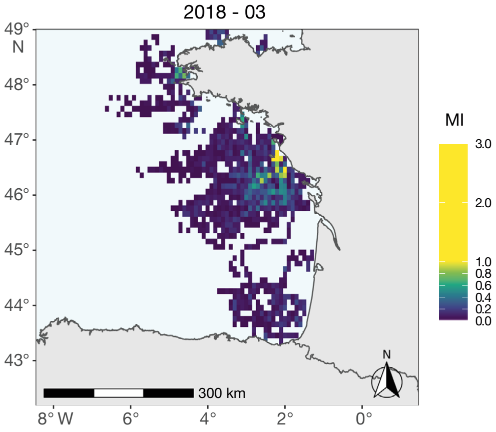

Fig. 2. Spatialized mortality index (MI) for March 2018. MI was computed from reverse drift modelling of stranded carcasses of common dolphins showing bycatch evidence. It allows us to locate potential mortality areas and to quantify the intensity of mortality events

5 to 15 d depending on the mortality window estimated from the decomposition state of the stranded carcasses. The computation of the MI on a daily basis, using a regular grid of 0.1° × 0.1° resolution (i.e. approximately 26 nmiles^2 or 89 km^2) for the Bay of Biscay, assumed an equal probability of bycatch occurring at each drift point. For a day *d*, a grid cell *c* and a carcass *i*, MI was defined as follows:

$$\mathrm{MI}_{d,c,i} = \frac{\text{No. of drift points of } i \text{ in grid cell } c}{\text{Total no. of drift points of } i} \quad (1)$$

The more a carcass stagnates in a grid cell, the higher MI reflects a higher probability that death occurred in that grid cell. For a given cell on a given day, there could be reverse drift points associated with several carcasses. The total MI for *d* and *c* was then:

$$\mathrm{MI}_{d,c} = \sum_{i} \mathrm{MI}_{d,c,i} \quad (2)$$

The greater the number of carcasses that have drifted through a grid cell, the higher its MI. Finally, daily MIs were summed for each grid cell over each month from 2012 to 2019 resulting in the following spatial monthly MI, for month *m* and grid cell *c* (Fig. 2):

$$\mathrm{MI}_{c,m} = \sum_{d \in m} \mathrm{MI}_{d,c} = \sum_{d \in m} \sum_{i} \mathrm{MI}_{d,c,i} \quad (3)$$

The total sum of MI over each month is equal to the number of stranded dolphins included in the dataset. In total, 1789 carcasses stranded all along the shore of the Bay of Biscay (Fig. 1) were used for the present study, with substantial seasonal and inter-annual variations (Fig. 3). Monthly numbers are provided in Supplement 1; www.int-res.com/articles/suppl/m679p195_supp/.

2.1.2. Stranding probability

A wide range of factors lead a carcass to strand, including buoyancy (the carcass must be floating) and drift conditions (wind being one of the main drivers). Consequently, not all carcasses of bycaught common dolphins do strand (Peltier et al. 2016). Drift conditions can sometimes keep carcasses at sea rather than push them to the coast. Buoyancy of carcasses is probably influenced by several parameters (i.e. depth at which death occurred, buoyancy at time of death; Moore et al. 2020) so that they may either sink or float when they are released from fishing boats. The calculated MI thus contained 'false' zeros, associated to grid cells where conditions would not have led to strandings if carcasses happened to drift through them. Conversely, 'true' zeros were associated to grid cells where conditions could have led drifting carcasses to strand. To account for this, we systematically included stranding probability as a covariate in all models. Stranding probabilities were estimated from drifts of simulated dolphin carcasses with MOTHY (Peltier et al. 2013, 2014, 2016). It was calculated over 10 d periods and averaged over each month. A conditional autoregressive (CAR) model was then applied to the result to leverage spatial dependence and smooth estimated probabilities. The spatial resolution of estimated probabilities was larger than that of MI (Fig. 4): each grid cell of the MI grid was matched to its closer neighbour in the stranding probability grid (using R package sf of Pebesma 2018). True zeros should be associated with high stranding probabilities whereas false zeros should be associated with low stranding probabilities.

2.2. Oceanographic data

Monthly EOVs and derived variables were computed from the 3-dimensional HYCOM numerical model of the French Service Hydrographique et Océanographique de la Marine (Shom). Based on the original HYCOM model (Bleck 2002), it was set with a number of numerical developments to optimize the model for coastal zones (Pichon & Correard 2006, Morel et al. 2008, Lahaye et al. 2011) and has already been successfully used over the Bay of Biscay area (e.g. Pichon et al. 2013). Hindcasts were calculated hourly from 1 January 2012 to 31 December 2019 to compute monthly EOVs and derived variables. EOVs are outputs of the model (temperature, salinity, cur-

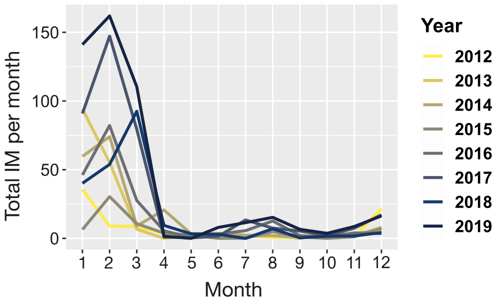

Fig. 3. Evolution of the total mortality index (MI) per month and per year. The monthly sum of spatial MI over the study area is equal to the number of stranded dolphin carcasses for which a reverse drift was calculated, thus giving a mortality signal

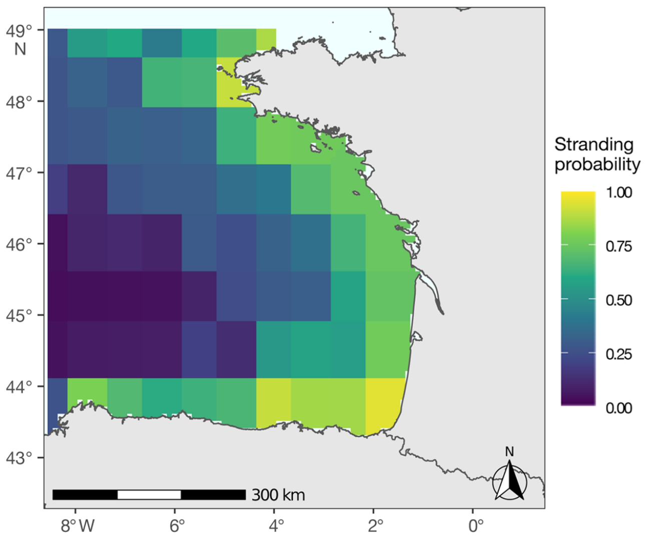

Fig. 4. Stranding probability in March 2018, estimated from simulated drifts of common dolphins, then smoothed with conditional autoregressive (CAR) model to account for spatial dependency between adjacent cells

rent), and derived variables have been calculated from these EOVs. One EOV and 2 derived variables, hereafter referred as oceanographic variables (OVs), were integrated in this study: (1) the sea surface temperature (*sst*), (2) the mean sea surface temperature gradient (*mean_sst_grad*), quantifying the intensity and wideness of thermal fronts, and (3) eddy kinetic energy (*eke*), quantifying the turbulent component of the residual (non-tidal) surface current. *sst* was chosen for its strong seasonal component (Lambert et al. 2017) but also as it is commonly integrated in habitat modelling of multiple marine taxa (Doniol-Valcroze et al. 2007, Mellin et al. 2012, Hughes et al. 2014, Castro et al. 2020). In addition, thermal fronts and eddies have been identified as key structures for the conservation of marine predators (Scales et al. 2014, 2018). Such interfaces might trigger bottom-up processes. As nutrient mixing and retention in the photic zone can boost primary productivity, interfaces like fronts and eddies might attract apex predators through a cascading effect from the lower trophic levels to the highest ones (Bakun 1996, 2006, Scales et al. 2014). This association was observed for several marine predators (Nel et al. 2001, Doniol-Valcroze et al. 2007, Bailey & Thompson, 2010, Miller et al. 2015, Snyder et al. 2017) along with further associations with bycatch events (Hahlbeck et al. 2017, Scales et al. 2018). Moreover, the Bay of Biscay encompasses a shelf area with complex dynamic mesoscale processes following a seasonal cycle (Yelekçi et al. 2017), and we meant to integrate some of these features in our analysis through the dynamic variables *eke* and *mean_sst_grad*.

As the spatial resolution of the oceanographic data was the nautical mile, it was upscaled to match that of the MI. All data can be visualized through maps and histograms at http://pelabox.univ-lr.fr:3838/pelagis/DdSeaByc/ (Tab: '1. Data').

2.3. Spatiotemporal modelling framework

Our goal was to elucidate if oceanographic conditions were associated with bycatch of common dolphins in fishing gear with statistical modelling. We considered a general set up MI ~ OVs where MI is the response variable whose variations are to be correlated with OVs, with linear effects for covariates.

2.3.1. Spatial and temporal considerations

Common dolphin bycatch — and stranding of animals showing bycatch evidence — is a seasonal phenomenon in the Bay of Biscay (Dars et al. 2019, ICES 2020). The mortality signal, defined here as the number of stranded common dolphin showing bycatch evidence, is higher in January to March (winter) and in July and August (summer) but is lower in between (Fig. 3). Oceanographic conditions also follow a seasonal cycle with different dynamics in winter and summer and transition regimes in between (Yelekçi 2017). Our exploratory analysis (not shown here) suggested that the relationship between the response variable and oceanographic covariates varies across months. Hence, we chose to fit one model per month to get a climatology over the study period. Each monthly model gathered data for the corresponding month from 2012 to 2019, resulting in 12 models (from January to December). A similar approach was used in Foravanti et al. (2021). This climatological approach had the advantage of reducing computational cost.

The relation between OVs and MI in one given month can vary from one year to the next, for instance because of a timelag in cyclic phenomena (Huret et al. 2018) or because of singular climatic events. The dynamic of mesoscale processes is complex in the Bay of Biscay (Yelekçi 2017). Singular phenomena could be especially attractive for preys of dolphins and predatory fish targeted by fisheries depending on their extent, their duration and their time of occurrence. The effect of OVs on bycatch risk (and thus on MI) must be varying in time, as suggested by the intensification in strandings from 2016 (Dars et al. 2019). This led us to consider annually varying coefficients for OVs (i.e. random slopes). We further added an annually varying intercept (random intercept) to account for different annual levels of bycatch. Using random slopes amounts to considering an interaction with year: time-series of the effect of OVs on MI for each month and each year were an output from models over the study period.

Generalized linear models (GLM) and generalized additive models (GAM) usually assume all relevant covariates have been included in the model (Zuur et al. 2007a,b). This assumption is unrealistic in most cases, and omitted variables may result in a residual dependence that, if not accounted for, may result in misleading inferences (Legendre et al. 2002, Valcu & Kempenaers 2010). Omitted variables bias may manifest in residual autocorrelation, either temporal, spatial, or both. Because there was one model per month, the time lag between each 'measurement' was 11 mo, and we assumed no temporal autocorrelation. Yet, spatial autocorrelation, if not taken into account, could suggest spurious correlations with OVs. Consequently, all models included explicitly a spatial component in addition to the (implicitly spatial) OVs.

2.3.2. Hierarchical Bayesian framework and Gaussian random field

We used a hierarchical Bayesian framework as they are adapted to the modelling of complex spatial or spatiotemporal phenomena (Cosandey-Godin et al. 2015, Martínez-Minaya et al. 2018). Including a spatial random effect, e.g. with a Gaussian random field (GRF), is straightforward (Blangiardo et al. 2013, Cosandey-Godin et al. 2015). The GRF, indexed on each grid cell, is a stochastic process that will gather all the spatially implicit information in the data that are not accounted for by other model components, in our case oceanographic covariates (Cosandey-Godin et al. 2015). To model this random field, we chose a CAR process (Besag et al. 1991, Besag & Kooperberg 1995) based on the notion of nearest neighbours (the so-called first law of geography: 'Everything is related to everything else, but near things are more related than distant things'; Tobler 1970, p. 236). For the vector of grid cells ($\eta_1, \eta_2, \ldots, \eta_n$, here n = 3487) it can be written as follows:

$$\eta_i \mid \eta_j,\ i \neq j,\ \tau \sim N\left(\frac{1}{n_i}, \frac{1}{n_i \times \tau}\right) \tag{4}$$

where n_i is the number of neighbours for grid cell i and τ is a precision parameter. $i \sim j$ means that the 2 grid cells i and j are neighbours.

2.3.3. Model set up

MI was first transformed to log(MI + 1) and then modelled by a Gaussian distribution with an identity link function. The spatial CAR process was considered constant over years, so that there would be one spatial field per month. The stranding probability (SP) was always included as a covariate with a linear effect. For oceanographic variables effects and for the intercept, we included the possibility for the coefficients to vary from one year to the next by specifying a Gaussian random (independent and identically distributed) effect on years (random slopes). For an overview of our monthly model, we had for the response variable MI in year t and grid cell c, with oceanographic covariates X:

$$\left\{\begin{array}{l} \text{For all } m \text{ in } 1:12 \text{ (dropping the } _m \text{ subscript below for clarity)} \\ \qquad \log(\mathrm{MI}_{c,t}+1) \sim N(\pi_{c,t}, \sigma) \\ \mathrm{Id}(\pi_{c,t}) = \gamma \times \mathrm{SP}_{c,t} + \beta_{0,t} + \sum_j \beta_{j,t} \times X_{j,c,t} + \eta_c + \varepsilon_{c,t} \end{array}\right. \tag{5}$$

where N defines the normal distribution of location parameter $\pi_{c,t}$ and scale parameter σ, Id is the identity link function, γ the coefficient associated with SP, $\beta_{0,t}$ the intercept for year t, $\beta_{j,t}$ the annual coefficient of covariate $X_{j,c,t}$ at cell c in year t and η_c the spatial effect associated to grid cell c, which is assumed to result from a CAR model. Finally, $\pi_{c,t}$ are unstructured errors, i.e. residuals. Parameters estimated in the linear predictor, i.e. γ, $\beta_{0,t}$, $\beta_{j,t}$, η_c and $\pi_{c,t}$ constitute the latent field. They are assumed to follow Gaussian distributions (Rue et al. 2009). These parameters depend on a vector of hyperparameters θ that are not necessarily Gaussian (Rue et al. 2009). In this manner, the monthly model defined in (Eq. 5) is a latent Gaussian model (LGM) (Rue et al. 2009). It presents a spatial component (η_c) along with annual components ($\beta_{0,t}$ and $\beta_{j,t}$).

2.3.4. Inference with integrated nested Laplace approximations (INLA)

Inference for such complex spatial models is computationally demanding and requires approximation to be fully scalable with a large amount of data. For a large dataset with 3487 grid cells observed 8 times (i.e. years) per analysis, i.e. 27 896 observations per month, classical methods like Markov Chain Monte Carlo may be prohibitively slow (Blangiardo et al. 2013). We used INLA, which offers a very efficient alternative giving fast and reasonable estimations (Rue et al. 2009). Especially adapted to LGMs, this algorithm uses a combination of analytical approximations and numerical integration for the inference of posterior marginals and likelihood, which greatly reduce computational demand while being extremely accurate (Rue et al. 2009, Moraga 2019). Inference with INLA was carried out with the R-INLA package in R statistical software v4.0.2 (R Core Team 2020).

Before model fitting, all oceanographic variables were standardized (mean-centered and scaled to unity), and *eke* and *mean_sst_grad* were log-transformed to account for skewness and strict positivity. Weakly informative priors were chosen so that estimations would mostly be driven by the data (Gabry et al. 2019). Fitted and predicted values that were negative after back transformation were set to zero.

2.3.5. Model selection

All possible combinations of the different effects and covariates were tested, with the SP systematically included as a confounding factor (list of tested models is provided in Supplement 2). The first combinations were the simplest models with only linear effects for oceanographic covariates (i.e. in Eq. 5, β_j replaces $\beta_{j,t}$) and no spatial field (8 possibilities with the null model). Second, coefficients were allowed to vary between years for oceanographic covariates (7 possibilities) with random slopes. Finally, the CAR process was added, with and without oceanographic covariates, considering strict linear effects or annual random slopes (15 possibilities). The 30th model was the more complex, defined in Eq. (5), where $j \in [1,3]$ and X_j are thus *sst*, *eke* or *mean_sst_grad*. Model selection was conducted using the Wanatabe Akaike information criterion (WAIC) (Watanabe 2010). WAIC gives an approximation of the out-of-sample predictive accuracy using the in-sample data (Gelman et al. 2014).

2.3.6. Model checking

The coefficient of determination R^2 for each monthly model was computed. R^2 is the proportion of variance in the response variable accounted for by explanatory variables (Johnson 2014). We apportioned the total variance to different model components, i.e. spatial or annual, and assessed their respective contributions. For random slopes models, some variance components depend on observations (Johnson 2014). For instance, the variance of $\beta_{sst,t}$, coefficient of variable *sst* on year *t*, depends on values of *sst* during year *t*. We used the matrix formula (11) of Johnson (2014); see Supplement 3 for further details.

Finally, we assessed the predictive power of models, first by conducting out-of-sample cross-validation (CV), then by testing different prediction scenarios. While the dataset was complete from 2012 to 2018, for 2019 only values of oceanographic variables were given to get predictions of MI for this year. As the intercept and covariates coefficients were estimated annually, there was an index associated to each year. For the CV procedure, we considered 2019 as a new year (predicted from the posterior distribution) and attributed to this year a new and unique index. In addition, we tested different repetition scenarios (RS): instead of attributing a new index to year 2019 and consider it as a new sample, we considered 2019 as a repetition of a previous year by attributing to 2019 its index. This way, all model components fitted during the 'repeated' year were used (covariates' coefficients, effect of the stranding probability, spatial CAR process) for the prediction of MI in 2019, still considering 2019's oceanographic conditions. We tested all 7 possibilities, i.e. we considered 2019 as a repetition of 2012, then of 2013, 2014, 2015, 2016, 2017 and 2018. Then, we confronted the predicted total mortality for 2019 to 2019's total mortality from the dataset (never seen by the models). We also computed a root mean squared error (RMSE) per RS and for the CV, based on the monthly differences between predicted and observed (from strandings) total monthly mortality. With these repetition scenarios, we aimed at addressing whether oceanographic conditions of past years affected bycatch mortality risk in the same way and could predict the observed mortality in 2019.

3. RESULTS

3.1. Model selection

For most months, the most complex model detailed in formula (Eq. 5) had the smallest WAIC values (table with WAIC of all tested models provided in Supplement 4). It included a CAR process, year-varying intercepts and year-varying slopes for the 3 covariates *sst*, *eke* and *mean_sst_grad*. In May, June and November the model with the smallest WAIC values excluded *eke* and for September *sst* was excluded. However, the difference in WAIC between these models and the most complex one selected for other months was small (relative difference of 0.01, 0.03, 0.1, 0.06% in May, June, September and November, respectively). Hence, we chose to keep the most complex model with all 3 covariates for all months to facilitate comparison of results over the 12 months.

3.2. Oceanographic covariates effects on the MI

Slope estimates of the effect of *sst*, *eke* and *mean_sst_grad* on spatiotemporal MIs were precise with tight credible intervals (see http://pelabox.univ-lr.fr:3838/pelagis/DdSeaByc/; Tab: '2. Results 2.1.'. There were no estimates for year 2019 as this year was not used in model fitting but in out-of-sample, 1-step-ahead cross-validation and predictions. Overall, effects were more intense in the winter season, from January to March (Fig. 5). They were close to zero for the rest of the year, except in July and August for 2016, 2017 and 2018 for *eke* and *mean_sst_grad*. The winter variation pattern of the effect of *eke* and *mean_sst_grad* was different every year. Their effect on MI was sometimes positive and sometimes negative, depending on years. In July and August, however, the effect of these 2 covariates was consistent from 2016 to 2018. It was negative for *eke* and positive for *mean_sst_grad*. The winter variation pattern of the effect of *sst* was consistent between years, with interannual differences in its intensity. It switched sign from one month to the next, for most years. In summer, the effect of *sst* was close to zero, except in 2017, when it was slightly negative. For all 3 covariates, 2017 emerged as a singular year.

The intercept was estimated as a mean level of MI with OVs being set at their mean values (given that they were standardized, that is mean-centered). It was greater in winter, with mostly positive values in January and February but negative values in March, except in 2017, when it was positive for all 3 months (Fig. 5). Its pattern of variation was more or less consistent over the study period, with differences in its intensity. In summer, the intercept was slightly positive only in 2016 and 2017.

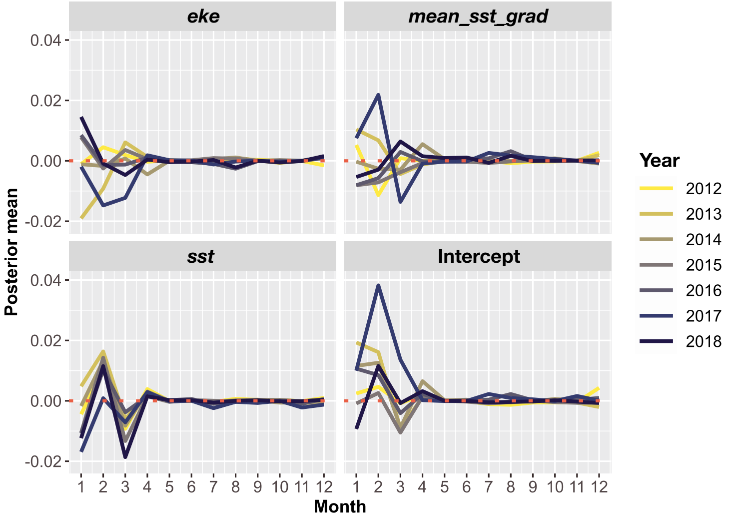

Fig. 5. Means estimates from the 12 separated monthly models of intercepts and coefficients of oceanographic covariates, for each month and each year. Spatiotemporal monthly models were inferred with integrated nested Laplace approximations (INLA). *eke*: eddy kinetic energy; *mean_sst_grad*: mean sea surface temperature; *sst*: sea surface temperature

3.3. Variance partitioning

The computation of R^2 allowed us to differentiate the contribution of the different model components to integrate MI variations (Fig. 6). The annual component included annual coefficients of covariates (random slopes) along with annual intercepts. The spatial component was the CAR process whose contribution in variance showed little between-month variation. The residual component included what was not accounted for by either of the 2 precedent components. In total, models better accounted for MI variations from January to April, the annual component being the most contributive component on this period. From January to March, 21 to 25 % of the variance were accounted for by annual and spatial components. A rise in the annual component contribution in July and in the spatial component contribution in August resulted in a rise in the overall variance accounted for these 2 months. Afterward, most of the variations of MI were integrated in residuals. Note that, using formula (11) of Johnson (2014), covariances between components were included: some negative covariances terms explain that contributions of the 3 components naïvely sum to more than 100 % for some months.

3.4. CV and predictions of 2019 mortality with repetition scenarios

For CV, 1-step-ahead prediction was performed. Each monthly model was calibrated on 2012–2018 data, so MI data from 2019 was not used in model fitting. 2019 oceanographic data were thus used for prediction, taking between-year variations into account. The total monthly MI of the dataset (observed) for 2019 fell within the confidence interval of total monthly predicted values, for both the winter and the summer mortality periods (Fig. 7). Total mean predicted values were below observed ones. In addition, 2019 was assumed as a repetition of each year between 2012 and 2018 (RS), to highlight if past oceanographic influences could predict observed mortality in 2019. Among the 7 RS, observed values of total monthly mortality of 2019 during the winter mortality period was within (or close to) confidence intervals of predicted values for 2 RS, when 2019 was considered as a repetition of 2013 (RS 2019 = 2013) and as a repetition of 2017 (RS 2019 = 2017) (Fig. 7). For RS of other years, predicted values and confidence intervals were lower than observed monthly mortality, from January to March. The summer mortality season was not reproduced by the models for RS of years before 2016. Overall, 2017 RS showed the lowest RMSE and gave the best prediction of 2019 monthly mortality levels (Table 1). RMSE for CV was below RMSE of RS of years 2012 and 2015 and close to that of 2018.

Additional results such as maps of fitted or predicted values and maps of the estimated spatial effects are available at http://pelabox.univ-lr.fr:3838/pelagis/DdSeaByc/ (Tab: '2. Results') for all 12 months. A temporal series of total monthly mortality of fitted values and observed values are provided in Fig. A1 in the Appendix.

4. DISCUSSION

We assumed bycatch risk could be correlated to the proximal relationship between the dynamic distribution of common dolphins, commercial predatory fish species targeted by fisheries and that of their common prey species, the latter being partially driven by oceanographic processes. Spatiotemporal information on at-sea bycatch mortality, fisheries, dolphins and fish prey species distribution is not easily accessible to study this proximal relationship. Thus, we used proxies, a mortality index inferred from strandings and oceanographic descriptors, to study the dis-

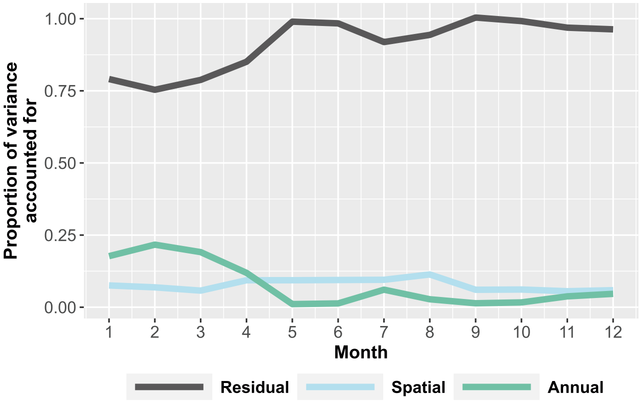

Fig. 6. For each of the 12 spatiotemporal monthly models inferred with integrated nested Laplace approximations (INLA), proportion (transformed with a square root) of variance accounted for by each model component. Residual: residual component; Spatial: spatial component (defined by a Gaussian random field); Annual: annual intercepts and coefficients of covariates

tal relationship between common dolphin bycatch and oceanographic processes. We mobilized 8 yr of stranding data (from 2012 to 2019) and explored spatial and temporal links between basal and apex nodes of the trophic network, from oceanographic processes to short-beaked common dolphins (and fisheries). We fitted a series of 12 spatiotemporal monthly models that included 3 oceanographic variables as covariates potentially contributing to the spatiotemporal structuring of bycatch risk of common dolphins in the Bay of Biscay. Results provided first insights into how the intensity of common dolphin bycatch in the Bay of Biscay might be modulated by key seasonal and dynamic oceanographic features.

4.1. Two seasons of mortality, two different underlying processes

Strandings highlight 2 seasons of high bycatch mortality in the Bay of Biscay: a main one from January to March and another (only observed from 2016 onward) in July and August (Fig. 3). Results reflected different patterns for these 2 mortality seasons, suggesting differences between the underlying phenomena leading to bycatch mortality. Outside these seasons, the explanatory power of oceanographic processes was very limited, and the effect of OVs on the mortality index was close to zero. Thus, it seems that OVs seasonally affect bycatch risk and should not be considered as season-invariant drivers of bycatch mortality.

4.1.1. Winter high mortality season, from January to March

The annual component, including OVs, accounted for most variations in bycatch risk during the winter mortality season (Fig. 6), suggesting a substantial influence of the oceanographic processes. Moreover, January, February and March were the months when OVs had the strongest effects on bycatch risk (Fig. 5). Depending on OVs, their effects (i.e. monthly estimated linear coefficients) showed different inter-annual patterns. The month-to-month effect of sea surface temperature was the only one to be consistent from one year to the next. Sea surface temperature partially drives the distribution and seasonal migrations of multiple marine taxa, from small pelagic fish (Lanz et al. 2009, Hughes et al. 2014,) to bigger fish (Hahlbeck et al. 2017) and high-level predators (Weltz et al. 2013). In the Bay of Biscay, the influence of sea surface temperature affects the distribution of identified prey species of common dolphins and commercial predatory fish species (Spitz et al. 2013), such as anchovies and sardines (Planque et al. 2007, Petitgas et al. 2014, Politikos et al. 2015). Therefore, a correlation between mortality and sea surface temperature can be expected if the underlying mechanisms are linked to preys of both common dolphins and commercial fish species targeted by fisheries. The effects of the mean temperature gradient and eddy kinetic energy were of the same magnitude as that of sea surface temperature but presented high inter-annual variations. Mean temperature gradient quantifies the intensity and wideness of thermal fronts, whereas eddy kinetic energy is associated with turbulent surface features such as eddies. Because they were averaged over each month, they should refer to relatively persistent structures. In winter, the Bay of Biscay environment is characterized by a seasonal cross-shore (west to east) surface temperature gradient with lowest temperature close to shore and intense frontal activity parallel to the coast (north to south) (Yelekçi et al. 2017). These frontal structures are freshwater fronts, correlated with the mixing of oceanic waters and cold freshwater inputs from river plumes (Yelekçi et al. 2017). Their location and timeline concur with observed patterns regarding bycatch mortality: during winter months, strandings were from all the Atlantic coast (http://seamap.env.duke.edu), and high mortality areas were previously identified on the continental shelf (Peltier et al. 2021). Moreover, most of highest MI values were located offshore of the coast from the south of the Finistère region to the south French border (not shown, see http://pelabox.univ-lr.fr:3838/pelagis/DdSeaByc/; Tab: '1. Data'), especially in 2017 when strandings were the more numerous over the 2012 to 2018 period. Together with the effects of the associated OVs on the MI, results suggested these seasonal fronts may be targeted by both fisheries and common dolphins as areas where fish aggregate, thereby putting the latter at risk of bycatch by the former.

4.1.2. Summer high mortality season in July and August

July and August were the only 2 other months when OVs accounted for a non-negligable fraction of variations in bycatch mortality (Fig. 6). The amount of total explained variance accounted for by OVs (included in the annual component) was more limited compared to the winter mortality season and was below the contribution of the CAR process. This could suggest that, during this summer season, other drivers (currently omitted in the model) might drive mortality risk. However, this was expected as strandings are at least one order of magnitude lower in summer and only became substantial from 2016 onward. Nevertheless, different patterns emerged regarding the effects of oceanographic covariates. Conversely to the winter season, the sea surface temperature coefficient was close to zero for all years, and the effects of mean temperature gradient and eddy kinetic energy on the MI were, respectively, quite consistent for all 3 years when a summer mortality peak was observed (2016, 2017, 2018). For these 3 years and in July and August, the effect of the mean temperature gradient was slightly positive, meaning that thermal fronts were associated with higher MI and that of eddy kinetic energy was slightly negative, meaning that bycatch mortality probably occurred in low turbulence waters. In July and August, the mesoscale dynamic activity of the Bay of Biscay is rather different than in winter. In winter, the frontal activity in the Bay of Biscay is dominated by freshwater fronts resulting from input of cold freshwater from rivers whereas in summer, there are mainly fronts due to tidal flow (Yelekçi 2017). Winter freshwater fronts display more spatiotemporal variability (on a given year and interannually) as they are directly correlated to river flows (Yelekçi et al. 2017). Summer tidal fronts are conversely quite consistent from one year to the next because they are correlated to a repetitive process (i.e. tides) (Yelekçi et al. 2017). During summer, the main frontal activity is a seasonal tidal front, called the Ushant Front, and it is located in front of the French Finistère region (Yelekçi et al. 2017). Its activity peaks in July and August (Yelekçi et al. 2017). Turbulent components of surface currents are relatively low around this structure (not shown, see http://pelabox.univ-lr.fr:3838/pelagis/DdSeaByc/; Tab: '1. Data'), except at its most northern part. Again, the location of this typical frontal structure concurred with the location of hot spots of fitted MI as well as with the location of bycaught common dolphin strandings, mainly occurring on the coast of the south Finistère region during the summer mortality season (http://seamap.env.duke.edu).

4.1.3. Other drivers of seasonal differences

The distribution of common dolphins in the Bay of Biscay differs between seasons (Laran et al. 2017). In winter, they are more numerous on the shelf, whereas in summer they are mainly distributed on the shelf break. This probably results in spatial differences in the local abundance of common dolphin between seasons, directly affecting bycatch risk. Seasonal differences in bycatch-induced mortality may further be linked to annual biological cycles of common dolphins and fish. The calving and mating season of short-beaked common dolphins of the northeast Atlantic is from April to September, with a likely peak of activity in July and August (Murphy et al. 2005, 2009). Feeding strategies and movement patterns of dolphins differ during those periods, resulting in a different response to oceanographic processes. This could also be true with respect to dolphins' preys, many of which present an annual biological cycle. As for the fisheries, they might likewise change their searching strategies, or their fishing gear, depending on the season and target species. The fishing effort and fishing targeted areas also likely differ between seasons (ICES 2020). A combination of those parameters might affect the difference between the 2 seasons regarding patterns of oceanographic variables effects on bycatch mortality.

Although the mechanisms were different between winter and summer mortality seasons, an influence of oceanographic processes and especially seasonal thermal front structures was highlighted for the 2 seasons of mortality. The association between marine predator and thermal fronts was shown and studied elsewhere (Doniol-Valcroze et al. 2007, Gannier & Praca 2007, Cox et al. 2018, Scales et al. 2018), and thermal fronts were identified as priority conservation areas for marine megafauna (Scales et al. 2014). If correlations are complex and not straightforward, this study still provides first hints of an association between short-beaked common dolphins and this type of mesoscale frontal structure in the Bay of Biscay, likely linked to bycatch mortality.

4.2. Between-month variations

For all 3 oceanographic covariates, in winter, interpretation is further complicated as their effects on the mortality index often switched sign from one month to the next. From a statistical point of view, there could be 2 reasons for this. First, because we conducted different models for each month, there is no dependence between consecutive months. This could be improved by putting additional model structure such as a first order random walk for example. However, this would also substantially increase the computational burden, multiplying the number of observations (3487 spatial cells 'observed' once per month and per year, so 334 752 observations for the complete dataset). Second, it is likely that the effect of oceanographic processes on the mortality of dolphins due to bycatch is not linear or additive. Non-linear relationships with environmental covariates are routinely evidenced in marine species distribution modelling (Forney 2000, Stoner et al. 2001, Tew Kai & Marsac 2010) and fisheries (Maury et al. 2001, Walsh & Kleiber 2001, Zagaglia et al. 2004) or even bycatch studies (Žydelis et al. 2011, Di Tullio et al. 2015, Hahlbeck et al. 2017). Given the extra complexity of our response variable, it is quite conceivable that the influence of oceanographic features on short-beaked common dolphins bycatch is not linear. Combined with the fact that oceanographic processes might have different effects depending on their location and timing of appearance (that might vary from month to month), it could explain changes in signs of mean monthly coefficients of the oceanographic covariates. Again, relaxing the linear assumption would be possible with, for example, functional regression, but is beyond the scope of the present study.

There could also be ecological reasons for these between month variations. The winter oceanographic dynamics of the Bay of Biscay is characterized by high-frequency processes with rapid changes, sometimes within a month. Changes in the sign of OVs effects on the MI could be due to dynamic processes affecting common dolphins and fisheries interactions. The possibility that the effect of OVs could change from one month to the next motivated the use of random slopes. Taking thermal fronts as an example: these can aggregate preys of both common dolphins and predatory fish and do not necessarily increase bycatch risk. If fronts are quite wide and persistent, they could be wide enough so that they could attract fisheries on, say, their shore side and common dolphin on their seaside: spatial overlap between common dolphins and fisheries would be limited. However, if thermal fronts are very spatially localized, then spatial overlap between common dolphin and fisheries could be substantial, and bycatch risk would be higher. Yet, the frontal dynamics in the Bay of Biscay shows seasonal and interannual variability (Yelekçi et al. 2017). The width and intensity of thermal fronts can therefore vary from one month to the next (and for a given month, from one year to the next), which may also explain fickle statistical relationships.

4.3. The bycatch mortality of 2019: a predictable event?

Bycatch mortality in 2019 was the highest ever observed on the French Atlantic coast (Peltier et al. 2019), exceeding 2017 levels that were also unprecedented at that time. Still, crossvalidation results suggested it was statistically predictable as the observed monthly mortality tally from the dataset was within the confidence interval of the prediction (Fig. 7). Furthermore, results of the repetition scenarios showed how 2019's mortality was possibly due to circumstances already met in the past, either related to oceanographic conditions, or to other component included in models through the spatial process. The MI in 2019 was more accurately predicted when 2019 was considered as a repetition of 2013 and 2017 (Table 1, Fig. 7). For RS 2019 = 2017, the observed monthly mortality of 2019 was close to predicted values from oceanographic covariates (in 2019) and past relationships with OVs, both for winter and summer mortality seasons. As mentioned above, bycatch mortality in 2017 was also unprecedented at that time as an all-high record. 2017 indeed stands out as a singular year regarding the effect of all 3 covariates on bycatch risk (Fig. 5). This suggests maybe singular oceanographic phenomena in 2017 that were especially conductive of bycatch events, phenomena which recurred in 2019. A more surprising result was the remarkable good prediction made for winter months, when 2019 was considered as a repetition of 2013 (RS 2019 = 2013). Observed mortality in 2013 from the dataset was 156 individuals (as fresher stranded carcasses showing bycatch evidence or stranded during an intense mortality event, see Section 2), whereas it was 317 in 2017 and 413 in 2019, through January, February and March. However, the observed mortality in January 2013 was close to that of January 2017 (Fig. 3) and was the second highest value for this month in the study period. In addition, mean coefficient estimates of *eke* and *sst* were part of the highest from 2012 to 2018. In January, the mean coefficient estimate of *mean_sst_grad* in 2013 was close to the mean coefficient estimate in 2017. In January, the mean effect of the mean temperature gradient was also the same in 2013 and in 2017. Despite the lower levels of observed mortality in 2013, it seems that winter oceanographic conditions in 2013, 2017 and 2019 favored common dolphin and fishery interactions, with an intensifying trend over the years. Given the complexity of our results regarding oceanographic covariate effects on bycatch risk (with inter-annual and between-month variations), the additional value of repetition scenarios was to highlight whether similar associations occurred in different years.

Overall, these results showed that, from a statistical point of view, with few oceanographic covariates,

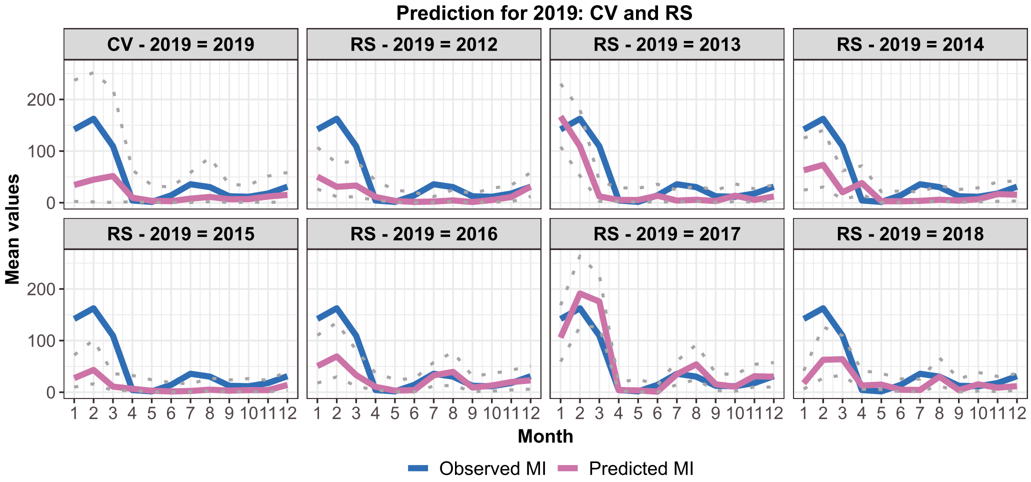

Fig. 7. Prediction for 2019. Monthly total mean mortality index from the dataset ('Observed MI') and from fitted values ('Predicted MI') for 2019 resulting from the 12 spatiotemporal models inferred with integrated nested Laplace approximations (INLA), with (1) a cross-validation (CV) procedure, i.e. the mortality index was predicted from previous years data and from values of oceanographic covariates for 2019 (2) repetition scenarios (RS), analogous to the latter except 2019 was considered as a repetition of a previous year of the study period. Grey dotted lines: 95%CI of fitted values

the unprecedented bycatch mortality of 2019 was at the very least unsurprising as the pattern observed in 2019 could be accurately predicted from 2012–2018 data. This highlights how gaining knowledge about environmental influences on interactions between short-beaked common dolphins and fisheries could have great conservation and management value (Scales et al. 2018). In this study, we adopted a modelling approach to determine whether bycatch mortality can be explained by oceanographic processes. However, with evidenced oceanographic influences on bycatch incidence, a similar analysis could be designed to forecast potential hotspots of mortality. The modelling approach would have to be different, as explanatory and predictive modelling are distinct and are associated with different 'modelling paths' (Shmueli 2010). For example, other sources of environmental data, available in a smaller timeframe, might have to be considered for near real-time prediction. Remote sensing could be an option, as it is already used in the support of fisheries activities (Santos 2000). The forecasting of high mortality zones might make it possible to define dynamic time–area closures for fisheries (Cosandey-Godin et al. 2015), which represent a promising tool to reduce bycatch pressure on the common dolphin population while limiting the economic impact (Dunn et al. 2011, Maxwell et al. 2015, Hazen et al. 2018). In this regard, further studies modelling the dynamic distribution of areas of co-occurrence of both short-beaked common dolphins and fisheries in the Bay of Biscay would be highly valuable for the conservation of this population.

4.4. Limitations and prospects for improvement

Several limitations can be imposed regarding the present work and results. First of all, strandings give only minimal estimations of bycatch-caused mortality. Some carcasses may never strand, and some others strand in advanced states of decomposition that do not allow their examination nor the identification of the cause of death of the animals. Moreover, due to the reverse drift modelling, the MI is associated with an uncertainty that is difficult to measure completely. Peltier et al. (2012) quantified the average distance between observed stranding locations of animals that were tagged when released from fishing boats and stranding locations predicted with MOTHY (27.1 ±

Table 1. Root mean squared error (RMSE) for cross-validation (CV) and repetition scenarios (RS)

	CV	RS						
	2019	2012	2013	2014	2015	2016	2017	2018
RMSE	48.4	51.2	32.8	43.6	54.2	45.0	30.1	48.1

24.5 km), which is accurate enough for practical purposes. Yet, there is no estimate of uncertainty associated with drift points as no information is available on where dolphins died. Developing the reverse modelling approach, on which the MI depends, was precisely motivated by infering high-probability at-sea mortality areas (Peltier & Ridoux 2015, Peltier et al. 2020).

The spatial scale for the present analysis (approximately 89 km^{-2}) was coarse compared to that of OVs. This coarse resolution required upscaling for OVs, which could have smoothed out too many high frequency processes such as fronts and eddies. It is thus possible that the relationship between the MI and OVs was weakened, impacting the results concerning oceanographic coefficients and explanatory power. The association between the MI and oceanographic variables is likely scale dependent as are associations between oceanographic covariates and marine top predators' distribution and foraging (Logerwell & Hargreaves 1996, Fauchald et al. 2000, Pinaud & Weimerskirch 2005, Pirotta et al. 2014). The link of interest here could be detectable at a specific spatial scale and not at another, and for high frequency processes the scale could be relatively small. Getting mortality data at a finer scale (and defining the spatial uncertainty associated with the reverse drift modelling) would then improve our understanding of the physical and ecological processes at stake.

Lastly, the models we developed for this study accounted for a low proportion of variance of the MI (25% at the highest, in February). This limits the range for interpretation, especially for months when this proportion was below 10%. This was expected: we aimed at quantifying links that are, at best, indirect between OVs and a marine top predator. Many trophic levels might be involved in the relationships of interest here, from phytoplankton to zooplankton and fish, each of these levels being influenced by several environmental and physiological factors. Moreover, the response variable we used is only a proxy of realized bycatch risk. Nonetheless, models performed well enough to reproduce annual patterns of total monthly MI from 2012 to 2018 (Appendix). Models performed better for the winter season with increased mortality and to a lesser extent for the summer mortality season, which were of particular interest regarding the seasonal pattern of bycatch. The CV results finally confirmed the acceptable performance of our models, suggesting an association between chosen oceanographic variables and bycatch-induced mortality of common dolphins in the Bay of Biscay.

This association should not be over-interpreted: relationships highlighted here are not straightforward, and they have been highlighted only for a few months, and not for all years. The limited explanatory power of the oceanographic covariates even for months when bycatch mortality was relatively high suggests that bycatch risk in the Bay of Biscay may be influenced by other non-environmental factors, e.g. characteristics of fisheries like the type of fishing gear used, the overall fishing effort or the timeline of the fishing operation (day or night). There were no significant changes in the pattern of the relationship between oceanographic processes and bycatch risk that could help explain the rise in bycatch observed from 2016 onward. This further suggests an influence of additional factors not considered in the present study. This rise of bycatch could be associated with a change in the distribution of common dolphins in the Bay of Biscay or a change in fishing practices. Bycatch risk is likely affected by a mix of different factors, oceanographic processes being one among others.

5. CONCLUSIONS

This study demonstrated the relevance of stranding data and modelled OVs from coastal operational oceanography to better understand this intense bycatch phenomenon which causes a serious threat to the short-beaked common dolphin population of the northeast Atlantic (Peltier et al. 2016, Murphy et al. 2019). The need to explicitly integrate spatial and temporal dimensions for such complex interactions was justified: our results effectively highlighted the spatiotemporal influences of structuring oceanographic processes on the risk of common dolphin bycatch in the Bay of Biscay. However, the underlying mechanisms remain unclear, and the relationship between environmental characteristics and dolphin bycatch must not be overinterpreted, as our model only indirectly links OVs with dolphin bycatch. Because of the dynamic aspects of both structuring oceanographic processes and dolphin and fishery distributions, further research focusing on smaller time scales is needed. For instance, extreme stranding events are observed on a weekly timeframe (Peltier et al. 2020), suggesting short periods of intense interactions between dolphins and fisheries, so a similar analysis on a weekly timeframe and focusing on these events might be more informative. Furthermore, we showed that the pattern of seasonal bycatch events can be directly inferred from past data on strandings and oceanographic conditions. This highlights the value of establishing functional relationships to eventually identify adapted and acceptable management measures to ensure both the long-term conservation of the population of short-beaked common dolphins of the Bay of Biscay and fisheries activities.

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Appendix.

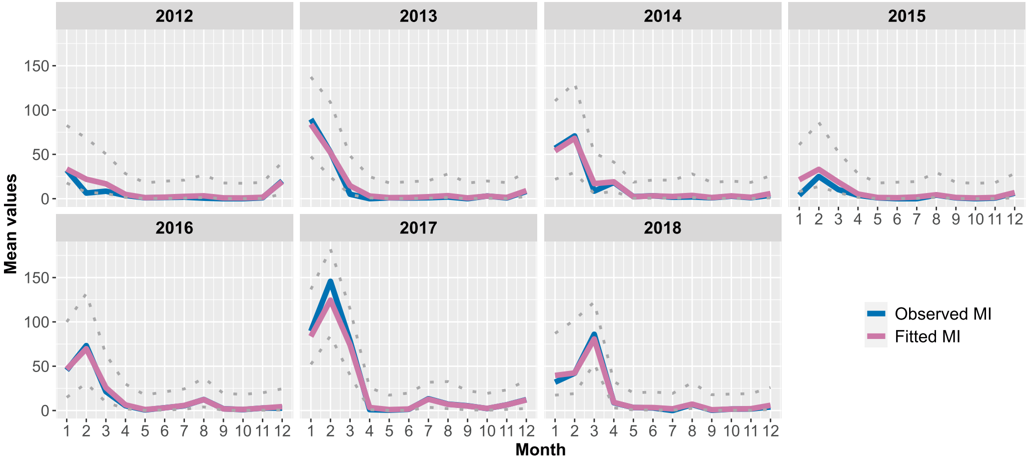

Fig. A1. Temporal series of the monthly total mean mortality index from the dataset ('observed', in blue) and from fitted values ('fitted', in purple) resulting from the 12 spatiotemporal models inferred with integrated nested Laplace approximations (INLA), from 2012 to 2018. Grey dotted lines: sum of the 0.025 (lower bound) and 0.975 (upper bound) quantiles of fitted values

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Estimating Cetacean Bycatch From Non-representative Samples (I): A Simulation Study With Regularized Multilevel Regression and Post-stratification

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Bycatch, the non-intentional capture or killing of non-target species in commercial or recreational fisheries, is a world wide threat to protected, endangered or threatened species (PETS) of marine megafauna. Obtaining accurate bycatch estimates of PETS is challenging: the only data available may come from non-dedicated schemes, and may not be representative of the whole fisheries effort. We investigated, with simulated data, a model-based approach for estimating PETS bycatch from non-representative samples. We leveraged recent development in the statistical analysis of surveys, namely regularized multilevel regression with post-stratification, to infer total bycatch under realistic scenarios of data sampling such as under-sampling or over-sampling when PETS bycatch risk is high. Post-stratification is a survey technique to re-align the sample with the population and addresses the problem of non-representative samples. Post-stratification requires to sub-divide a population of interest into potentially hundreds of cells corresponding to the cross-classification of important attributes. Multilevel regression accommodate this data structure, and the statistical technique of regularization can be used to predict for each of these hundreds of cells. We illustrated these statistical ideas by modeling bycatch risk for each week within a year with as few as a handful of observed PETS bycatch events. The model-based approach led to improvements, under mild assumptions, both in terms of accuracy and precision of estimates and was more robust to non-representative samples compared to more design-based methods currently in use. In our simulations, there was no detrimental effects of using the model-based even when sampling was representative. Estimating PETS bycatch ideally requires dedicated observer schemes and adequate coverage of fisheries effort. We showed how a model-based approach combining sparse data typical of PETS bycatch and recent methodological developments can help when both dedicated observer schemes and adequate coverage are challenging to implement.

Keywords: marine megafauna, conservation, modeling, statistics, Bayesian, anthropogenic removals

1. INTRODUCTION

Bycatch, the non-intentional capture or killing of non-target species in commercial or recreational fisheries, is a world wide threat to protected, endangered or threatened species (PETS) of marine megafauna (Gray and Kennelly, 2018), including seabirds (Martin et al., 2019), elasmobranchs (Pacoureau et al., 2021) and cetaceans (Avila et al., 2018). Bycatch in fishing gears, such as gillnets, is currently driving some small cetacean species to extinction (Brownell et al., 2019; Jaramillo-Legorreta et al., 2019). The European Commission recently issued infringement procedures against several Members States for failing to correctly transpose some provisions of European environmental law (the Habitats Directive, Council Directive 92/43/EEC), in particular the obligations related to the establishment of a coherent monitoring scheme of cetacean bycatch[1]. The Data Collection Framework (DCF) provides a common framework in the European Union (EU) to collect, manage, and share data within the fisheries sector (Anonymous, 2019a). The Framework indicates that the Commission shall establish a Multi-Annual Union Programme (EU-MAP) for the collection and management of fisheries data which should be inclusive of data that allows the assessment of fisheries' impact on marine ecosystems. With respect to PETS (including cetaceans), the collection of high quality data usually requires a dedicated sampling scheme and methodology, and is generally different from those applied under the DCF (Stransky and Sala, 2019): "EU MAP remains not well-suited for the dedicated monitoring of rare and protected bycatch in high-risk fisheries since its main focus is the statistically-sound random sampling of all commercial fisheries (Ulrich and Doerner, 2021, p. 126)." In practice, the introduction of any programme on PETS bycatch under the DCF may be met with caution because of its perceived potential to disrupt data collection for fisheries management (Stransky and Sala, 2019). This perception implicitly relegates PETS bycatch as a side issue for fishery management rather than an integral part of it. It may explain the usually poor quality of bycatch data on PETS (ICES, 2020a).

Recent EU legislation (Regulation 2019/1241), referred to as the Technical Measures Regulation (TMR), requires Members States to collect *scientific data* on cetacean bycatch for the following métiers: pelagic trawls (single and pair), bottom-set gillnets and entangling nets; and high-opening trawls (Anonymous, 2019b). Unlike its predecessor (Council Regulation EC No. 812/2004), this Regulation does not require the establishment of dedicated observer schemes for cetacean bycatch data collection (Dolman et al., 2020). Furthermore, only vessels of an overall length of 15 m or more are to be monitored, but these represent a small fraction of the European fleet (less than 10% in 2019)[2]. This vessel length criterion introduces bias in the bycatch monitoring data as the sample of vessels larger than 15 m is almost certainly dissimilar to smaller vessels. Even within the sample of vessels that are monitored, pragmatic considerations can complicate sampling. For example, in the United States, observer sampling trips are allocated first by region, port, and month, then randomly to vessels of particular categories within those monthly and spatial strata (ICES, 2009). Random allocation of observers to vessels follows sound statistical methodology and increases the likelihood of collecting unbiased data (Babcock and Pikitch, 2003). In France, observer days are allocated by port and by month for each fishery, but the exact vessel allocation is then negotiated and left at the discretion of skippers (ICES, 2009). Allocation is no longer random as skippers may only accept observers when cetacean bycatch risk is low (Benoît and Allard, 2009). Non-random allocation means potential bias in the collected data for monitoring bycatch as the sub-sample of skippers accepting an observer may be very different from skippers refusing to do so (Babcock and Pikitch, 2003).

One pragmatic solution bypassing observers is to mandate skippers to self-declare the non-intentional capture or killing of any PETS, as already required under the DCF (Anonymous, 2019a). In France, a national law from 2011 mandate fisheries to declare (without fear of prosecution) the bycatch of any cetacean species, but this law remained largely unknown to French fishermen until late 2019 (Cloâtre, 2020). In general, self-reported PETS bycatch data are sub-optimal as they may be heavily biased, non-representative (ICES, 2009) and typically provide poor information on which to base management decisions (National Marine Fisheries Service, 2004). Once again, the set of skippers who choose to declare bycatch may differ markedly from those who do not: for example the former take the extra time required to fill logbooks and thus provide accurate data while the latter do not. If this behavior is correlated to other attributes, e.g., a more acute awareness of threats to PETS resulting in practices that tend to minimize impact on PETS, data collected from skippers reporting bycatch would not be representative. There may also be an element of skippers genuinely forgetting to log PETS bycatch in the bustle of the fishing operation but this is random and unlikely to introduce bias. In addition, ground-truthing, for example with remote-electronic monitoring (REM; Course et al., 2020), would be required in order to ensure the quality and accuracy of self-reported data before their statistical analyses.

Another hurdle, of the statistical kind, with cetacean bycatch is the low frequency of these events. Assuming that implementing a representative sampling program were feasible, if bycatch is a rare event (Komoroske and Lewison, 2015), then few events would be observed for realistic sampling effort (Babcock and Pikitch, 2003; ICES, 2009). This paucity of observed event means a large uncertainty in statistical estimates: with a bycatch rate of the order of 0.01 event per fishing operation, a sample size of 1,100 observed operations would be required to obtain, in the best case scenario (no bias, statistical independence, etc.), the US recommended coefficient of variation of 30% (National Marine Fisheries Service, 2005, 2016; ICES, 2009; Carretta and Moore, 2014). The amount of observer coverage needed to reach this precision depends on fishery size and trip duration (Babcock and Pikitch, 2003). In practice, the sampling error depends on the overall design of the survey, of which the sample size

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[1] https://ec.europa.eu/info/news/july-infringements-package-commission-moves-against-member-states-not-respecting-eu-energy-rules-2019-jul-26_en

[2] https://appsso.eurostat.ec.europa.eu/nui/show.do?dataset=fish_fleet_alt&lang=en

is only one factor: for example a larger sample size could be needed if there are large "skipper-effects" as the same vessels would contribute fishing operations, and these would not be statistically independent. With a small sample size, uncertainty may be so large as to prevent using estimates altogether, even if one were to assume no bias in the data (Babcock and Pikitch, 2003). Given this challenge and the lack of uptake of dedicated monitoring programmes of cetacean bycatch in Europe over the last decade or more (Sala et al., 2019), it would appear prudent to seek methods of analysis that can handle the few and non-representative data available to robustly estimate bycatch rates.

The problem of having non-representative samples to carry out statistical analyses is ancient (Hansen and Hurwitz, 1946) and widespread: it pops up in many applied disciplines, including election forecasting (Wang et al., 2015; Kiewiet De Jonge et al., 2018), political sciences (Lax and Phillips, 2009; Zahorski, 2020), social sciences (Halsny, 2020), addiction studies (Rhem et al., 2020) or epidemiology (Zhang et al., 2014; Downes et al., 2018). In these disciplines, there are also intrinsic limits on improving the representativeness of sampling. For example, in polling, non-response rates can be above 90% (Forsberg, 2020). In other cases, some populations of interest may be hard to reach (Rhem et al., 2020), or answers may not be honest (St. John et al., 2014). Challenges lie in the accurate estimation of quantities of scientific interest (e.g., the true magnitude of bycatch in a fishery; Babcock and Pikitch, 2003) with the construction of statistical weights that can calibrate a non-representative survey sample to the population targets. Such weights are implicit with simple random sampling where each unit in a population has the same, non-nil, probability of being included in the sample. When inclusion probabilities differ between units, weights inversely proportional to the former can be used to adjust the sample. However, constructing survey weights is in general more elaborate than using inverse probabilities of selection in the sample (Gelman, 2007). Model-based approaches, and multilevel regression modeling with post-stratification in particular, has become an attractive alternative to weighting to adjust non-representative samples (Gelman, 2007).

Multilevel regression modeling allows researchers to summarize how predictions of an outcome of scientific interest vary across statistical units defined by a set of attributes or covariates (Gelman et al., 2021, p. 4): for example bycatch events are a binary outcome at the fishing operation level (a unit) associated with attributes, such as date-time, location, gears and vessels (e.g., Palka and Rossman, 2001). Post-stratification is a standard technique to generalize inferences from a sample to the population by adjusting for known discrepancies between the former and the latter. Post-stratification is a form of adjustment whereby statistical units are sorted out according to an auxiliary variable (hereafter a stratum) after completion of data collection; stratum-level effects (i.e., effects within each stratum or cell) are then estimated, and finally averaged with weights proportional to stratum size to obtain the population-level estimate. Post-stratification differs from blocking as the latter is done before data collection to ensure balance and representativeness at the design stage. Post-stratification is a *post hoc* statistical adjustment done at the analysis stage: it can remove bias, but at the price of an increased variance of estimates. Lennert et al. (1994) provided an early example of model-based estimates of bycatch with post-stratification.

In small samples post-stratification can degrade estimate precision, especially if the number of strata is large as each stratum will typically include very few data, or even not a single datum (the so-called "small-area" problem). In practice, adequate post-stratification may require handling hundreds of cells (the crossing of several attributes; e.g., week by statistical area by gears). Some predictions for each cell may be too noisy, especially if there are sparse or no data for that particular combination of attributes. Multilevel regression can offer a solution as it borrows strength from similar units to improve and stabilize (i.e., regularize) these predictions (Cam, 2012). In other words, multilevel regression allows an efficient use of a sparse sample to estimate the outcome of interest within each cell, even if these cells are very numerous (e.g., several hundreds). The key insight of combining multilevel regression modeling with post-stratification is thus: even if observations are not a representative sample of the population of interest, it may be possible to construct a regression model to first *predict* unobserved cases, and then *post-stratify* to average the fitted regression model's predictions over the population of interest (Gelman et al., 2021, p. 313). Good predictions may be obtained with regularization by means of multilevel models with structured priors (including so called "random-effects" models). The latter can increase precision by inducing shrinkage of parameter estimates across similar post-stratification cells, where similarity is encoded in the model specification (e.g., by using random effects that assume exchangeability). The amount of shrinkage, or partial-pooling across cells, is model-based and thus data-driven. However, in order to be able to leverage the information in the data, some model structure on the parameters of interest is necessary hence the need for structured priors. Relying on a model rather than just empirical means of the response variable addresses the bias-variance problem intrinsic to having a large number of cells in post-stratification, and leverages the large toolbox of regression-based models.

Technically, when data arise as signal plus noise, overfitting occurs when a regression model captures too much of the noise compared to the signal; that is in using an ill-conditioned (unstable) model that will provide an excellent in-sample fit but make poor out-of-sample predictions (Authier et al., 2017b; George and Ročková, 2021). Overfitting may result when using richly parametrized models without using adequate estimation methods such as regularization to stabilize parameter estimates and buffer them against noise (Gelman et al., 2021, p. 459–460). Weakly-informative priors in a Bayesian framework regularize the estimation of the large number of parameters that may be present in a multilevel model. Multilevel modeling takes into account complex data structures with structured prior models for batches of parameters; the simplest example are so-called "random effects" whereby a common (Gaussian) distribution centered on zero and with an unknown variance to be estimated for data is assumed for a group of parameters; for example years or sites (Cam, 2012). This common distribution for the parameters is a prior model, and this model for parameters means that the latter are not independently estimated but in tandem according to the postulated prior model. For example, Sims et al. (2008) used a model-based approach to obtain spatially smoothed estimates of bycatch in a gillnet fishery. Spatial-smoothing (also known as "small-area estimation"; Fay and Herriot, 1979) was used to stabilize estimated bycatch rates by using a Conditional Autoregressive prior model that leverages information from spatial neighbors to improve the prediction at a specific location. Prior models add some soft constraints to the overall model and these constraints are very useful in data sparse settings to mitigate variance and bias in predictions. In other words, these prior models represent additional assumptions about the data, assumptions, which if approximately correct, add information in the analyses and increase the precision and stability of predictions at the cost of a usually small estimation bias. Introducing bias to reduce variance is a common statistical technique known as shrinkage or regularization (George and Ročková, 2021).

Regularized multilevel regression with post-stratification is thus the combination of several important ideas to obtain accurate predictions (Gao et al., 2019). First, post-stratification is a survey technique to re-align the sample with the population and addresses the problem of non-representative samples. In practice, post-stratification requires to sub-divide the population of interest into many cells corresponding to the combination of important attributes. Multilevel regression can be used to accommodate all these cells in a single model, but the problem has now moved to how to obtain useful estimates for all these cells, which can number in the several hundreds. Regularization solves this estimation problem: it introduces model-driven bias in statistical estimates in order to stabilize them. These new developments in the statistical analysis of non-representative samples may help in obtaining a better quantification of bycatch rates and numbers. Our aim is to assess with simulations, the potential of regularized multilevel regression with post-stratification for analyzing already collected bycatch data, with the full knowledge that these data are non-representative and biased in several respects. These biases in sampling are manifold (see above): bias may be due to regulation exempting certain vessels (e.g., no monitoring for vessels smaller than 15 m); to non-dedicated observers or because sampling is driven for other purposes than bycatch monitoring of PETS (commercial discards, stock assessment); or in the case of dedicated schemes, to over-sampling a few "cooperative" skippers or focusing sampling in métiers with the highest or lowest bycatch risk. Our focus will be narrower, honing in on specific sampling scenarios whereby observer coverage is correlated to bycatch risk. In other words, we will assess the potential of regularized multilevel regression with post-stratification to estimate accurately bycatch numbers with samples preferentially collected either during low- or high-bycatch risk periods. Our investigation is largely framed from our knowledge on small cetacean bycatch in European waters, such as short-beaked common dolphin (*Delphinus delphis*, lower observer coverage when bycatch risk is higher) in the Bay of Biscay (Peltier et al., 2021) or harbor porpoises (*Phocoena phocoena*, higher observer coverage when bycatch risk is higher) in the Celtic Seas (Tregenza et al., 1997). In the remainder, we first introduce methods and notations to detail the proposed model to perform multilevel regression with post-stratification with bycatch data, using dolphins as an example. Next, we explain our data simulation scenarios and how we emulate non-representative sampling. We then compare the results (i.e., estimates of bycatch) from the proposed modeling approach with those from the method currently used by the working group on bycatch of protected species from the International Council for the Exploration of the Sea (ICES WGBYC) before concluding on some recommendations for future investigations.

2. MATERIALS AND METHODS

We carried out Monte Carlo simulations to assess the ability of regularized multilevel regression with post-stratification to estimate bycatch risk and bycatch numbers from representative and non-representative samples. ICES WGBYC collate data through an annual call from dedicated and DCF surveys collecting data on the bycatch of PETS through onboard observers or REM. These surveys may be qualified as "design-based" in the sense that, ideally, a representative coverage of fisheries would be sought in order to scale up the observed sample to the whole population using ratio-estimators. There are many caveats around the use of these ratio-estimators as EU MAP is not well-suited for monitoring PETS bycatch (Ulrich and Doerner, 2021). Given these shortcomings in the collection of bycatch data under EU MAP, the data available to ICES WGBYC are unlikely to be representative of fisheries of interest but nevertheless, ratio-estimators are used as part of a Bycatch Risk Approach (BRA) to identify relative risk of bycatch across species and metiers (ICES, 2018). Cetacean bycatch observer programmes may aim at achieving a pre-specified precision for bycatch rates (with a coefficient of variations less than 30%; National Marine Fisheries Service, 2005, 2016; ICES, 2009; Carretta and Moore, 2014). Achieving this is very difficult in practice, and a given coverage of effort deployed by the total fleet is, instead, aimed at: for example 10% (5%) for pair-trawlers (level-3 métier PTM) larger (smaller) than 15 m in France. Data from onboard observer programmes are then used to estimate total bycatch using ratio estimators (Lennert et al., 1994; Julian and Beeson, 1998; Amandè et al., 2012) and the bootstrap or a classical approach (Clopper-Pearson) for uncertainty quantification (ICES, 2018, p. 57). We used an approach similar to that of WGBYC (hereafter referred to as a "design-based" approach) as a benchmark to compare against results from regularized multilevel regression with post-stratification. We honed in on the accurate estimation of the number of bycatch events for a complete fleet. We assume that information on the total effort deployed by a fleet operating in a spatial domain are available and measured without error. This assumption is necessary to scale estimates from the sample to the population. We also assumed that there are no false-negatives in the sample, that is no bycatch event went unrecorded by onboard observers (assuming thereby a dedicated observer programme). These two assumptions are customary with ratio estimators, whether design- or model-based, and do not deviate from current norms. We assume however that these population data on total effort can be disaggregated at a finer temporal scale in order to post-stratify on calendar weeks. This assumption of accurate measurement of effort at the week-level is crucial for post-stratification.

2.1. Notations

The logit transform maps a quantity $p \in]0, 1[$ to the real line: $\text{logit}(p) = \log\left(\frac{p}{1-p}\right)$. Its inverse is denoted by $\text{logit}^{-1}(x) = \frac{1}{1+e^{-x}}$ (sometimes called the "expit" transform). Let y_{ijkl} denote the ith fishing operation of vessel j in week k of year l, with $y_{ijkl} = 1$ if a bycatch event occurs and 0 otherwise:

$$y_{ijkl} \sim \text{Bernoulli}\left(\mathrm{p}_{jkl} = \text{logit}^{-1}\left(\mu + \beta_{kl} + \alpha_j\right)\right) \qquad (1)$$

where p_{jkl} is the product of the probability of a bycatch event occurring and the probability of dolphin presence. This unconditional probability p_{jkl}, or "bycatch risk" hereafter, is not indexed by i: although there may be several fishing operations of vessel j in week k of year l, the risk is assumed constant over these. Bycatch risk is a function of several parameters (on a logit scale): μ is the intercept (overall risk), $\alpha_j \sim \mathcal{N}(0, \sigma_{\text{vessel}})$ are (unstructured, normal random effects) vessel-effects accounting for heterogeneity (e.g., "fishing style" of skippers); and β_{kl} are time effects, modeled with a Gaussian Process. A Gaussian process is written as $\mathcal{GP}(m, c)$ where m and c are the mean and covariance functions respectively (Gelman et al., 2014, p. 501). The Gaussian Process prior on the vector of week effects in year l, $\boldsymbol{\beta}_l$, defines this vector as a random function for which the values at any week $1, \ldots, k, \ldots, w$ are drawn form a w-multivariate normal distribution:

$$\beta_{1l}, \ldots, \beta_{wl} \sim \mathcal{N}\left(\left(m(1), \ldots, m(w)\right), \Omega\right) \qquad (2)$$

with mean m and covariance Ω. The function c specifies the covariance between any 2 weeks k and k', with Ω an $w \times w$ covariance matrix with element $\Omega\left(k, k'\right) = c(k, k')$. A Matérn covariance function of order $\frac{3}{2}$ and range parameter fixed to $\frac{3}{2}$ was assumed: $c\left(k, k'\right) = \sigma^2_{\text{year}} \times \left(1 + \frac{2\sqrt{3}\times d(k-k')}{3}\right) \times \exp -\frac{2\sqrt{3}\times d(k-k')}{2}$, where $d(k - k')$ is the temporal distance (in weeks) between weeks k and k'. The distance function was the absolute difference between calendar weeks within the same year: $d(k-k') = |k-k'|$. The choice of the Matérn covariance function translate an assumption of smoothness in the temporal profile of bycatch risk: bycatch risk is assumed to change gradually across weeks, with no abrupt increase or decrease. The range parameter is fixed and not estimated from data. This choice represents an additional assumption whereby the temporal correlation is 0.05 after 4 weeks corresponding to temporal independence after a month. This choice is to some extent arbitrary and represents an additional assumption. In theory, the range parameter could also be estimated from data but we assumed a data sparse setting with limited information (more so with Bernoulli data) to estimate this parameter.

The mean function m of the Gaussian process was modeled (on a logit scale) with a first order random walk, which was evaluated at specific values $k_{\in[1,\ldots,w]}$ corresponding to week number within a year:

$$\begin{cases} \left(m(1), \ldots, m(w)\right) = (\varepsilon_1, \ldots, \varepsilon_w) & \\ \varepsilon_k = 0 & k = 1 \\ \varepsilon_{k+1} \sim \mathcal{N}(\varepsilon_k, \sigma_{\text{week}}) & k > 1 \end{cases} \qquad (3)$$

The order of the random walk prior was assumed fixed at 1 and not estimated from data. This prior choice smooths the first order differences between adjacent elements of $\boldsymbol{\varepsilon}$ and represents an additional assumption, mainly to limit the number of parameters to estimate from the typically sparse data on bycatch. A random walk was chosen as an effective way to reveal the shape of the average risk profile without specifying a family of parametric curves.

The model in Equation (1) is a decomposition of bycatch risk into a time-varying component (at the week-scale, Equation 3; and with an interaction with year, Equation 2) and time-invariant component which can be interpreted as fishing-style effects whereby some skippers may have consistent practices that increase or decrease bycatch risk. Importantly, bycatch risk is modeled here with no attempt to model dolphin presence directly as relevant data to do so may be missing in the general case. Bycatch risk is thus to be estimated for each week of a year, and each of these weeks represent *de facto* a stratum. In any applied case, additional factors, such as statistical area, may need to be included in Equation (1) for improved realism. For simplicity, we did not consider space in simulations, and solely focused on time.

2.2. Data Simulation

To test the ability of model 1 to estimate bycatch risk, data were simulated (**Figure 1**).

1. Bycatch probability conditional on dolphin presence was constant and set to 0.3, that is roughly one fishing operation out of 3 generates a bycatch event when dolphins are present (corresponding to a high risk fishery, e.g., the trawl fishery in the Bay of Biscay).
2. Dolphin presence is seasonal (loosely inspired from the observed pattern of common dolphin in the Bay of Biscay where abundance is higher closer to the coasts in winter; Laran et al., 2017): it peaks at the beginning and end of the year, but quickly drops to 0 for roughly 2 thirds of a year.
3. A fishery of 20 vessels is operating all year round, with an overall activity rate of 80% each week (that is, for any week, $20 \times \frac{80}{100} = 16$ vessels are fishing). Each fishing day (5 days per week), on average 2.3 fishing operations are carried out. The expected total number of fishing operations for a year is $5 \times 52 \times 2.3 \times 16 \approx 10{,}000$. These values were loosely taken from an exploratory analysis of onboard observer data collected on PTM flying the French flag. During each of these operations, a bycatch event may occur depending on dolphin presence at the time and on a skipper-specific risk factor (drawn randomly from a normal distribution with scale parameter set to $\frac{\log(2)}{3}$ to induce moderate heterogeneity on a logit scale; Authier et al., 2017a).

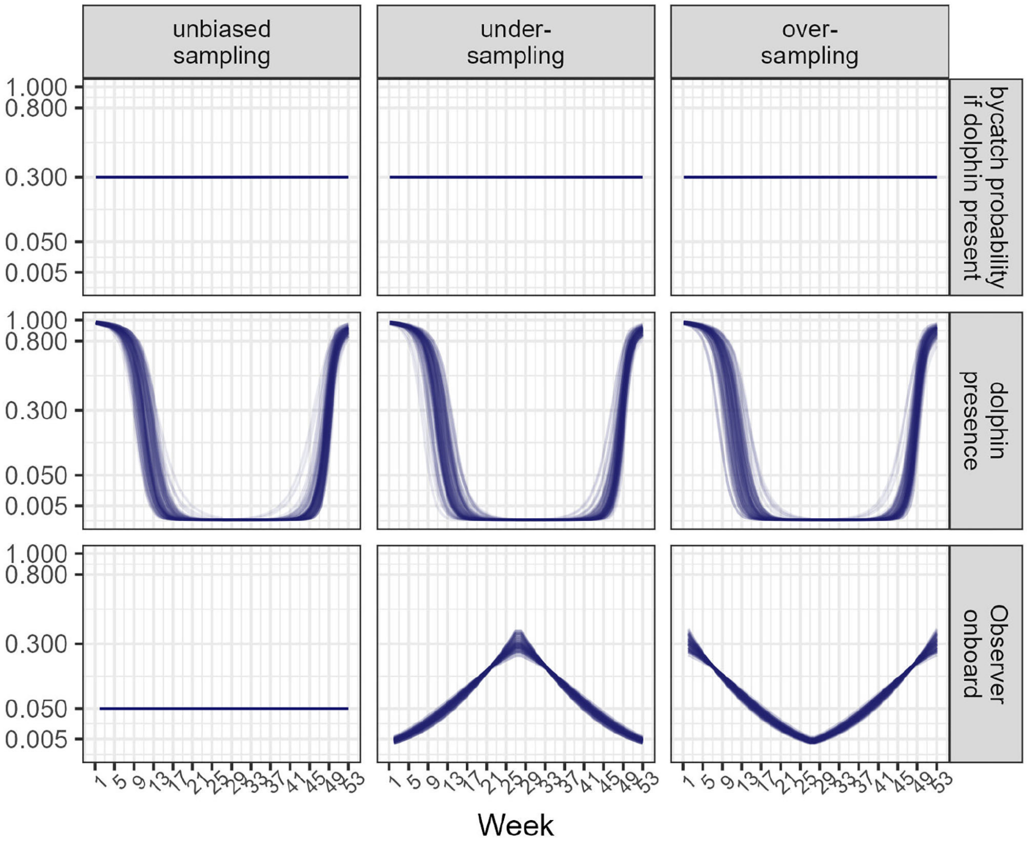

FIGURE 1 | Inputs for data simulation. **Top:** bycatch probability if dolphins are present during a fishing operation. **Middle:** dolphin presence during a year. **Bottom:** Probability for a skipper to accept an observer onboard. **Left:** sampling is unbiased; **Middle column:** sampling is biased downwards (under-sampling). **Right:** sampling is biased upwards (over-sampling). Each line corresponds to one of the 100 data simulations that were carried out. The *y*-axis is on a square-root scale to better visualize small values.

4. Observers are accepted onboard vessels either with a constant probability of 0.05 corresponding to a coverage of 5% of all fishing operations (unbiased sampling scenario) or with a probability that covaries with dolphin presence (biased sampling scenarios). In the latter case, realized coverage is a random variable. With under-sampling, the bulk of the observer data is collected when bycatch risk (the product of dolphin presence and bycatch probability) is nil (**Figure 1**). With over-sampling, the bulk of the observer data is collected when bycatch risk is high but no data are collected when the risk is nil (**Figure 1**).
5. In a year, the number of fishing operations is ≈ 10,000, and the number of bycatch events ≈ 300, which yields a rate of ≈ 3%. This rate is not large, but is not extremely rare either.

Bycatch events were simulated for each fishing operations during a day when an observer was present from a Bernoulli distribution according to the product of bycatch probability given dolphin presence and dolphin presence probability for that day. If no observer was present, no data were recorded. The data-generating mechanism used a parametric function for dolphin presence probability and was different from the statistical model used to analyzed the data (see https://gitlab.univ-lr.fr/mauthier/regularized_bycatch). For each sampling scenario, 100 datasets were generated for 1, 5, 10, or 15 years. All data simulations were carried out in R v.4.0.1 (R Core Team, 2020). When simulating only 1 year of data, Equation (2) is not necessary as there is no between-year variation to estimate: the model can be simplified with the omission of $\boldsymbol{\beta}_l$. Our Monte Carlo study had a comprehensive factorial design crossing (a) sampling regime (either unbiased or not) and (b) sample size as controlled with the number of years for which the observer programme was assumed to have been in operation.

2.3. Estimation

Estimation of the parameters of model 1 from simulated data was carried out in a Bayesian framework using programming language `Stan` (Carpenter et al., 2017) called from `R` v.4.0.1 (R Core Team, 2020) with library `Rstan` (Stan Development Team, 2020). `Stan` uses Hamiltonian dynamics in Markov chain Monte Carlo (MCMC) to sample values from the joint posterior distribution (Carpenter et al., 2017). Weakly-informative priors were used for regularization: $\begin{cases} \mu \sim \mathcal{N}(0, \frac{3}{2}) \\ \text{prop} \sim \mathcal{D}(1, 1, 1) \\ \sigma_{\text{total}} \sim \mathcal{GG}(\frac{1}{2}, \frac{1}{2}, \frac{\log 2}{10}) \end{cases}$

where $\mathcal{D}()$ denotes the Dirichlet distribution for modeling proportions (such that $\sum_{i=1}^{3} \text{prop}_i = 1$) and $\mathcal{GG}()$ the Gamma-Gamma distribution for scale parameters (Griffin and Brown, 2017; Pérez et al., 2017). With this simplex parametrization, chosen to improve mixing and ease estimation with Monte Carlo methods (He et al., 2007), the several variance components of the model were: $\begin{cases} \sigma^2_{\text{vessel}} = \sigma^2_{\text{total}} \times \text{prop}_1 \\ \sigma^2_{\text{week}} = \sigma^2_{\text{total}} \times \text{prop}_2 \\ \sigma^2_{\text{year}} = \sigma^2_{\text{total}} \times \text{prop}_3 \end{cases}$

These priors are weakly-informative (Gabry et al., 2019): the prior for the intercept covers the whole interval between 0 and 1 on the probability scale but is informative on the logit scale. The prior for the scale (square-root of the variance) is heavy tailed and has a median set to $\frac{\log 10}{2}$ (Griffin and Brown, 2017; Pérez et al., 2017), which translate an assumption about the plausible range of variations in bycatch risk spanning *a priori* two full order of magnitude from one tenth to a ten-fold increase compared to the mean bycatch rate. Thirty random realizations from our choice of priors are depicted on **Figure 2**: the whole interval between 0 and 1 is covered, and between-week variations can be large or small.

For each simulated dataset, four chains were initialized from diffuse random starting points (Carpenter et al., 2017, p. 20) and run for a total of 1,000 iterations, discarding the first 500 as warm-up. Default settings for the No-U-Turn Sampler (NUTS) were changed to 0.99 for `adapt delta` and 15 for `max treedepth` (Hoffman and Gelman, 2014). NUTS uses Hamiltonian Dynamics in MCMC and typically requires shorter runs than other MCMC algorithms both to reach convergence and to obtain an equivalent Effective Sample Size from the posterior (Hoffman and Gelman, 2014; Monnahan et al., 2017). Parameter convergence was assessed using the $\hat{R}$ statistics (Vehtari et al., 2019) and assumed if $\hat{R} < 1.025$. Upon diagnosing convergence of all parameters, a combined sample of $4 \times 500 = 2,000$ MCMC values were obtained to approximate the joint posterior distribution. Let $\hat{\mu}^{[m]}, \hat{\beta}^{[m]}_{kl}, \hat{\sigma}^{[m]}_{\text{vessel}}$ denote the mth MCMC sample for parameters μ, β_{kl} and σ_{vessel}. Bycatch risk $\hat{\text{p}}_{j^*kl}$ for a randomly chosen vessel j^* operating in week k of year l was computed from the mth MCMC draw from the joint posterior distribution as:

$$\hat{\text{p}}^{[m]}_{j^*kl} = \text{logit}^{-1}\left(\hat{\mu}^{[m]} + \hat{\beta}^{[m]}_{kl} + \hat{\alpha}^{[m]}_{j^*}\right) \qquad (4)$$

where $\hat{\alpha}^{[m]}_{j^*} \sim \mathcal{N}(0, \hat{\sigma}^{[m]}_{\text{vessel}})$. This predicted bycatch risk incorporates between-vessel variability, that is it takes into account the fishing style of skippers. The predicted risk (on a logit scale) for a random chosen skipper is $\hat{\alpha}^{[m]}_{j^*}$ and was drawn from the posterior predictive distribution: not all skippers may be observed in the sample, and but the subset of skippers that accept an observer can be used to estimate a between-skipper variance in bycatch risk. In practice, the number of fishing operations carried out in the course of a week in a year by individual skippers is unknown, although the aggregated number of fishing operations may be known. If totals by skippers were available, and all skippers had been sampled, it would be more efficient to use skipper-specific estimated risk, but we did not assume that this would necessarily be the case.

The total number of bycatch events, T_{bycatch} was estimated as the average over the 2,000 MCMC draws from the posterior:

$$\hat{T}_{\text{model}-\text{based bycatch}} = \frac{1}{2000}\sum_{m=1}^{2000}\left(\sum_{l=1}^{n_{\text{year}}}\sum_{k=1}^{n_{\text{week}}} \hat{\text{p}}^{[m]}_{j^*kl} \times N_{kl}\right) \qquad (5)$$

where N_{kl} is the total number of fishing operations that took place is week k of year l. The total number of strata for post-stratification was $n_{\text{year}} \times n_{\text{week}}$, with a maximum of $15 \times 52 = 780$ cells. Highest Posterior Density credible intervals at the 80% level were computed with function `HPDinterval` from package `coda` (Plummer et al., 2006) for uncertainty evaluation. Equation (5) is an instance of a ratio-estimator with post-stratification, except that it uses model-based estimates of bycatch risk. This model-based approach regularizes estimates with partial pooling (Gelman and Shalizi, 2013): the variance of estimates is greatly reduced by introducing some bias with structured priors (Gao et al., 2019). Our results were benchmarked against an approach similar to that of ICES WGBYC whereby total number of bycatch events was estimated1 as:

$$\hat{T}_{\text{design}-\text{based bycatch}} = \sum_{l=1}^{n_{\text{year}}}\left(\bar{p}_l \times \sum_{k=1}^{n_{\text{week}}} N_{kl}\right) \qquad (6)$$

where $\bar{p}_l$ is the average bycatch risk estimated as the mean from the observed sample in year l. Confidence intervals at the 95% level were computed using either the bootstrap or the Clopper-Pearson approach as customary in ICES WGBYC. Both were considered as the Clopper-Pearson approach is known for being more conservative: it produces confidence intervals that above the nominal level (i.e., wider than necessary) but generates non-nil confidence intervals even if no bycatch has been observed (Northridge et al., 2019). In practice, ICES WGBYC often pooled several years to stabilize the estimate of $\bar{p}$ (e.g., ICES 2018, p. 57–58; Carretta and Moore, 2014): Equation (6) translate an ideal case that is rarely met in practice.

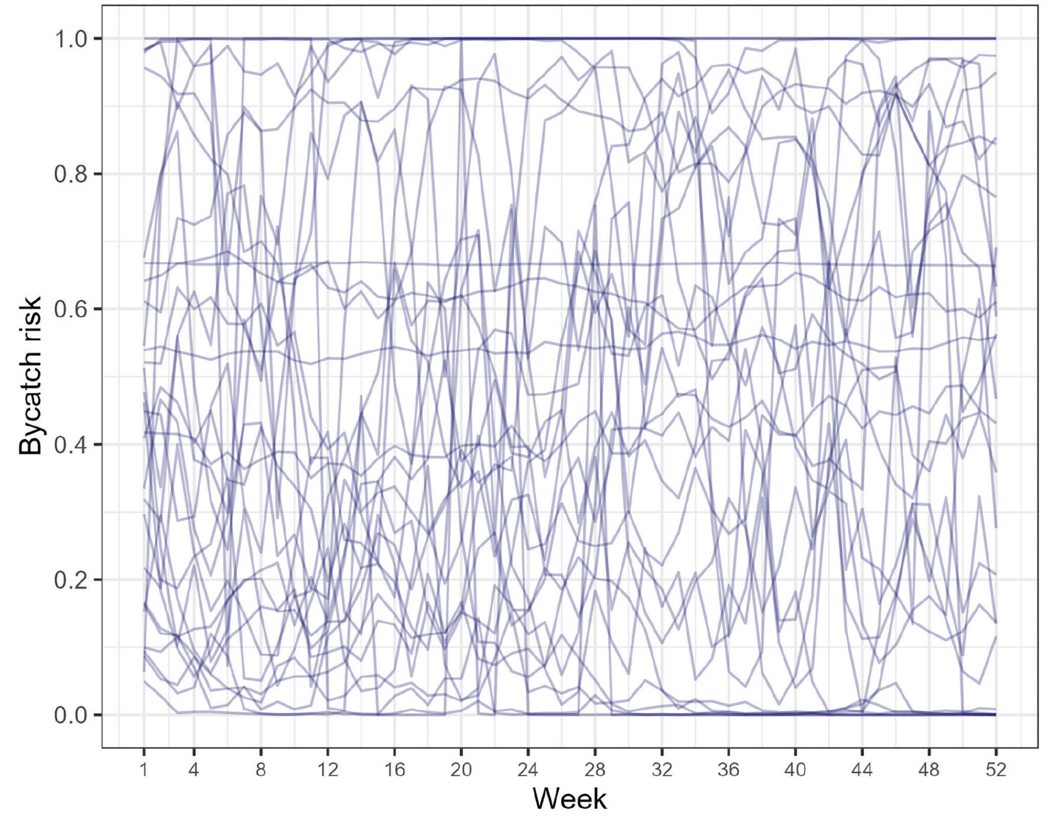

FIGURE 2 | Prior predictive checks *sensu* (Gabry et al., 2019). Bycatch risk (p_{ijkl} in Equation 1) is depicted: 30 random realizations from the priors are depicted.

ICES WGBYC usually works on bycatch rates (in number of PETS per unit effort), not bycatch risk. We focused on risk for simplicity, but scaling bycatch risk to a rate is straightforward by multiplying with the average number of PETS bycaught in a bycatch event. Dolphin presence was seasonal in the data-generating mechanism for simulations: pitching a method that can explicitly accommodate such seasonality against one that does not may be viewed as knocking down a strawman. However, current estimates of PETS bycatch in Europe are stratified by flag, ICES statistical areas, and métiers but not by season (e.g., Table 2 p. 17 in ICES 2019; Northridge et al., 2019, p. 27). The comparison remains relevant and topical as it matches current practices.

3. RESULTS

Convergence across all simulations and scenarios was assumed to be reached, with all $\hat{R} < 1.025$, for all parameters. For each simulation, chains were combined in a single sample of 2,000 values to approximate the joint posterior distribution of the model defined by Equations (1), (2), and (3).

3.1. Design- vs. Model-Based Approach

Comparing the design- and model-based approach was done with simulating 1 year of data. When data sampling was unbiased, both the design- and model-based approach were able to recover the true number of bycatch events (**Figure 3**; **Table 1**). Estimates of bycatch events were statistically unbiased but their precision low with a (frequentist 95%) confidence or (Bayesian 80%) credible interval (CI) as large as 100% of the point estimate (**Table 1**), as could be expected with only 15 bycatch events were recorded on average by onboard observers (**Table 1**). With under-sampling, design-based estimates were negatively biased (that is, they were under-estimates) whereas model-based estimates were still unbiased on average (**Figure 3**; **Table 1**). With over-sampling, design-based estimates were positively biased (that is, they were over-estimates) but so were model-based estimates, although bias was 5 times smaller (**Figure 3**; **Table 1**). In all cases, coverage was 100% but largely as a result of low precision:

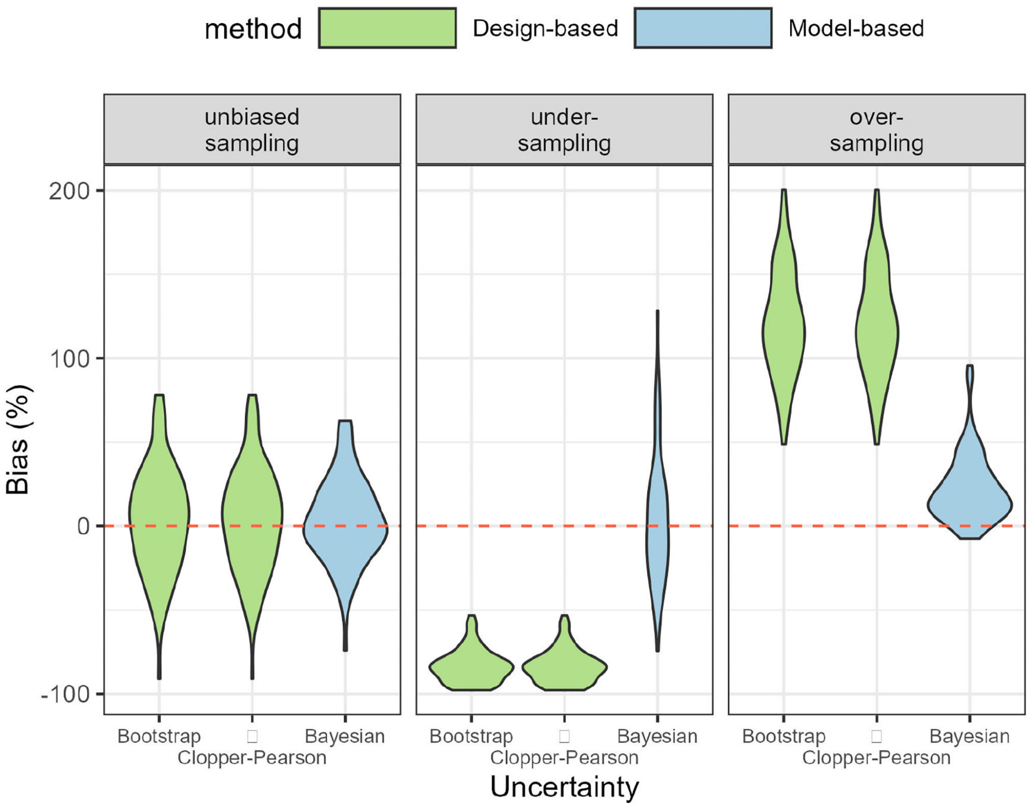

FIGURE 3 | Violin plot of bias in point estimates of total bycatch events. **Left:** data sampling was unbiased and all methods yielded statistically unbiased estimates. **Middle:** Under-sampling scenario: only the model-based approach was accurate. **Right:** Over-sampling scenario: both the design- and model-based approaches were biased upwards. Violin plots are based on 100 simulations.

TABLE 1 | Statistical properties of estimates from the design- and model-based approach.

Method	Uncertainty	Data sampling	n_{years}	Bias (%)	Coverage (%)	Width of CI (%)	n_{obs}
Design-based	Bootstrap	Unbiased	1	3.5	100.0	102.5	15
Design-based	Clopper-Pearson	Unbiased	1	3.5	100.0	115.0	15
Model-based	Bayesian	Unbiased	1	3.6	100.0	120.4	15
Design-based	Bootstrap	Under-	1	−83.5	100.0	195.0	5
Design-based	Clopper-Pearson	Under-	1	−83.5	100.0	259.6	5
Model-based	Bayesian	Under-	1	3.0	100.0	204.3	5
Design-based	Bootstrap	Over-	1	121.0	100.0	46.1	63
Design-based	Clopper-Pearson	Over-	1	121.0	100.0	50.1	63
Model-based	Bayesian	Over-	1	22.1	100.0	78.6	63

One year of data was simulated a 100 times. Bias of point estimate, coverage of (frequentist 95%) confidence or (Bayesian 80%) credible interval (CI) and precision (as CI width relative to the point estimate) are reported. The last column indicates the average number of bycatch events ($n_{\text{obs}} = \mathbb{E}\left[\sum_{ijk} y_{ijk}\right]$) *that were recorded by onboard observers during data sampling.*

precision was very low with CI spanning some 200% of the point estimate for the unbiased and under-sampling scenarios. This low precision was the result of having to work with as few as 5 observed bycatch events on average (**Table 1**). Precision improved with over-sampling, but was still as high as 50% of the point (over-)estimate. The model-based approach was well-calibrated in both the unbiased and under-sampling scenarios (**Figure 4**): model-based estimates were on average equal to the truth whereas this was only the case with design-based estimates when sampling was unbiased. In addition, the model-based approach was able to recover the temporal profile of bycatch risk (**Figure 5**) in these two scenarios, but with an increased accuracy and precision if sampling was unbiased. In the over-sampling scenario, both the design- and model-based approaches were not well -calibrated (**Figure 4**) and the model-based approach over-estimated bycatch risk when no data were collected (**Figures 1**, **5**).

3.2. Model-Based Approach With Several Years of Data

With several years of data, the model-based approach was able to yield nearly unbiased estimates: the bias was smaller than 3 bycatch events when sampling was unbiased, but as large as 10 (on average) with biased sampling and 3 years of data. The precision of estimates improved with several years of data, as expected with larger sample size. Precision of model-based estimates with over-sampling were already acceptable with 3 years of data: an 80% credible interval width of 50% corresponds to a coefficient of variation of $\frac{50}{2.5} \approx 20\%$ assuming a normal distribution for the posterior. The model-based approach allowed to obtain estimates at the weekly scale (**Figure 6**): these estimates were approximately unbiased in the unbiased and over-sampling scenarios, but were biased for the under-sampling scenario. In that latter case, the bias was correlated with the temporal pattern used to simulate dolphin presence (**Figure 1**): it was the largest when dolphin presence was at its highest but positive at the beginning of a year and negative at the end of the same year. Both biases were greatly attenuated with increased sample size.

4. DISCUSSION

Using Monte-Carlo simulations, we investigated the statistical properties of a model-based approach, regularized multilevel regression with post-stratification, to estimate the total number of bycatch events in a fishery operating year-round. Simulations were broadly informed from the case of common dolphins and pair-trawlers in the Bay of Biscay and from harbor porpoises and set-gillnets in Celtic Seas. A salient feature of simulations was biased sampling with observers being preferentially accepted onboard when bycatch risk was either high or low. Data simulations in that latter case, which is the most realistic one in the Bay of Biscay (Peltier et al., 2016), resulted in as few as 5 observed bycatch events per year on average (**Tables 1**, **2**). This aligns with the ubiquitous description of small cetacean bycatch being a rarely observed event. It was nevertheless possible to fit a regularized multilevel regression model on these data. Importantly, estimates from this model-based approach were statistically less biased than the design-based estimates when sampling was biased. Model-based estimates were, however, imprecise but this is largely to be expected (Amandè et al., 2012), especially with as few as 5 observed bycatch events per year. The design-based approach was also imprecise, even in the unbiased data sampling scenario of 5% coverage of the fleet, which is not reached in practice (Anonymous, 2016; ICES, 2020b). The design-based approach was very sensitive to how data were collected: this approach severely under- or over-estimated bycatch when sampling was biased, whereas the model-based approach was still well-calibrated with under-sampling, but not with over-sampling (**Figure 4**).

Biases in onboard observer data are pervasive and widely acknowledged (Babcock and Pikitch, 2003; Benoît and Allard, 2009; Peltier et al., 2016). Enforcing coverage as required to achieve a pre-specified precision in estimates can be challenging in practice. For example, in 2016, France only achieved a coverage rate less than 2% for most métiers and concluded on the impossibility of scaling-up observed bycatch rates to the whole fleet (Anonymous, 2016, p. 24). There were, however, 9 bycatch events of common dolphins in pair-trawlers targeting European hake (*Merluccius merluccius*). From these numbers, bycatch was described a “rare” event (Anonymous 2016, p. 23). Such a conclusion would be warranted if sampling were representative, in which case the design-based estimate could be used, even though its precision would still be very low. On the other hand, with under-sampling, this conclusion is misleading as our simulations further illustrated: although only 5 bycatch events were observed on average (**Figure 4**), the true number of bycatch events was on average 60 times larger (**Figure 4**). In our simulations, the true bycatch rate was on average ≈ 3% over a year, which is not rare, but not frequent either. Moreover, interviews with French skippers deploying trawls or gillnets in the Bay of Biscay revealed that more than 80% of respondents declared to having experienced at least one small cetacean bycatch event in a year (Cloâtre, 2020). Such a large proportion contradicts the idea of common dolphin bycatch being a rare event in the Bay of Biscay, but rather suggest severe biases in onboard observer data that result in the rare reporting of bycatch events, rather than a rarity of events *per se*. The common dolphin in the Bay of Biscay illustrates how under-sampling may distort the perception of bycatch as a very rare event when it can, in fact, be widespread. This is a catch-22 situation whereby cetacean bycatch is described as a rare event because it is rarely reported, and this perceived rarity may serve to argue against ambitious dedicated monitoring programmes out of cost-effective considerations, thereby preventing to dispel the initial misconception.

Finding an optimal sampling plan for fisheries with rare bycatch events is a long standing problem (ICES, 2009). Several strategies have been attempted: for example in the United States, one strategy is “pulsed sampling” whereby a particular fishery or métier is very heavily sampled for a short period of time in order to maximize the chance for observers to record any bycatch that might occur (ICES, 2009). This pulsed sampling strategy corresponds to our over-sampling scenario wherein monitoring effort is positively correlated with bycatch

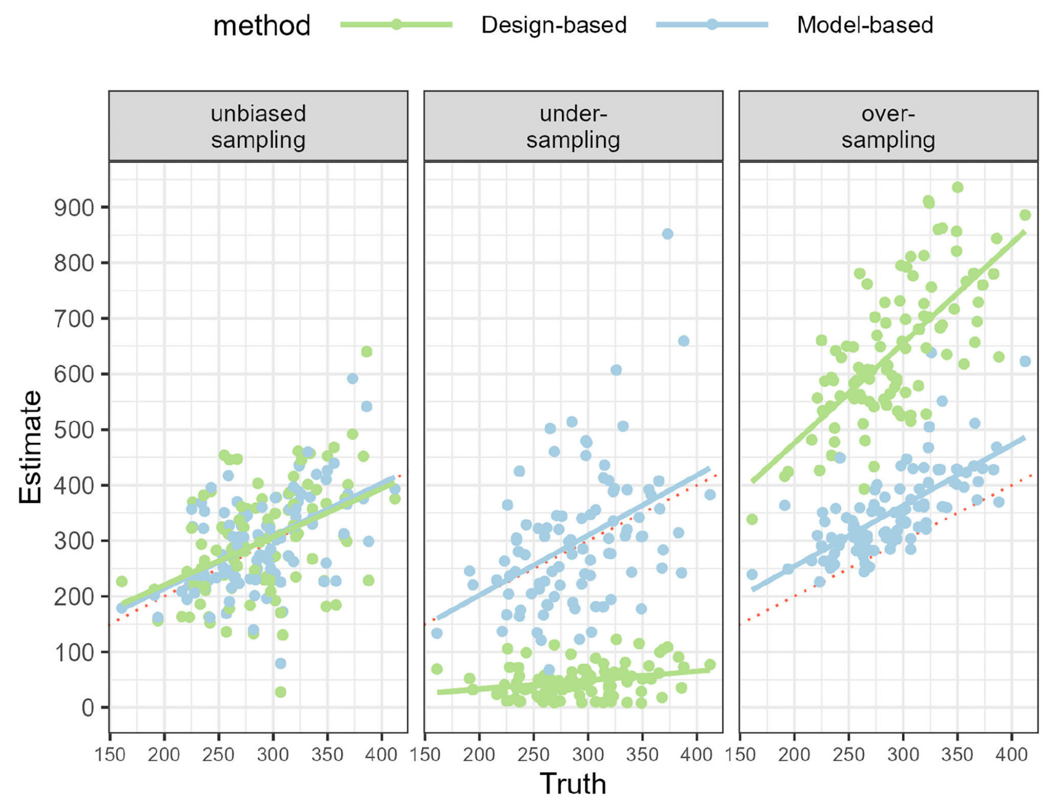

FIGURE 4 | Regression lines of point estimates against the true number of bycatch events, showing the calibration of the design- and model-based approach. The *x*-axis shows the true number of bycatch events across 100 simulations, spanning between 150 and 400 events. The red dotted line shows the identity line, i.e., no bias. **Left:** data sampling was unbiased and all methods yielded statistically unbiased estimates. **Middle:** Under-sampling scenario: only the model-based approach was well-calibrated. **Right:** Over-sampling scenario: both the design- and model-based approaches were not calibrated to the truth.

risk. Under this scenario, the absence of any sampling at all when bycatch risk was low was detrimental to the accurate estimation of bycatch events with our model. Model-based estimates were, however, less biased than design-based estimates. Arguably, this comparison is somewhat artificial as a correct comparison would use all the available information and uses estimators that are season-specific to account for under-sampling when bycatch risk is low if such a period is known to the investigator. Notwithstanding this shortcoming, model-based estimates represented an improvement and allowed to infer the bycatch risk profile accurately, especially with several years of data.

We showed with our Monte-Carlo simulations that regularized multilevel regression with post-stratification can nevertheless be used to analyze bycatch data despite concerns about non-representative sampling. Model-based approaches (Palka and Rossman, 2001), with post-stratification (Lennert et al., 1994), or machine learning (Carretta et al., 2017), or multilevel regression (Sims et al., 2008; Martin et al., 2015) have previously been used to estimate bycatch rates. Traditional, design-based, ratio estimates are biased if sampling is biased; imprecise if observer coverage is low (as is the usual case in the North East Atlantic; see for example Figure 14, p. 114 in ICES, 2020b); and volatile if bycatch events are only observed occasionally (Carretta et al., 2017). The traditional remedy to stabilize estimates and improve precision is to bypass year-specific estimation and pool several years together (Carretta and Moore, 2014; ICES, 2018). This pragmatic solution improves precision but does not address the problem of biased sampling. It also introduces estimation bias for any year-specific estimates by pooling completely several years in order to stabilize the variance of estimates (ICES, 2009, p. 36): any between-year differences are thus ignored in order to obtain a better precision of estimates. It is a reasonable approach in practice, but one

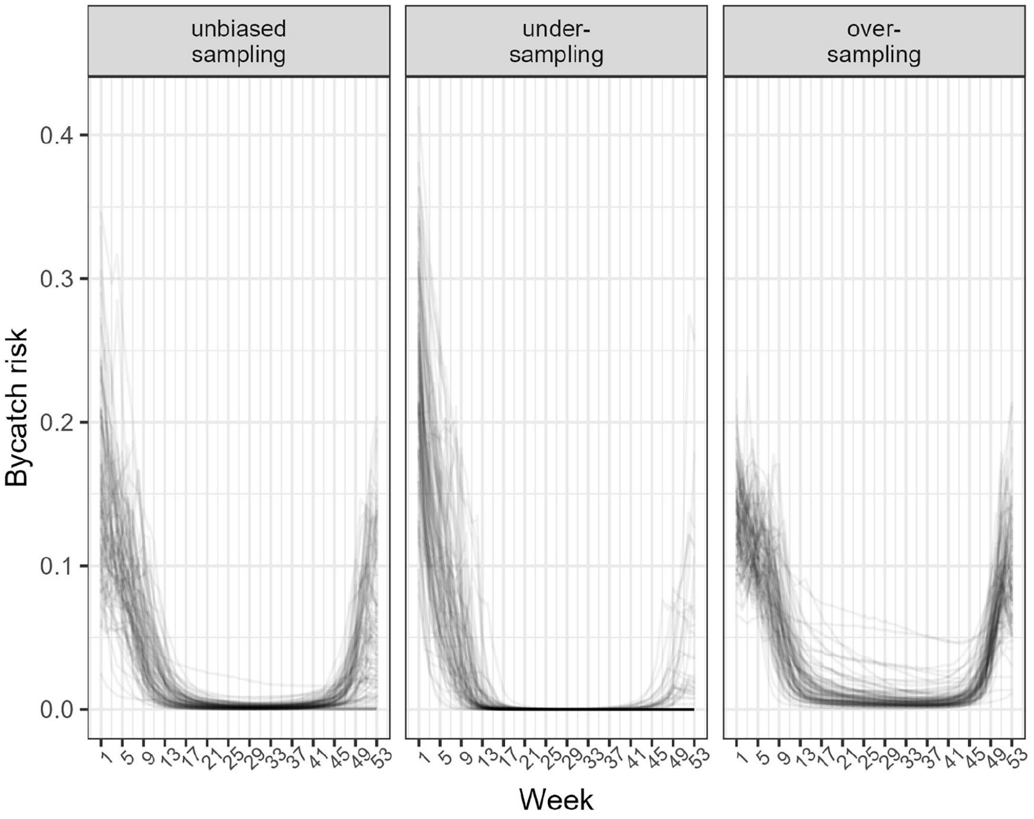

FIGURE 5 | Estimated temporal pattern in mean bycatch risk from the model-based approach. **Left:** data sampling was unbiased. **Middle:** Under-sampling. **Right:** Over-sampling. The model-based approach recovered the correct pattern overall, but overestimated risk in the over-sampling scenarios when risk was, in fact, nil but no data were collected.

that can be improved. Model-based approaches offer a trade-off between no-pooling (keeping all years separate) and complete-pooling with a third option: partial pooling or regularization (Gelman and Shalizi, 2013). Regularization is a general term for statistical procedures that give more stable estimates. Our model-based approach achieves regularization by leveraging, via a structured prior model (Equations 2 and 3, see section 2), the within-year information at the weekly scale. The result were more stable and accurate annual bycatch estimates at the cost of some modeling assumptions and weakly-informative priors. Importantly, weekly estimates could also be obtained with our model-based approach.

Our model-based approach is semi-parametric as it uses a random walk prior to learn from the data the weekly pattern in bycatch risk. This prior is also ensuring some smoothness in the temporal risk profile as it translates an assumption on the correlation between 2 consecutive weeks. This random walk model remains simple as the order is fixed to 1. We further expanded this model to allow for between-years variation in the weekly risk profile with a Gaussian Process prior (Neal, 1998; Goldin and Purse, 2016). Importantly, these two prior choices (a random walk and a Gaussian Process prior) add structure to the model and help in leveraging the information present in the sparse data typical of onboard observer programmes. Even when with over-sampling, these choices were not detrimental as model-based estimates were statistically unbiased and precise with 3 years of data (**Table 2**). The explicit consideration of time effects is key to mitigate bias in sampling. In our simulations, dolphin presence was caricaturally seasonal, and observers could be preferentially allowed on fishing vessels when dolphins were less or more likely to be present (**Figure 1**). Our model was still able to provide statistically unbiased estimates of bycatch in those scenarios, although these estimates were very imprecise with under-sampling. However, they were not

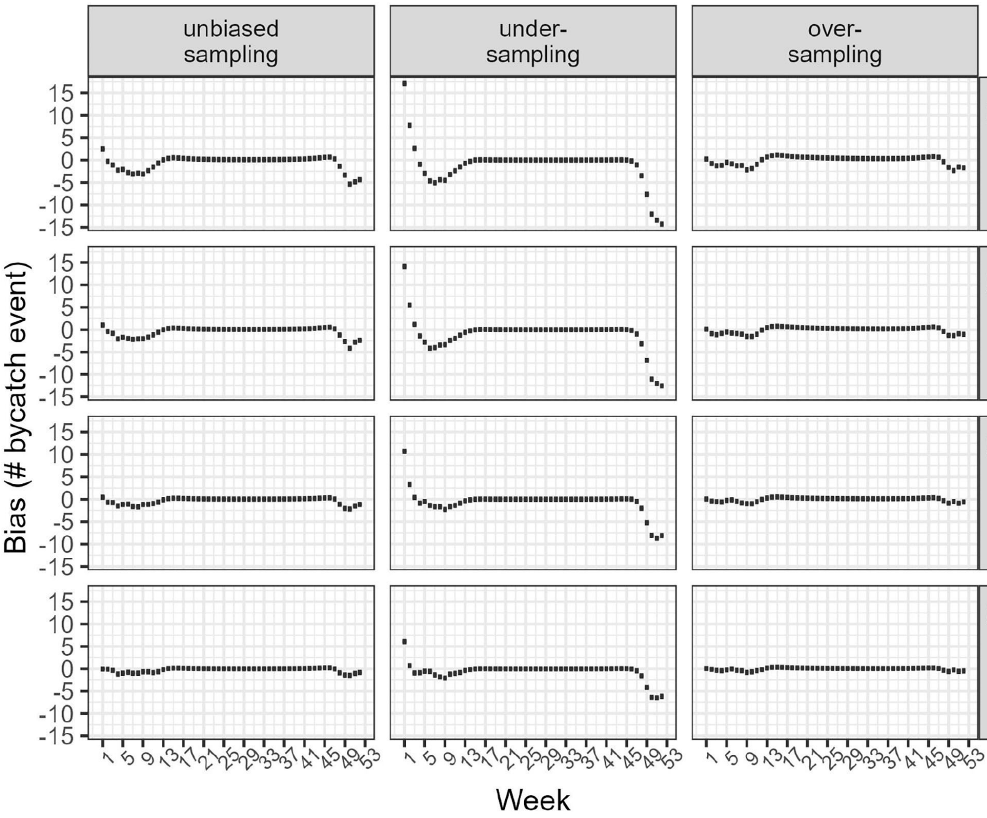

FIGURE 6 | Box plots of bias (in number of estimated bycatch events compared to the truth) in the weekly model-based estimates of bycatch events. **Left:** data sampling was unbiased. **Middle:** Under-sampling. **Right:** Over-sampling. Each row corresponds to data simulated for a different number of years.

more imprecise than the traditional (but biased) design-based estimates (**Table 1**) if 80% credible interval were used. In addition to being unbiased, these estimates could also reveal with accuracy the temporal risk profile (**Figure 5**). It is important to keep in mind here that our model is different from the data-generating model used in simulating data: our results were not simply an instance of using a true model, which is impossible in practice as a model is by definition a simplification used to capture the salient features of a phenomenon. Our model had some shortcomings: for example, bias increased with 3 years of data compared to 1 year for the under-sampling scenario (contrast **Tables 1**, **2**). This increased bias (toward the prior model) was the result of partial pooling but came with a gain in precision as evidenced in the width of credible intervals. The bias progressively wore off with more years of data, illustrating thereby the attractiveness of partial pooling and structured priors to regularize estimates (Gelman and Shalizi, 2013; Gao et al., 2019). The gain in reducing bias in estimates and increasing their precision was most evident with over-sampling (**Tables 1**, **2**).

Our model could also provide weekly bycatch estimates which were largely unbiased except in the under-sampling scenario where a positive and negative bias remained at the beginning and end of a year respectively, even with 15 years of data (**Figure 6**). With under-sampling, few observed bycatch events can be collected by design because observers are very unlikely to be accepted on board by skippers. Weekly estimates were too high at the beginning of a year but too low at the end, but this somewhat canceled out at the year-level. There was still a slight overestimation bias resulting from our choice of a non-symmetric pattern for dolphin presence and a symmetric pattern for biased coverage: observing bycatch events at the end of a year was comparatively more difficult than at the beginning of a year because overlap between a non-nil coverage and dolphin presence was smaller at the end of year (**Figure 1**). These shortcomings illustrate that a model-based approach should

TABLE 2 | Statistical properties of estimates from the model-based approach.

Method	Uncertainty	Data sampling	n_{years}	Bias (bycatch events)	Coverage (%)	Width of CI (%)	n_{obs}
Model-based	Bayesian	Unbiased	3	3.0	100.0	91.1	45
Model-based	Bayesian	Unbiased	5	2.1	100.0	76.3	75
Model-based	Bayesian	Unbiased	10	1.1	100.0	59.1	150
Model-based	Bayesian	Unbiased	15	1.9	100.0	50.9	225
Model-based	Bayesian	Under-	3	10.0	100.0	164.6	15
Model-based	Bayesian	Under-	5	6.4	100.0	142.0	25
Model-based	Bayesian	Under-	10	8.3	100.0	112.9	50
Model-based	Bayesian	Under-	15	5.3	100.0	97.8	75
Model-based	Bayesian	Over-	3	7.4	100.0	53.2	63
Model-based	Bayesian	Over-	5	4.8	100.0	42.6	126
Model-based	Bayesian	Over-	10	3.5	100.0	32.6	630
Model-based	Bayesian	Over-	15	3.3	100.0	27.7	756

Several years of data were simulated a 100 times. Bias of point estimate (in number of bycatch events), coverage of (Bayesian 80%) credible interval (CI) and precision (as CI width relative to the point estimate) are reported. The last column indicates the average number of bycatch events ($n_{\text{obs}} = \mathbb{E}\left[\sum_{ijkl} y_{ijkl}\right]$) that were recorded by onboard observers during data sampling.

be tailored to the context of the study, and we designed our simulations largely from our knowledge on the common dolphin in the Bay of Biscay. However, the framework of regularized multilevel regression with post-stratification is very flexible and we believe our proposed model has large potential for generality as it simply translates a decomposition of bycatch risk into a smooth time-varying and (unstructured) time-invariant effects. The model can easily be made more complex, data permitting, to accommodate spatial effects with, for example, a Besag-type prior (Sims et al., 2008; Morris et al., 2019).

Several important assumptions are structurally built into our model: in particular, a first order random was assumed for the mean function of the Gaussian Process prior, with no attempt to estimate from data the correlation parameter (e.g., using an AR(1) prior instead). The choice of a first order random walk was not aiming at uncovering the true data-mechanism: our aim were to reveal a temporal pattern in bycatch risk from sparse data using a flexible, yet parsimonious approach. This was particularly true in the under-sampling scenario where few bycatch events could be observed in any given year of simulated data. In the other scenarios, other choices than the first order random walk could be considered as more data are collected. We also assumed that the range parameter of the covariance function in the Gaussian Process prior for week effects was known and such that bycatch risk was temporally uncorrelated after 4 weeks. Fixing the range parameter is usually not recommended but was motivated by consideration of the data-to-parameter ratio, and computation convenience. Bycatch data are binary and can be sparse: these two features underscore how little information may be available. In this context, limiting the number of parameters to estimate can be justified on pragmatic consideration. The model we are proposing is parameter-rich, but some structure are assumed on these parameters in the form of the prior used. These priors represent choices from the analyst and may be reconsidered and tested, data permitting. There was some evidence that bycatch risk was under-smoothed in the over-sampling scenario which resulted in an over-estimation of bycatch risk (**Figure 5**, rightmost panel). Model expansion is seamless with `Stan` (Gabry et al., 2019), and the above mentioned parameters could be estimated, rather than fixed, with adequate data. Despite somewhat arbitrary prior and modeling choices, our model provided more accurate estimates of bycatch numbers and bycatch risk in under- and over-sampling scenarios. This satisfactory predictive ability points to another important limitation.

Our model is phenomenological, i.e., it is agnostic of the causes behind the temporal variations in bycatch risk. Bycatch risk is the product of dolphin presence and bycatch probability given presence (the latter was constant in our simulations). The model only estimates this product of two probabilities and thus cannot disentangle them without other sources of data. This limitation seems inconsequential in our simulations for the aim of accurate estimation of the total number of bycatch events as interest lies in the effects of causes (how much bycatch?) rather than in the causes of effects (why bycatch occurred?). A straightforward model expansion (as pointed out by a reviewer) would be the consideration of p vessel-level covariates $(z_{1j}, \ldots, z_{pj})$ in Equation (1):

$$\alpha_j \sim \mathcal{N}\left(\sum_{b=1}^{p} \left(\xi_b \times z_{jb}\right), \sigma_{\text{vessel}}\right) \tag{7}$$

Candidate covariates such as vessel length or gear-attributes (e.g., mesh size) could be incorporated in the analysis to improve the exchangeability assumption on vessel-effects. An obvious covariate to consider for detecting self-selection of skippers into observer programme participation is to include whether a skipper has ever accepted an observer, or the number of times it did so in the past: a negative regression coefficient could be interpreted as voluntary skippers having an intrinsically lower risk of bycatch. Including skipper-level covariates could reduce the between-skipper variance σ^2_{vessel}, and improve ultimately precision of bycatch estimates. Consideration of other distributions than the normal (e.g., a skew-normal, or a Student-t distribution with a fixed degree of freedom) would be straightforward with `Stan` but is probably worthwhile only with large enough amount of data for all practical purposes (McCulloch and Neuhaus, 2011).

An important assumption underlying accurate estimation is that the information on the total effort must also be accurate and available at the scale of weeks for post-stratification. This assumption is crucial to scale-up estimates from the (potentially biased) sample to the population, but it does not necessarily hold with fisheries effort as the latter is more often estimated rather than measured directly (Julian and Beeson, 1998; ICES, 2018, 2020b). Here we assumed that the total number of fishing operations (e.g., number of tows for trawls; Tremblay-Boyer and Berkenbusch, 2020) are available as auxiliary information for post-stratification. This assumption about the availability of disaggregated data stems from the explicit consideration of time as an important predictor of variations in bycatch risk. This assumption is necessary for using post-stratification to align the sample with the population targets but may be difficult to meet in practice. Currently, ICES WGBYC uses in its BRA a coarse, but admittedly comparable proxy across fisheries and countries to quantify fishing effort, namely days at sea (ICES, 2019). A day at sea is any continuous period of 24 h (or part thereof) during which a vessel is present within an area and absent from port (Anonymous, 2019a). Importantly, this definition is not at the level of a fishing operation, and effort thus quantified is already aggregated at a level above that at which bycatch data are collected. This coarsening of fisheries effort data is fundamentally a measurement problem, and one that modeling should not be expected to remedy easily. BRA uses an estimate of total fishing effort for the fisheries of concern in a specific region, together with some estimate of likely or possible bycatch rates that might apply for the species of concern, in order to evaluate whether or not the total bycatch in that area might be a conservation issue. A regularized multilevel regression model could be used to obtain estimates of bycatch rates to be used in BRA. Post-stratification could also be attempted using the coarse days at sea proxy for effort, and thus our framework could be adapted to match the requirements of ICES WGBYC.

Assuming that our framework were to be adopted to produce bycatch estimates, how would both fisheries and Non-Governmental Organizations (NGOs) react given the salience of bycatch as a policy issue in Europe? Such a prospective question inevitably entails some speculations (as with all "what-if" questions), but may nevertheless bring some insights as highlighted by a reviewer. Within Europe, the conservation reference currently available for assessing bycatch is that established under the Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas. The agreement has the conservation objective to minimize anthropogenic removals of harbor porpoises (and other small-sized cetaceans), and to restore and/or maintain population depletion to/at 80% or more of the carrying capacity in each assessment unit (ASCOBANS, 2000; ICES, 2020c). Methods for setting conservation reference points were agreed in March 2021 at the meeting of the Biodiversity Committee of the Olso-Paris Regional Sea Convention. This committee adopted the use of the Removals Limit Algorithm for harbor porpoises in the North Sea assessment unit and a modified Potential Biological Removal (Wade, 1998) for common dolphins in the North-East Atlantic (Genu et al.)[3]. Accurate bycatch estimates will be needed for assessment against these reference points. However, fisheries may challenge the accuracy of estimates precisely because they will result from a new statistical model. While a healthy skepticism is warranted, and model improvements are certainly possible, it must be kept in mind that our model only addresses the issue of having a correlation between observer coverage and bycatch risk, and does so with some assumptions. There would remain many biases to be addressed in bycatch data (Babcock and Pikitch, 2003), and many of them would be best addressed with a proper random allocation of professional observers to vessels (that is better design and better measurement). A purely model-based solution can be brittle (Sarewitz, 1999), and may lead to displacement of the problem of bycatch assessment to a never-ending problem of model improvement that would delay any corrective measures or decision (Rayner, 2012). Model-based estimates offer a pragmatic approach to the analysis of already collected data, but should not deflect from improving survey design where possible. Assuming that model-based estimates would be endorsed by a fishery industry, NGOs could challenge in court any reference point that is not zero for PETS, since by definition, it *ought* to be zero. The Habitats Directive requires strict protection and prohibits "all forms of *deliberate* capture or killing" (emphasis added) of all species listed on its Annex IV which includes all cetacean species. The Court of Justice of the European Union has consistently ruled that the adjective "deliberate" is to be understood in the sense of "conscious acceptance of consequences" (Trouwborst and Somsen, 2019): in other words, using knowingly a gear that may potentially catch a protected species contravenes the Habitat Directives. What will eventually play out remains to be seen, but strongly hinges on how polarized the bycatch issue is. As scientists, our duty remains to provide the best available evidence on bycatch and to outline all management actions and their consequences in light of this evidence (Pielke, 2007). Our model is unlikely to change bycatch management in France in the near term: both fisheries and NGOs are at loggerheads, vying for public and official support. They are building constituencies and advertising unyielding positions in diverse medias: we content that a legal confrontation at a national or supra-national level is extremely likely and probably being prepared. We nevertheless think our model, by making use of data already collected within the DCF framework and by encouraging further, ideally dedicated, monitoring; can be part of

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[3] Genu, M., Gilles, A., Hammond, P., Macleod, K., Paillé, J., Paradinas, I. A., et al. (in preparation). Evaluating strategies for managing anthropogenic mortality on marine mammals: an R Implementation with the Package RLA.

a messy solution to the wicked problem (Frame, 2008) of dolphin bycatch in the medium to long term, once the gavel hits and the dust settles.

5. CONCLUSION

We investigated with simulations the ability of multilevel regularized regression with post-stratification to estimate cetacean bycatch for observer programmes when coverage is correlated to bycatch risk. Our aims were to provide a first investigation on model-based estimates obtained from samples preferentially collected either during low- or high-bycatch risk periods. The unbiased sampling case is unrealistic (Babcock and Pikitch, 2003): biased sampling, either under-sampling or over-sampling (ICES, 2009), may be the general case. We considered both of these cases, under quite extreme scenarios whereby data collection was highly correlated with bycatch risk, resulting in either very few observed events with under-sampling, and a large number of observed events with over-sampling. In both cases, multilevel regularized regression with post-stratification was able to produce nearly unbiased bycatch estimates with as few as 5 observed events data. With only 1 year of data, precision was low, especially with under-sampling, and there was some estimation bias with over-sampling one. These results stemmed from the extreme scenarios we considered but illustrate nevertheless that a model cannot be expected to solve all the deficiencies of data collection and measurement. Good measurement is key for accurate estimation and our results actually re-emphasize the importance of design. However, they also show that a good data collection design *and* an adequate modeling framework are synergistic and allow to extract a lot of information for sparse data. Assuming a normal distribution for the bycatch estimates (which is not necessary as the posterior is available, but the following are back-of-the-envelope calculations to be used for deriving heuristics), a 80% Bayesian CI width divided by 2.5 gives an idea of the associated coefficient of variation: the model-based approach can yield a coefficient of variation of 50% with as few as 15 observed events if sampling is unbiased. With under-sampling, one would need 10 years of data (under our data simulation schemes) to obtain the same precision. This re-iterates the need to (i) have dedicated observer schemes, (ii) ensure adequate observer coverage and (iii) use a model-based approach tailored to extract as much information as possible from sparse data, as the first two points are very difficult to live up to in practice.

The key assumptions behind regularized multilevel regression with post-stratification in our simulations are that bycatch risk changes smoothly through time and that accurate data on the number of fishing operations at the same temporal scale are available (e.g., number of tows for trawls; Tremblay-Boyer and Berkenbusch, 2020). When both assumptions can be reasonably entertained, we showed how a model-based approach using recent methodological developments is attractive, irrespective of how data were collected. A further asset of the explicit consideration of a temporal scale is that it may help in pinpointing more precisely windows of heightened risk in order to target adequate mitigation measures (e.g., spatio-temporal closures). The framework of multilevel modeling is very flexible and can accommodate spatial effects, etc., data permitting. Regularization will, in general, be needed to mitigate data sparsity and leverage partial pooling in order to obtain stable estimates of bycatch. Given the satisfactory performance of regularized multilevel regression with post-stratification in our simulations, we recommend further investigations using this technique to estimate bycatch rate and numbers from both representative or non-representative samples. The modeling choices we made (e.g., a first order random walk for the mean function, or fixing the range parameter in the covariance function of the Gaussian Process prior) are not prescriptive, and other choices of prior models for parameters should be investigated. Investigations should be tailored to the context, and modeling choices motivated by the latter: given the complexity of PETS bycatch, a one-size-fits-all solution is unlikely. A re-analysis of > 15 years of observer data on common dolphin bycatch in pair trawlers flying the French flag is currently underway (Rouby et al.)[4] in order to obtain better bycatch estimates that could be further used to estimate conservation reference points in order to better manage this fishery in the long run (Cooke, 1999; Punt et al., 2021).

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://gitlab.univ-lr.fr/mauthier/regularized_bycatch.

AUTHOR CONTRIBUTIONS

MA: led the analyses, the conception, and writing of the paper. ER and KM: support in analyses, paper conception, and writing. All authors contributed to the article and approved the submitted version.

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[4] Rouby, E., Dubroca, L., Cloâtre, T., Demanèche, S., Genu, M., Macleod, K., et al. (in preparation). Estimating cetacean bycatch from non-representative samples (II): a Case Study on Common Dolphins in the Bay of Biscay.

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Estimating Bycatch From Non-representative Samples (II): A Case Study of Pair Trawlers and Common Dolphins in the Bay of Biscay

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Marine megafauna plays an important functional role in marine ecosystems as top predators but are threatened by a wide range of anthropogenic activities. Bycatch, the incidental capture of non-targeted species in commercial and recreational fisheries, is of particular concern for small cetacean species, such as dolphins and porpoises. In the North-East Atlantic, common dolphin (*Delphinus delphis*, Linné 1758) bycatch has been increasing and associated with large numbers of animals stranding during winter on the French Atlantic seashore since at least 2017. However, uncertainties around the true magnitude of common dolphin bycatch and the fisheries involved have led to delays in the implementation of mitigation measures. Current data collection on dolphin bycatch in France is with non-dedicated observers deployed on vessels for the purpose of national fisheries sampling programmes. These data cannot be assumed representative of the whole fisheries' bycatch events. This feature makes it difficult to use classic ratio estimators since they require a truly randomised sample of the fishery by dedicated observers. We applied a newly developed approach, regularised multilevel regression with post-stratification, to estimate total bycatch from unrepresentative samples and total fishing effort. The latter is needed for post-stratification and the former is analysed in a Bayesian framework with multilevel regression to regularise and better predict bycatch risk. We estimated the number of bycaught dolphins for each week and 10 International Council for the Exploration of the Sea (ICES) divisions from 2004 to 2020 by estimating jointly bycatch risk, haul duration, and the number of hauls per days at sea (DaS). Bycatch risk in pair trawlers flying the French flag was the highest in winter 2017 and 2019 and was associated with the longest haul durations. ICES divisions 8.a and 8.b (shelf part of the Bay of Biscay) were estimated to have the highest common dolphin bycatch. Our results were consistent with independent estimates of common dolphin bycatch from strandings. Our method show cases how non-representative observer data can nevertheless be analysed to estimate fishing duration, bycatch risk and, ultimately, the number of bycaught dolphins. These weekly-estimates improve upon current knowledge of the nature of common dolphin bycatch and can be used to inform management and policy decisions at a finer spatio-temporal scale than has been possible to date. Our results suggest that limiting haul duration, especially in winter, could serve as an effective mitigation strategy.

Keywords: additional mortality, anthropogenic activities, modelling, non-representative samples, conservation, small cetaceans, fisheries, post-stratification

1. INTRODUCTION

Over the last 50 years, the conservation status of cetaceans has been deteriorating (Brownell et al., 2019). Over 80 species of cetaceans occur worldwide and bycatch, the non-intentional capture or killing of non-target species in commercial or recreational fisheries (Hall, 1996; Davies et al., 2009), remains a threat, especially to small-sized species (Scarff, 1977; Read et al., 2006; Avila et al., 2018; Anderson et al., 2020). Success stories in small cetacean conservation are the exception rather than the rule (e.g., Bessesen, 2018). Both Rogan et al. (2021) and Bearzi and Reeves (2021) opined of institutional failures to conserve cetaceans in European Waters in spite of current legislation (for example, the Habitats Directive, the Marine Strategy Framework Directive) or regional agreements such as the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS, see **Table 1** for acronyms; ICES, 2020c). Over 20 species of small cetaceans have been registered in the North-East Atlantic, with roughly half of which occurring regularly (Course, 2021). Because of their slow life histories and their limited potential rates of increase, small cetaceans are particularly at risk of decline when anthropogenic activities induce additional mortality on populations (Read, 2008). Anthropogenic activities and their cumulative impacts can take a heavy toll on populations. Common species may disappear, such as short-beaked common dolphins (*Delphinus delphis*, hereafter called common dolphins) in the Adriatic Sea (Bearzi and Reeves, 2021), or are under many threats, e.g., in the Bay of Biscay (García-Baron et al., 2019; Murphy et al., 2021).

In 2013, the common dolphin's conservation status in the European Marine Atlantic, as assessed under Article 17 of the Habitats Directive, was "Unfavourable–Inadequate" because of fishery bycatch (Murphy et al., 2021). Common dolphin bycatch in the Bay of Biscay, in particular, has attracted a lot of media coverage since 2017 in international outlets[1] and motivated (with bycatch of Harbour porpoise *Phocoena phocoena* in the Baltic Sea) a special request of Non-Governmental Organisations to the European Commission in 2019. The International Council for the Exploration of the Sea (ICES) advised in 2020, for the common dolphin in the Bay of Biscay, a combination of temporal closures of all métiers (*i.e* the combination of gear, target species, and fishing area) of concern and application of pingers on pair trawlers to mitigate bycatch outside of the period of closure (ICES, 2020b). Temporal closures, restricted to winter months in which strandings of common dolphins with evidence of bycatch have increased in recent years (ICES, 2020d), could have been implemented as emergency measures under the provisions of the Common Fisheries Policy. For 2021, France instead required the mandatory use of acoustic repulsive devices (pingers) on all pair trawlers flying the French Flag (code métier Pair trawlers and hereafter referred to as PTM) operating in the Bay of Biscay[2], a technical mitigation measure whose efficiency was found wanting (Ulrich and Doerner, 2021). This decision against the advice of ICES was motivated by a lack of knowledge on common dolphins, including its abundance at the level of the whole North-East Atlantic (the currently recognised management unit: Murphy et al., 2013) and the extent of bycatch. The issue of managing uncomfortable knowledge through interpretation of scientific uncertainty can be raised (Schweder, 2000; Rayner, 2012); yet it should not eclipse that there are genuine difficulties in estimating accurately the true magnitude and the extent of bycatch of small cetaceans (Moore et al., 2021).

Several types of fishing gear are known to cause cetacean bycatch: drift nets, set gill, trammel nets, both pair and single midwater trawls, and some demersal trawls (Rogan and Mackey,

TABLE 1 | List of acronyms.

Acronym	Meaning
ASCOBANS	Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas
DCF	Data collection framework
DPMA	"Direction des pêches maritimes et de l'aquaculture"
GNS	Gillnetters
GTR	Gill trammel netters
ICES	International Council for the Exploration of the Sea
Ifremer	Institut Français de Recherche pour l'Exploitation de la Mer
ObsMer	Observation des captures en Mer (French national observer scheme for monitoring fisheries)
PBR	Potential Biological Removal
PTM	Pair trawlers
PTB	Bottom pair trawlers
VAST	Vector-Autoregressive Spatio-Temporal
WGBYC	ICES Working Group on Bycatch of Protected Species
WKEMBYC	ICES Workshop on fisheries Emergency Measures to minimise BYCatch of short-beaked common dolphins in the Bay of Biscay and harbor porpoise in the Baltic Sea

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[1] https://www.nytimes.com/2019/05/02/world/europe/france-dolphins-fishing.html

[2] https://www.mer.gouv.fr/protecting-cetaceans-annick-giradin-presents-7-commitments-made-french-state-fishermen-and

2007; Fernández-Contreras et al., 2010; Peltier et al., 2016). Accurate quantification of bycatch rates by fishing gears or métiers remains a challenging endeavour (Babcock et al., 2003; ICES, 2019). Traditionally, bycatch data are collected by onboard observers monitoring fishing operations and recording the unwanted catch of non-commercial species (Course, 2021). Ratio estimators, based on the number of observed hauls with bycatch over the total number of monitored hauls, are used (Alverson et al., 1994; page 18) but are plagued by large uncertainties due to low coverage and the usual small number of hauls with small cetacean bycatch (Babcock et al., 2003; Authier et al., 2021; Course, 2021). It may also happen that some bycatch events may not be reported by non-dedicated observers since they may drive observations for other purposes than report bycatch (e.g., commercial discards or stock assessments). A critical assumption behind the use of such ratio-estimators is that of a representative sample: this assumption is difficult to sustain unless monitoring is dedicated to marine mammals, and allocation of observers to fishing vessels is truly randomised (that is, not at the discretion of skippers). Even if we are willing to assume representative sampling, if coverage is low, the main challenge remains to extrapolate from sample to the whole fisheries. In France, monitoring of cetacean bycatch in fisheries is non-dedicated (Cornou et al., 2018), and the collected data are described as non-representative of the bycatch events, preventing the use of ratio-estimators (Anonymous, 2016; page 24).

This non-dedicated nature and the sparseness of the bycatch data complicates the use of state-of-the-art spatio-temporal models such as Vector-Autoregressive Spatio-Temporal (VAST) (Thorson, 2019). This framework accommodates density-dependence, spatial and temporal scales to estimate biomass or abundance or presence of a species (Thorson et al., 2015). Spatio-temporal models are also used to model the co-occurrence of commercial and bycaught species, allowing the estimate of bycatch risk with time-varying spatial effects (Ward et al., 2015). These types of model-based approaches methodologies allow modelling spatial and temporal auto-correlation through the use of Gaussian process priors. It is difficult to transfer a priori the same model-based structure to analyse small cetacean bycatch. Models such as VAST capitalise on the availability of catch data that are collected as part of fisheries monitoring. In contrast, bycatch monitoring is not as developed or efficiently enforced in many fisheries in Europe (ICES, 2019, 2020a; Sala et al., 2019), and bycatch data are typical of low quality and unrepresentative (Authier et al., 2021). In Europe, fisheries monitoring is carried out under the Data Collection Framework (DCF) but "remains not well-suited for the dedicated monitoring of rare and protected bycatch in high-risk fisheries since its main focus is the statistically-sound random sampling of all commercial fisheries" (Ulrich and Doerner, 2021). Because of these data quality issues, Authier et al. (2021) conducted a simulation study to gauge the potential of investigating recent methods for the analysis of non-representative samples (for a recent example of a model-based approach to estimate bycatch, refer to Luck et al., 2020) in the context of small cetacean bycatch: they concluded the potential of regularised multilevel regression with post-stratification to infer more accurately bycatch rates (although uncertainties remained large). The approach of Authier et al. (2021) also makes use of Gaussian process priors but does not necessarily assume that a large dataset has been collected.

We analysed historical bycatch monitoring data collected by onboard observers (from 2004 to 2020) on PTM, a métier historically associated with high levels of dolphin bycatch in the Bay of Biscay (ICES, 2019; Murphy et al., 2021). Leveraging recent modelling developments (see companion article; Authier et al., 2021), we jointly estimated bycatch risk, haul duration, and number of hauls per days at sea (DaS) from an updated and revised observer dataset on common dolphin bycatch. The modelling procedure accounts for the sparseness of the bycatch incident dataset and the low observer coverage through constraints. This type of constraint (which can be viewed as some sort of penalisation) is also called regularisation. We used structured priors, such as Gaussian processes, to achieve regularisation and leverage the within-year information at the weekly scale (inducing correlation between some weeks). Structured priors allow inducing some spatial- or temporal-dependency between so called random-effects whereas unstructured priors do not induce such dependency (but both assume exchangeability). Importantly, we used this model-based approach to disaggregate bycatch risk at the level of calendar weeks in order to document within-year variations. Estimates were summed over a whole year to investigate between-year variations in the number of bycaught dolphins. We compared these model-based estimates with strandings, both within- and between-years. Finally, we concluded with recommendations on conservation and mitigation.

2. MATERIALS AND METHODS

2.1. Materials

2.1.1. Study Division

The study area (**Figure 1**) encompasses 10 ICES divisions within area 27: it includes the Bay of Biscay, the English Channel, and part of the Celtic seas. These zones are associated with submesoscale and mesoscale oceanographic processes, such as eddies and upwelling, that enhance ecosystem productivity and result in high availability of fishes, including commercial species (e.g., European seabass *Dicentrarchus labrax*, Sardine *Sardina pilchardus* or Anchovy *Engraulis encrasicolus*). Each division can roughly be classified as oceanic or neritic: divisions 7.d, 7.e, 7.f, 7.g, 7.h, 8.a, 8.b, and 8.c are related to neritic ecosystems while divisions 7.j, and 8.d are related to oceanic ecosystems.

2.1.2. Data Sources

Two main sources of data were used. The first dataset, called ObsMer[3] ("Observation des captures en Mer"), is collected as part of an onboard observer program set up within the Data Collection Framework of the Common Fisheries Policy. The ObsMer program is carried out by Ifremer ("Institut Français de Recherche pour l'Exploitation de la Mer"), under the supervision of the Directorate of Fisheries and Aquaculture ("Direction

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[3] https://sih.Ifremer.fr/Ressources/ObsMer

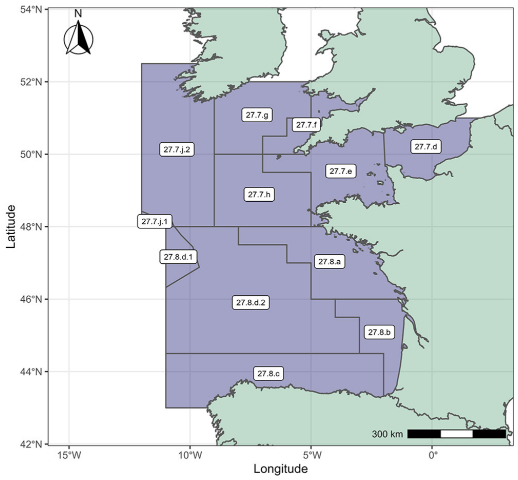

FIGURE 1 | Study area in the North-East Atlantic ocean, with ICES divisions overlayed.

des pêches maritimes et de l'aquaculture," DPMA). ObsMer observers' primary duty is to register the length and weight composition of catches. Still, they have to report any bycatch event if they witness such events. ObsMer data on PTM cover 4, 484 hauls between 2004 and 2021, of which 82 were associated with a bycatch event of at least 1 and up to 50 common dolphins. ObsMer provides, among other information, the geographic position, timing, and duration of hauls. Although ObsMer is aiming at a coverage of 10 and 5% of fishing effort for (level-3 métier) PTM for vessels of more than 15 m and less than 15 m, respectively, these figures are rarely, if ever, reached in practice: accepting onboard observers remains entirely at the discretion of skippers. The effort is quite low overall, ranging from 0 to 11% of Days at Sea (DaS) (**Table 2**). A DaS is any continuous period of 24 h (or part thereof) during which a vessel is present within an area and absent from the port (Anonymous, 2019). The number of observed hauls with at least one bycatch record is very small because the yearly percentage of observed hauls with a bycatch event never exceeded 4.5% and was 0 in nearly half of the surveyed years. ObsMer data on pair-trawlers are an unrepresentative sample of hauls, largely because allowing an observer remains largely at the discretion of skippers (Babcock et al., 2003; Benoît and Allard, 2009).

The second dataset provides monthly estimates of total fishing effort in each division. This dataset is generated from the algorithm SACROIS developed by Ifremer and integrates data from Vessel Monitoring System, log-books, and landing statistics (for boats longer than 18 m from January 1, 2004, and longer than 15 m from January 1, 2005; Système d'Information Halieutique, 2017). SACROIS aims at (1) correcting errors that could exists in the integrated dataset due to recording or collecting errors and (2) reconstitute métiers during the fishing trip as they are not recorded in logbooks or fish market data (Cornou et al., 2018). The SACROIS dataset provides the best available estimates of total effort, in DaS, between 2004 and 2020 (**Table 2**). There are also refusals from skippers due to administrative and security reasons. Skippers must file an application for authorisation to embark observers and even if they decide to file, the authorisation may be declined due to security reasons (e.g., not enough room or rails not high enough).

These two datasets are complementary for our purposes: ObsMer provides micro-level data on marine mammal bycatch at the resolution of hauls. From these data, bycatch risk may be estimated (Luck et al., 2020). Fishing trips effort data, on the other hand, are macro-level: they provide spatialised effort data at the scale of a whole fishing fleet. These population-level data on effort allows the post-stratification of bycatch risk estimated from observer data to obtain the number of bycaught dolphins (Authier et al., 2021). Descriptive statistics of both datasets are displayed in **Table 2**. Used in tandem, both datasets allow using regularised multilevel regression with post-stratification to estimate cetacean bycatch from non-representative samples (Authier et al., 2021).

Estimates were finally compared to strandings along the French Atlantic seaboard. The French Stranding Network, founded in the 1970s, is dedicated to the monitoring of marine mammal strandings along the shores of France (mainland and overseas). Around 400 trained volunteers are currently taking an active part in the network. These volunteers make the complete coverage of French coastlines possible. Standardised training of volunteers by permanent Observatoire Pelagis staff, which takes place two times a year, ensure the homogeneity, comparability, and standardisation of data collection procedures in the field. Observatoire Pelagis is mandated by the French Ministry of Ecology to train and deliver authorisation to handle carcasses of marine mammals (which are all protected species under national law). It also collates the data and analyse it to inform on the status of marine mammal populations. Stranding data for the period 2004–2020 were used. Only common dolphins found with lesions diagnostic of bycatch in fishing gear were considered (Kuiken, 1994) as well as those stranded during multiple stranding events, or "unusual mortality events" related to lesions diagnostic of bycatch. Multiple stranding events were defined as high numbers of strandings occurring in a restricted area with a common cause of death. The threshold was defined at 30 cetaceans over 10 consecutive days recorded along a maximal distance of 200 km in the Bay of Biscay, and 10 individuals per 10 days per 200 km of coastline along the coast of the western Channel (Peltier et al., 2014). Reverse drift modelling uses a deterministic drift model developed by Meteo France (Peltier et al., 2012) to reconstruct the trajectory of every stranded common dolphin from its stranding location to its likely area of death at sea. The number of dead stranded animals in each cell is then corrected by the cell-specific probability of being stranded (Peltier et al., 2016). These probabilities were estimated by numerical experiment in which the drift of carcasses in the study area was simulated in order to assess with which frequency they would reach a coastline (Peltier and Ridoux, 2015).

TABLE 2 | Descriptive statistics for Observation des captures en Mer (ObsMer) and SACROIS data displayed for each year.

Dataset	ObsMer						SACROIS
Year	**Hauls**	**Average Duration (hours)**	**Bycatch events**	**Median nb of dolphins**	**Max. nb of dolphins**	**DaS (Coverage %)**	**Total Effort (DaS)**
2004	4	2.80	0	-	-	4 (0.0)	8 530
2005	5	4.26	0	-	-	4 (0.0)	8 790
2006	122	4.62	0	-	-	90 (1.1)	7 853
2007	727	3.89	6	1.5	5	401 (6.4)	6 305
2008	554	4.81	6	1.5	4	328 (10.9)	3 011
2009	464	5.50	20	2	50	326 (7.4)	4 413
2010	305	3.52	1	4	4	159 (3.5)	4 486
2011	173	3.99	2	3	3	86 (2.1)	4 001
2012	210	3.58	4	4	8	96 (2.4)	4 005
2013	128	3.81	2	5.5	9	75 (1.8)	4 192
2014	114	4.44	0	-	-	78 (1.9)	4 136
2015	136	2.77	1	2	2	78 (1.7)	4 597
2016	156	4.75	5	3	10	106 (2.3)	4 603
2017	196	5.23	12	2	20	124 (2.6)	4 835
2018	184	3.85	1	1	1	102 (2.8)	3 613
2019	438	5.45	11	2	8	289 (7.4)	3 139
2020	123	3.69	2	2	3	70 (4.0)	1 686

2.2. Methods

2.2.1. Modelling Bycatch Risk and Duration of Hauls

Observation des captures en Mer data allow both bycatch risk and haul duration to be modelled. The two may be correlated as a longer towing time may result in an increased likelihood of bycatch, all else being equal. Bycatch risk is defined at the level of a haul. Hauls can differ in duration as skippers may target different commercial species at different times of the year. However, the population-level data on effort is aggregated and available as DaS, the metric currently used in international fora (e.g., ICES Working Group on BYCatch, WGBYC). The number of hauls per DaS was also modelled from the ObsMer dataset in order to scale up bycatch risk per haul by the number of hauls per DaS. We modelled jointly bycatch risk, fishing duration of hauls, and the number of hauls per DaS of pair-trawlers flying the French flag at the week-level for each year between 2004 and 2020 (**Table 2**) and each ICES division (**Figure 1**). The goal of the approach is to model bycatch rates at the weekly scale for each year within each ICES division using a simple autoregressive model. To smooth the fluctuations of estimated bycatch rates in weekly estimates we constrained estimation using Gaussian Process structured priors. These priors allow (i) to estimate an average bycatch risk profile at the weekly scale and from this weekly average, (ii) to estimate year- and division-level deviations.

2.2.2. Notations

Let $\mathcal{N}(d, s)$ denote a normal distribution of location parameter d and scale parameter s. Let $\mathcal{G}(a, b)$ denote a gamma distribution of scale parameter a and rate parameter b. Let $\mathcal{LN}(d, s)$ denote a log-normal distribution of location parameter d and scale parameter s. The gamma and the log-normal distribution are used and compared to model the likelihood of the haul duration since they assume a positive continuous distribution. These distribution laws are appropriate modelling choices for positively skewed data with a constant coefficient of variation. Let $\mathcal{GP}(m, c)$ denote a Gaussian process of mean function m and covariance function c. A Gaussian Process is a prior distribution on a function f in which, for any vector $\boldsymbol{x} = (x_1, \ldots, x_n)$, $f(\boldsymbol{x})$ is drawn from a $n-$dimensional normal distribution with mean $m(\boldsymbol{x})$ and covariance matrix depending only on the distances of the point x from each other (Gelman et al., 2021, page 465). In the following, we will drop the $\boldsymbol{x}$ and write in a shorthand manner $\boldsymbol{\theta} \sim \mathcal{GP}(\boldsymbol{m}, \boldsymbol{S})$ to mean that the vector $\boldsymbol{\theta}$ of n parameters has a Gaussian process prior and follows a multivariate normal distribution whose mean vector $\boldsymbol{m}$ is equal to $m(\boldsymbol{x})$ and whose covariance matrix $\boldsymbol{S}$ is defined for any pairs (x, x') as $S\left(x, x'\right) = c(x, x')$, where c is the covariance function of the Gaussian process prior.

2.2.3. Joint Modelling Approach

Let i denotes the i^{th} haul (fishing operation) happening in ICES statistical division j in week t of year k. Let y_{ijkt}, d_{ijkt}, and n_{jkt} denote, respectively, bycatch event (0 or 1), fishing duration (in hours, $d_{ijkt} > 0$), and the number of hauls per DaS$_{jkt}$. Bycatch risk p_{jkt} is estimated from

$$y_{ijkt} \sim \text{Bernoulli}\left(\mathrm{p}_{jkt} = \text{logit}^{-1}\left(\alpha^{1}_{jkt}\right)\right) \tag{1}$$

To account for strict positivity, fishing duration is modelled either with a Gamma or a log-normal likelihood:

$$d_{ijkt} \sim \mathcal{G}\left(\beta, \frac{\beta}{\bar{d}_{jkt}}\right) \tag{2a}$$

$$d_{ijkt} \sim \mathcal{LN}\left(\bar{d}_{jkt}, \sigma\right) \tag{2b}$$

The number of hauls per DaS is modelled assuming a zero-truncated Poisson likelihood:

$$n_{jkt} \sim \mathcal{P}^{+}\left(\mathrm{DaS}_{jkt} \times \lambda_{jkt}\right) \tag{3}$$

Parameters $\bar{d}_{jkt} = e^{\alpha^2_{jkt}}$ and $\lambda_{jkt} = e^{\alpha^3_{jkt}}$ are rates. The linear predictors $\boldsymbol{\alpha}_{jk}$ are vectors of week-level parameters related to ICES division j and year k (dropping the superscript for convenience):

$$\begin{cases} \boldsymbol{\alpha}_{jk} \sim \mathcal{GP}\left(\boldsymbol{\delta}_k, \boldsymbol{\Sigma}_{\text{division}}\right) & \\ \boldsymbol{\delta}_k \sim \mathcal{GP}\left(\boldsymbol{\epsilon}, \boldsymbol{\Sigma}_{\text{year}}\right) & \\ \epsilon_t = \mu & t = 1 \\ \epsilon_{t+1} \sim \mathcal{N}(\varepsilon_t, \sigma_{\text{week}}) & t > 1 \end{cases} \tag{4}$$

Parameter μ is the intercept. The vector $\boldsymbol{\epsilon}$ aggregates the mean weekly effects (on the linear predictor scale) which are modelled with a first-order random walk to ensure some smoothness in between-week variations (Authier et al., 2021). The vector $\boldsymbol{\delta}_k$ are year-specific deviations from the mean weekly pattern $\boldsymbol{\epsilon}$. The vector $\boldsymbol{\alpha}_{jk}$ are division-specific deviations from the mean yearly pattern $\boldsymbol{\delta}_k$. Smoothness in $\boldsymbol{\alpha}_{jk}$ and $\boldsymbol{\delta}_k$ is controlled via the covariance matrices $\Sigma_{\text{division}} = \Delta_{\text{division}}\Omega\Delta_{\text{division}}$ and $\Sigma_{\text{year}} = \Delta_{\text{year}}\Omega\Delta_{\text{year}}$.Matrices $\Sigma_.$ have dimensions $\mathrm{n}_{\text{week}} \times \mathrm{n}_{\text{week}}$ (53×53). These covariance matrices are decomposed into a product of a diagonal matrix $\Delta_.$ (of dimension 53×53) with the common scale parameter on the diagonal, and a correlation matrix Ω (of dimension 53×53; Chen and Dunson, 2003):

$$\Delta_. = \begin{bmatrix} \sigma_. & 0 & \dots & 0 & 0 \\ 0 & \sigma_. & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & \sigma_. & 0 \\ 0 & 0 & \dots & 0 & \sigma_. \end{bmatrix} \tag{5}$$

$\Omega = \Omega\left(t, t^{'}\right)$ is a matrix with the correlation between week t and week $t^{'}$ of dimensions $\mathrm{n}_{\text{week}} \times \mathrm{n}_{\text{week}}$ (53×53). A Matérn correlation function of order $\nu = \frac{3}{2}$ and range parameter fixed to $\rho = \frac{3}{2}$ was assumed: $\Omega\left(t, t^{'}\right) = \left(1 + \frac{2\sqrt{3} \times d(t-t^{'})}{3}\right) \times \exp -\frac{2\sqrt{3} \times d(t-t^{'})}{2}$ where $d(t - t^{'}) = |t - t^{'}|$ is the temporal distance (in weeks) between weeks t and $t^{'}$. The choice of the range parameter induces a temporal correlation of 0.05 after 4 weeks (that is, temporal independence after a month; Authier et al., 2021). The correlation matrix Ω is assumed known and is depicted in **Figure 2**. Equations 4 and 5 allow modelling an interaction between week, year, and division. The joint model defined in Equations (1), (2a), and (3) includes a time-varying component at the week-scale with interaction with year and division.

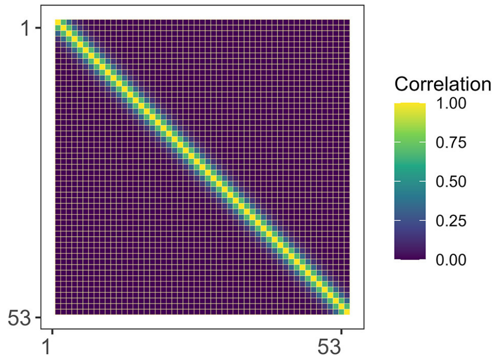

FIGURE 2 | Graphical representation of the assumed correlation matrix Ω.

Simpler models without such interactions, and with only additive effects, were also fitted to the data. The simplest model included only additive random (unstructured) effects (dropping the superscript for convenience):

$$\begin{cases} \alpha_{jkt} = \epsilon_t + \delta^*_k + \alpha^*_j & \\ \alpha^*_j \sim \mathcal{N}\left(0, \sigma_{\text{division}}\right) & \forall\, j \\ \delta^*_k \sim \mathcal{N}\left(0, \sigma_{\text{year}}\right) & \forall\, k \\ \epsilon_t = \mu & t = 1 \\ \epsilon_{t+1} \sim \mathcal{N}(\varepsilon_t, \sigma_{\text{week}}) & t > 1 \end{cases} \tag{6}$$

Models are multilevel, accommodating week-, year-, and division-level variations. They also use structured priors such as Gaussian processes or random walks to regularise estimation (Gao et al., 2019). More information on these models, and on applying (regularised) multilevel regression with post-stratification in the context of estimating bycatch, are detailed by Authier et al. (2021). Estimation was carried out in a Bayesian framework using programming language `Stan` (Carpenter et al., 2017) called from `R` v.4.0.1 (R Core Team, 2020) with library `Rstan` (Stan Development Team, 2020). `Stan` uses Hamiltonian dynamics in Markov chain Monte Carlo (MCMC) to sample values from the joint posterior distribution (Carpenter et al., 2017). Four chains were initialised from diffuse random starting points and run for a total of 2,000 iterations, discarding the first 1,000 as a warm-up. Default settings for the No-U-Turn Sampler (NUTS) were changed to 0.99 for `adapt delta` and 15 for `max treedepth` (Hoffman and Gelman, 2014). Priors are reported in **Table 3**. We fitted a total of 6 models of differing complexity (**Table 4**): we compared models assuming either gamma or a log-normal likelihood for haul duration, and models assuming additive effects vs. interactive effects of the week, year, and divisions. Model fitting was carried out

TABLE 3 | Prior specifications.

Parameter	Specification	Response variable	Meaning
μ	$\sim \mathcal{N}(0, \frac{1}{2})$	Bycatch risk	Intercept (on linear predictor scale).
prop	$\sim \mathcal{D}(1, 1, 1)$		Variance partitioning proportions
σ_{total}	$\sim \mathcal{GG}(\frac{1}{2}, \frac{1}{2}, \frac{\log 10}{2})$		Total variability (on linear predictor scale)
σ_{week}	$= \sigma_{\text{total}}\sqrt{\text{prop}_1}$		Week-level variability
σ_{year}	$= \sigma_{\text{total}}\sqrt{\text{prop}_2}$		Year-level variability
σ_{division}	$= \sigma_{\text{total}}\sqrt{\text{prop}_3}$		Division-level variability
μ	$\sim \mathcal{N}(0, 5)$	Fishing duration	Intercept (on linear predictor scale).
prop	$\sim \mathcal{D}(1, 1, 1)$		Variance partitioning proportions
σ_{total}	$\sim \mathcal{GG}(\frac{1}{2}, \frac{1}{2}, \frac{\log 2}{3})$		Total variability (on linear predictor scale)
σ_{week}	$= \sigma_{\text{total}}\sqrt{\text{prop}_1}$		Week-level variability
σ_{year}	$= \sigma_{\text{total}}\sqrt{\text{prop}_2}$		Year-level variability
σ_{division}	$= \sigma_{\text{total}}\sqrt{\text{prop}_3}$		Division-level variability
μ	$\sim \mathcal{N}(0, 5)$	Haul numbers	Intercept (on linear predictor scale).
prop	$\sim \mathcal{D}(1, 1, 1)$		Variance partitioning proportions
σ_{total}	$\sim \mathcal{GG}(\frac{1}{2}, \frac{1}{2}, \frac{\log 2}{2})$	per Days	Total variability (on linear predictor scale)
σ_{week}	$= \sigma_{\text{total}}\sqrt{\text{prop}_1}$		Week-level variability
σ_{year}	$= \sigma_{\text{total}}\sqrt{\text{prop}_2}$	at Sea	Year-level variability
σ_{division}	$= \sigma_{\text{total}}\sqrt{\text{prop}_3}$		Division-level variability
ρ	$\frac{3}{2}$	All	Range of Matérn correlation function
ν	$\frac{3}{2}$		Smoothness of Matérn correlation function

*$\mathcal{D}()$ denotes the Dirichlet distribution for modelling proportions (such that $\sum_{l=1}^{3}$ **prop**$_l = 1$) and $\mathcal{GG}()$ the Gamma-Gamma distribution for scale parameters (Griffin and Brown, 2017; Pérez et al., 2017).*

on the supercomputer facilities of the "Mésocentre de calcul de Poitou Charentes (Université de Poitiers/ISAE-ENSMA/La Rochelle Université)." Codes are available at https://gitlab.univ-lr.fr/mauthier/cdptmbycatch. For confidentiality reasons, the actual dataset cannot be shared: a synthetic dataset, generated by predicting from the posterior distribution, is provided instead.

2.2.4. Estimating the Total Number of Hauls and Bycatch Events

The number of unobserved hauls N_{jkt} that happened in ICES statistical division j in week t of year k can be estimated from the number of observed DaS in ObsMer ($\text{DaS}_{jkt}^{\text{ObsMer}}$) and from total effort $\text{DaS}_{jkt}^{\text{tot}}$ (and accounting for zero-truncation):

$$\hat{\text{N}}_{jkt} = \frac{\hat{\lambda}_{jkt}}{1 - e^{-\hat{\lambda}_{jkt}}} \times \left(\text{DaS}_{jkt}^{\text{tot}} - \text{DaS}_{jkt}^{\text{ObsMer}}\right) \tag{7}$$

The total number of bycatch events in ICES statistical division j in week t of year k is estimated as the sum of events observed in ObsMer ($\text{Bycatch}_{jkt}^{\text{ObsMer}}$) and the number of unobserved hauls multiplied by bycatch risk ($\hat{\text{p}}_{jkt}$):

$$\widehat{\text{Bycatch}}_{jkt} = \text{Bycatch}_{jkt}^{\text{ObsMer}} + \hat{\text{N}}_{jkt} \times \hat{\text{p}}_{jkt} \tag{8}$$

Similarly, for each year, the number of common dolphins bycaught in pair-trawlers can be estimated using the observed number of bycaught dolphins in ObsMer, the estimated number of unobserved hauls (Equation 7), bycatch risk, and either the median number of dolphins involved in a bycatch event (**Table 2**, or the grand median of $m = 2$ for years with no observed bycatch event). We used the median to attenuate the influence of some bycatch events involving up to 50 dolphins (**Table 2**). These estimates are thereafter referred to as model-based estimates.

2.3. Comparing Model-Based Estimates With Strandings

The sample provided by ObsMer, a non-dedicated observer scheme of marine mammal bycatch, may not be representative of all bycatch. In addition, it provides very sparse data, with less than 100 observed events over 17 years (**Table 4**) when strandings have reached several hundred per week in recent years (ICES, 2020d) (for all causes of death). Despite this, the weekly pattern of bycatch risk provided by ObsMer roughly matches that of strandings, with an increase in winter (**Figure 3**). Despite this rough match, the ObsMer data also suggest a heightened risk in summer, especially in the 2000s, whereas strandings suggest such an increased risk in very recent years (Peltier et al., 2021).

The number of stranded common dolphins with evidence of bycatch can be used to estimate the total bycatch mortality with reverse drift modelling (Peltier et al., 2016). These stranding-based estimates are now used in international working groups (ICES, 2020d). Reverse drift modelling corrects for at-sea drifting conditions, but cannot inform on which fishing gears were responsible for bycatch. Hence, strandings-based estimates are total estimates of bycatch and can be compared to model and observation based estimates of bycatch by French pair-trawlers. These model-based estimates use data independent from strandings, but they should not exceed stranding-based estimates. Second, whether model-estimates correlate with strandings-based ones is of interest to shed light on the increased mortality witnessed in the Bay of Biscay (Peltier et al., 2021). For each year, we checked the magnitude of model-based estimates against stranding-based ones and computed Pearson's correlation coefficient between the two time-series at the month level. To account for drift, these correlations were computed with and without a lag of 2 weeks when aggregating model-based estimates at the month level.

3. RESULTS

We built and compared six models (**Table 4**). Convergence was reached for all parameters with all $\hat{R} < 1.05$. Model $\mathcal{M}_6$ had the lowest WAIC and was selected as the best model for

TABLE 4 | Model selection.

Model	Likelihood for duration	Specification	$\widehat{WAIC}_{se}$	$\Delta_{\widehat{WAIC}}$	Computation time (h)
$\mathcal{M}_6$	Gamma	ICES division × week × year	$18,265_{169}$	0	50
$\mathcal{M}_5$	Log-normal	ICES division × week × year	$18,746_{185}$	481	47
$\mathcal{M}_4$	Gamma	ICES division + week × year	$19,065_{151}$	800	10
$\mathcal{M}_3$	Log-normal	ICES division + week × year	$19,475_{167}$	1,210	11
$\mathcal{M}_2$	Gamma	ICES division + week + year	$21,553_{133}$	3,288	4
$\mathcal{M}_1$	Log-normal	ICES division + week + year	$21,886_{148}$	3,621	3

Models are ordered in increasing order of $\widehat{WAIC}$ (the smaller, the better the fit). se stands for "standard error".

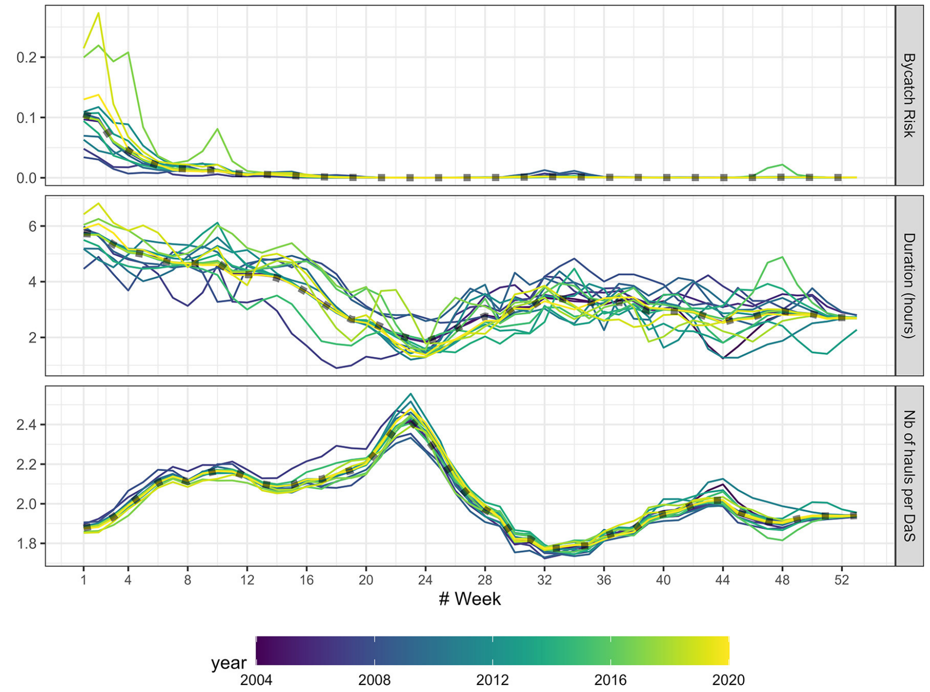

FIGURE 3 | Model-based estimates (posterior medians) of bycatch risk, haul duration, and number of hauls per Days at Sea (DaS) of pair-trawlers (PTM) flying the French flag operating in the study area. Each colour represents a different year (parameters α_{jkt} in Equation 4) and the dotted black line the yearly average (parameters ϵ_t in Equation 4).

further inferences. Model $\mathcal{M}_6$ included an interaction between week, year, and ICES division (Equations 4 and 5). All codes to fit models are available at https://gitlab.univ-lr.fr/mauthier/cdptmbycatch.

3.1. Bycatch Risk, Haul Duration, and Haul Number Per DaS

Haul duration, hauls per DaS, and bycatch risk per haul (Equations 7 and 8) were jointly estimated. Their temporal variations are displayed in **Figure 3** for each week between 2004 and 2020. Haul duration was the highest in week 1 with a posterior median estimate of 5.8 h that decreased to 4.0 h in week 16, before dropping to 2 h in week 24. Haul duration increased up to 3 h in week 32 and plateaued until the end of the year. Remarkable years were 2017, 2019, and 2020 with the longest haul durations estimated from week 1 to 10. From week 10 onwards, years before 2012 displayed some variations in haul duration. In particular, duration was consistently smaller in 2004. In 2016, an increase in haul duration was estimated in week 48 (5 vs. 3 h on average across years).

Bycatch risk was maximum in week 1 (around 0.1) and decreased to almost 0 from week 8 onwards. 2017, 2019, and 2020 were the years with the highest estimated bycatch risk in the first 8 weeks. In particular, the risk was as high as 0.20 in 2017 for the first four consecutive years of the year. Two years prior to 2012 were associated with an increased risk between weeks 30 and 36. The year 2016 showed a rise in bycatch risk in week 48. Bycatch risk and haul duration were positively correlated with weeks in years associated with the highest risk and also having the longest haul duration. Numbers of hauls per DaS were negatively correlated with weeks with longer haul duration. There was little variation across years in numbers of hauls per DaS, but substantial within year variations.

Spatial variations in bycatch risk and haul duration are available as supplementary information. There were noteworthy differences between divisions regarding bycatch risk (see supplementary information). The overall signal was similar to the one observed in **Figure 3** with the highest risk values estimated between weeks 1 and 8. Risk in 2017 and 2019 was higher by a factor of 5 in week 1 compared to other years. After week 8, this difference disappeared. With respect to divisions, division 8.a. was the one with the highest bycatch risk, with an estimate as high as 0.50 in winter 2017 and 2019.

3.2. Number of Bycaught Dolphins

The estimated total number of bycaught dolphins for each year is reported in **Table 5**. The study area was further divided into three strata: a neretic stratum in ICES subarea 7 (divisions 7.defgh) and another in subarea 8 (divisions 8.abc); and an oceanic stratum spanning subareas 7 and 8 (divisions 7.j and 8.d). Estimates were the lowest in the oceanic stratum of the study area and the largest in the neretic stratum spanning ICES subarea 8. The largest bycatch estimate was in 2017, with a posterior median of > 600 common dolphins bycaught in PTM operating in the neretic stratum spanning ICES subarea 8. There were large between-year variations in estimates, ranging from less than a hundred (in 2018) to more than one thousand (in 2017). Uncertainties around model-based estimates were also large.

3.3. Comparison and Correlations With Strandings

Strandings data were used to estimate common dolphins mortality due to fisheries following method described in Peltier et al. (2016) for each month from 1990 to 2020. Stranding-based estimates aggregate mortality due to all fisheries and do not distinguish between gears or métiers. Nevertheless, we correlated stranding-based estimates with our model-based estimates of mortality from PTM flying the French flag both between years (**Figure 4**) and within each year (**Figure 4**). For yearly estimates, correlations were computed on raw and standardised (mean centered and unit variance) values (**Figure 4**). Model-based estimates of bycatch by PTM were always below stranding-based estimates (which do not allow to disaggregate by métiers) save for 2010 (**Figure 4**). In 2010, model-based and stranding based estimates were 465 and 343, respectively, with a large overlap in credibility interval. At the year level, the Pearson correlation between stranding-based and model-based estimates was 0.25. Yearly variations between the two time series were more in phase from 2015 onwards (**Figure 4**). At the within year (between month) level, correlations between the two time-series were always positive. These within year correlations generally increased by 47% (median) when model-based estimates were aggregated by month with a lag

TABLE 5 | Model-based estimates of common dolphin bycaught in PTM in the study area.

Year	Neretic 7	Neretic 8	Oceanic	Total
2004	$_{0}48_{248}$	$_{0}177_{876}$	$_{0}1_{10}$	$_{0}227_{1134}$
2005	$_{0}56_{302}$	$_{0}235_{1101}$	$_{0}2_{15}$	$_{0}293_{1417}$
2006	$_{0}77_{378}$	$_{0}208_{923}$	$_{0}0_{3}$	$_{0}286_{1303}$
2007	$_{15}45_{102}$	$_{0}29_{111}$	$_{1}2_{8}$	$_{16}77_{219}$
2008	$_{1}18_{63}$	$_{11}46_{125}$	$_{0}0_{4}$	$_{12}65_{190}$
2009	$_{10}94_{248}$	$_{172}315_{568}$	$_{0}1_{6}$	$_{183}412_{820}$
2010	$_{0}119_{537}$	$_{4}112_{454}$	$_{0}0_{3}$	$_{4}232_{994}$
2011	$_{9}128_{359}$	$_{0}61_{270}$	$_{0}1_{7}$	$_{9}191_{635}$
2012	$_{22}233_{667}$	$_{0}129_{511}$	$_{0}3_{13}$	$_{23}366_{1190}$
2013	$_{13}315_{1086}$	$_{0}105_{442}$	$_{0}5_{25}$	$_{13}426_{1552}$
2014	$_{0}33_{158}$	$_{0}50_{224}$	$_{0}0_{3}$	$_{0}84_{384}$
2015	$_{0}14_{71}$	$_{2}78_{368}$	$_{0}1_{8}$	$_{2}94_{446}$
2016	$_{0}15_{76}$	$_{55}255_{852}$	$_{0}0_{3}$	$_{55}270_{929}$
2017	$_{0}18_{61}$	$_{156}600_{1355}$	$_{0}0_{1}$	$_{156}618_{1415}$
2018	$_{0}2_{15}$	$_{1}31_{147}$	$_{0}0_{2}$	$_{1}35_{163}$
2019	$_{0}12_{40}$	$_{59}203_{391}$	$_{0}1_{6}$	$_{59}216_{441}$
2020	$_{0}6_{27}$	$_{4}50_{159}$	$_{0}0_{5}$	$_{4}57_{190}$

Divisions 7.j and 8.d are labelled "Oceanic," divisions 7.defgh are labelled "Neretic 7," and divisions 8.abc are labelled "Neretic 8." Estimates (posterior median) are reported with the lower and upper bound of a 80% credibility interval (Louis and Zeger, 2009).

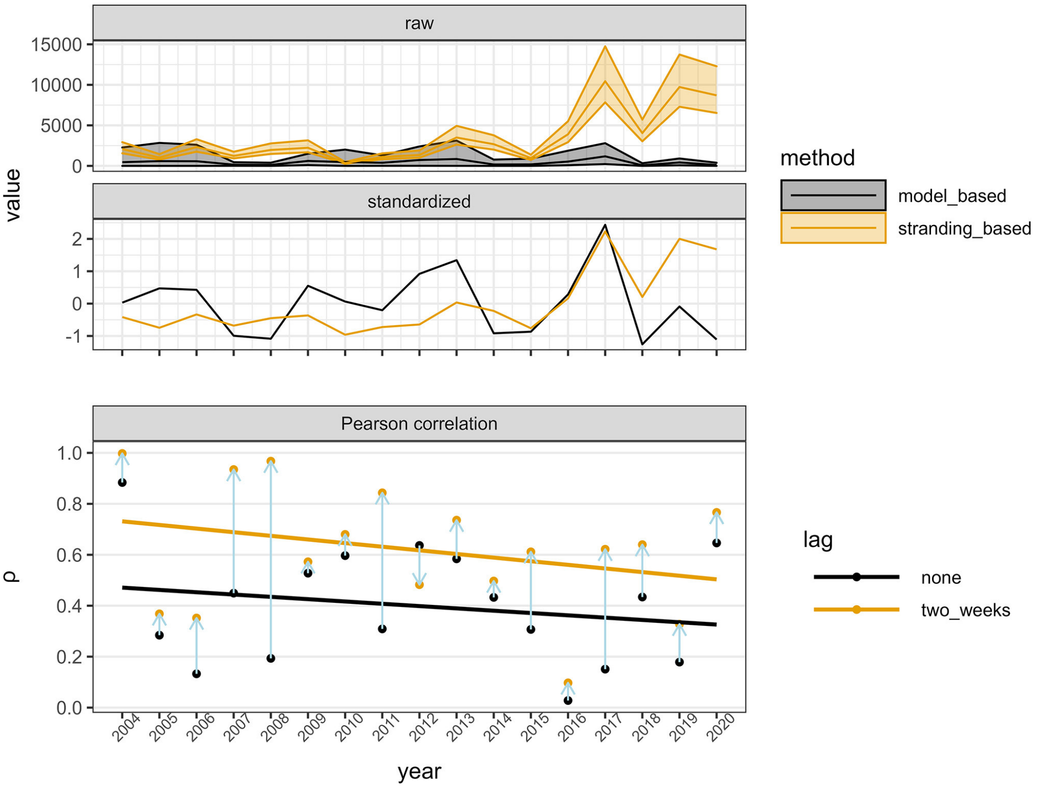

FIGURE 4 | Comparison of model-based (orange solid line) and stranding-based estimates (dark violet solid line) of common dolphin bycatch. **Upper**: Raw estimates with uncertainty intervals (80% for model-based estimates and 95% for stranding-based estimates); **Middle**: standardised (mean centred and unit variance) estimates. **Bottom**: Year-level and month-level (within each year) correlations were computed. At the within year (between month level), correlations were computed with and without 2-weeks lag. Change in the magnitude of the Pearson correlation coefficient is shown with an arrow.

of 2 weeks to account for drift (**Figure 4**). The temporal trend in within year correlation was negative over the study period.

4. DISCUSSION

From a non-representative sample of bycatch events of common dolphins collected over more than 15 years, we estimated bycatch risk and number of dolphins bycaught in PTM. Leveraging recent methodological developments in the analysis of non-representative samples (Gao et al., 2019; Authier et al., 2021), we built a joint model of bycatch risk, haul duration, and haul number per DaS to investigate changes within and between years in common dolphin bycatch. The years 2017 and 2019 were associated with the highest bycatch risk and the longest haul duration in winter.

4.1. Within-Year Variations in Bycatch Risk

We uncovered the within-year pattern in bycatch risk of common dolphins. Bycatch risk is the highest in winter, during the first weeks of a calendar year. This pattern is largely congruent with the pattern seen in strandings of common dolphins in the Bay of Biscay (Gilbert et al., 2021). Both stranding and observer data, which are independent, identified 2017 and 2019 as years with the highest risk of bycatch (Gilbert et al., 2021; Peltier et al., 2021). A limitation of stranding data is how the location of bycatch events must be inferred with reverse drift modelling (Peltier and Ridoux, 2015). The ObsMer data in contrast included geolocalised bycatch events, with a spatial resolution at the level of ICES divisions kept for analysis. Despite this coarse resolution, we could identify divisions 8.a and 8.b as the ones with the highest risk of bycatch by PTM.

The ICES Working Group on Bycatch (WGBYC) estimate bycatch of protected species, including common dolphins, in the

North East Atlantic. Using data collected by onboard observers collected between 2005 and 2017, bycatch rates for ICES divisions on the continental shelf of the Bay of Biscay were estimated with ratio estimators (ICES, 2019). These estimates are not produced at the week level, but ICES (2019) also identified divisions 8.a and 8.b as the ones with the highest of bycatch in midwater trawls for common dolphins over the period 2005–2017 (p. 61). ICES (2019) estimated yearly rates ranging between 0.285 and 0.372 dolphins per DaS and warned against extrapolation given the low observer coverage (p. 61). Our model-based approach overcomes this limitation (Authier et al., 2021) and was able to identify, within each year, that weeks 3 to 5 were the ones with the highest bycatch numbers for both divisions 8.a and 8.b. These results were concomitant with the seasonal stranding pattern observed each year on the French seashore (that is, winter strandings; Gilbert et al., 2021): around 80% of all common dolphin strandings on the French Atlantic seashore is observed between the end of January and the beginning of April.

A key feature of our model-based approach is how it leverages correlations between bycatch risk, haul duration, and number of hauls per DaS (**Figure 3**). Some of the correlations are expected, such as the negative correlation between haul duration and the number of hauls per DaS. However, average haul duration is not constant within a year, with the variations reflecting the change in the commercial fish species targeted by PTM at different time of the year. These variations at the week-level were quite substantial and were taken into account when estimating bycatch in our model. There was a positive correlation between haul duration and a bycatch risk, with at least a two-fold increase in the later when haul duration exceeds 5 h (**Figure 3**). This was particularly evident in weeks 1 to 5 in 2017 and 2019 and week 48 in 2016. The latter was due to a single fishing trip with 5 hauls that lasted > 10 h, each of which resulted in a bycatch event. We recommend, in light of the within-year pattern in haul duration (**Figure 3**), to investigate management actions and mitigation measures on limiting haul duration in winter to assess whether bycatch may also be reduced.

Another possible mitigation measure is to manage common dolphin interactions with PTM with spatio-temporal closures (and acoustic repulsive devices such as pingers) during the first week of a year, when bycatch is the highest. Such measures were explored by WKEMBYC (ICES, 2020d) to reduce bycatch mortality across several scenarios. The performance of each scenario was assessed with the Potential Biological Removal (Wade, 1998), bycatch reduction rate, and fishing effort reduction rate. WKEMBYC (ICES, 2020d) defined an efficiency score by the ratio between the latter two rates. This efficiency score is a trade-off between the expected bycatch reduction and the cost for the fishing industry (without direct economic consideration). WKEMBYC (ICES, 2020d) identified one scenario (scenario L) wherein 2 months closure from mid January to mid March for all fishing métier (and the use of pingers for "Bottom pair trawlers" (PTB) and PTM the rest of the year) was efficient. This scenario appears as a good compromise between bycatch reduction and a reduced cost for the industry. Another efficient scenario (scenario N) involves a 3-month closure from January to March and another 1 month from mid July to mid August for all métier (and the use of pingers for PTB and PTM the rest of year). This scenario can achieve the highest level of bycatch reduction but incurs a high cost to the industry. However, scenarios considered by WKEMBYC are emergency measures meant to reduce punctually common dolphin bycatch. Systematic spatio-temporal closures, which are usually not favoured by the fisheries, were not considered and remained to be explored. In contrast, mitigation measures relying on the large scale deployment of acoustic repulsive devices and the development of new such devices are underway (e.g., in the CetAMBICion project[4]).

4.2. Between-Year Variations in Bycatch Risk

There were large between-year variations in model-based estimates of common dolphin bycatch in the study area. To some extent, these variations were explained by other factors than bycatch risk. For example, the (posterior median) estimate is >600 dolphins in 2017 down to <100 in 2018. The total effort in DaS in the Bay of Biscay (divisions 8.a and 8.b) in the first 10 weeks of 2017, when bycatch risk was highest, is two times the value of total effort in 2018. The median number of dolphins involved in a bycatch event in 2017 was also two times the number in 2018 (2 and 1, respectively, **Table 2**). All else being equal, the estimate for 2017 is expected to be at least four times that of 2018. A further improvement of the model-based approach is to jointly model the number of dolphins involved in a bycatch event. This improvement will require accomodating a large overdispersion, but there were however less than 100 such events in the dataset and we chose to use the median. This is a cautionary choice since the median is less sensitive to the few events for more than 10 dolphins. The uncertainty in the median number of dolphins involved in a bycatch event is currently ignored: incorporating it in future development will further widen credibility intervals (which are already large; Authier et al., 2021). Thus, the model-based estimates are conservative estimates of bycatch by PTM.

Bycatch risk was also very variable between years: the large between-year variations may be due to ecological factors. Bycatch risk results from both fisheries activity within a particular division at a particular time and dolphin presence. The highest bycatch risk values were estimated for the 8 or 10 first weeks of each year within each division of the study area (**Figure 3**). Astarloa et al. (2021) found evidence of an increased abundance of common dolphins in the Bay of Biscay in recent years but weak correlations with biological and oceanographic variables, such as chlorophyll a concentration or sea surface temperature. ICES divisions 8.a and 8.b cover the continental shelf parts of the Bay of Biscay (**Figure 1**). These neritic divisions are witness to sub-mesoscale oceanographic processes and nutrient offloads from the Gironde estuary. Gilbert et al., 2021 correlated eddies and frontal structures with common dolphin mortality areas at sea in the Bay of Biscay (although these authors also concluded that oceanographic accounted for a small fraction of the overall variance in stranding numbers). In winter, the Bay of Biscay

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[4] https://www.cetambicion-project.eu/

environment is characterised by a seasonal cross-shore (West to East) surface temperature gradient with the lowest temperature close to shore and intense frontal activity parallel to the coast (North to South) (Yelekçi et al., 2017). These frontal structures are freshwater fronts, correlated to the mixing of oceanic waters and cold freshwater inputs from river plumes (Yelekçi et al., 2017). These seasonal fronts may be targeted by both fisheries and common dolphins as areas where fish aggregate, thereby putting the latter at risk of bycatch by the former. In July and August, the mesoscale dynamic activity of the Bay of Biscay is rather different than in winter. In summer, there are mainly fronts due to tidal flow (Yelekçi et al., 2017). Summer tidal fronts are quite consistent from 1 year to the next because they are correlated to a repetitive process (i.e., tides) (Yelekçi et al., 2017). During summer, the main frontal activity is a seasonal tidal front, called the Ushant Front and located in front of the French Finistère county (Yelekçi et al., 2017). Its activity peaks in July and August (Yelekçi et al., 2017). We can speculate that the years associated with a high bycatch risk were also those when oceanographic processes favouring the spatial overlap (mediated by fish species; Spitz et al., 2013; Astarloa et al., 2021) between fisheries and common dolphins were particularly operant.

Stranding records are an independent source of data for estimating the number of bycaught dolphins (Peltier et al., 2016). Reverse drift modelling allows the death location of each stranded dolphin showing bycatch evidence for each month between 1990 and 2020 to be inferred. Observed stranding tallies for each month can be corrected for both stranding and buoyancy probabilities (Peltier and Ridoux, 2015). Reverse drift modelling cannot disaggregate estimates by métiers or fisheries but provides an independent estimates of total mortality due to bycatch in the study area: bycatch mortality due to PTM should be lower than the total estimated from strandings. This was verified for all years save for 2010, but uncertainties were large and credibility intervals had a large overlap. While the correlation between model-based and stranding-based estimates was modest at the year level, it was larger at the within-year level, especially after accounting for a lag due to drift (**Figure 4**). The magnitude of the within-year correlation decreased between 2005 and 2020. One interpretation is that of a change in the relative contribution of PTM in total dolphin mortality over time, with PTM having a lesser impact on common dolphins in recent years compared to the 2000s.

4.3. Limitations and Improvements

The model used to estimate the bycatch of common dolphins in PTM has been developed to address the issue of non-representative sampling (Authier et al., 2021). It relies on a post-stratification step that requires accurate effort data at the scale of the whole fleet. The effort measurement retained was that of DaS as in international working groups (e.g., ICES WGBYC; ICES, 2019). Leveraging this important piece of information required the joint modelling of risk at the haul level, haul duration, and that of the average number of hauls per DaS. This modelling choice proved successful for PTM but need not be so for other métiers, in particular for passive gears such as gillnets and setnets. In the later case, a better measure of effort at haul level is soak time, taking into account net length and height, and possible mesh size. These pieces of information may be difficult to collect and retrospectively obtain for post-stratification. Any method seeking to scale up a sample from onboard observer to the whole fleet must confront the difficult issue of accurate measurement and quantification of effort. The model developed for PTM may not necessarily transfer seamlessly to other gears or métiers.

Since 2021, PTM flying the French flag are required to use deterrent acoustic devices (pingers[5]). If these devices are efficient to reduce bycatch risk, this may be taken into account in the model, by adding a covariate in Equation (1). Doing so requires on the other hand to post-stratify on that covariate, which is likely to be a major hurdle. Ignoring the deployment of pingers need not be problematic as the model allows for between- and within-year variations in bycatch risk. Large-scale deployment of pingers in 2021, if effective in reducing risk, will manifest itself in an estimated risk lower compared to previous years. In other words, the model does not have to necessarily take into account all haul-level covariates as long as the aim is prediction rather than explanation (Authier et al., 2021). Taking explicitly into account the pinger effect is only required to make sense of the between- and within-year variations in risk, but not necessarily to estimate those variations.

While Authier et al. (2021) concluded on increased accuracy of using regularised multi-level regression with post-stratification to estimate bycatch with observer data, they also found that estimated precision was low. This was also the case in this study (**Table 5**). A simple way to increase precision is to include self-declared positive bycatch events from fishermen in Equation (7) and (8). Doing so provides a strong incentive for compliance on self-declaration and would result in increased precision as a greater number of hauls (and possibly DaS) would be monitored. Ultimately, full compliance would render modelling moot as bycatch would be perfectly known, if all events were properly recorded (e.g., with Electronic Remote Monitoring) or reported systematically and accurately in logbooks.

4.4. Implications for Common Dolphin Conservation

The common dolphin is one of the most abundant delphinid species within the North-East Atlantic (Hammond et al., 2021). This species may be described as a "keystone species" and an "umbrella species" considering its ecological importance (Murphy et al., 2021). The large additional mortality due to anthropogenic activities on this species triggered a dedicated working group on emergency measures in 2020: the workshop on fisheries emergencies measures to minimise bycatch of short-beaked common dolphins in the Bay of Biscay and harbour porpoises in the Baltic Sea (WKEMBYC) took place remotely in spring 2020 (ICES, 2020d) and informed an ICES advice that same year (ICES, 2020c). This advice led to an infringement procedure issued in July 2020 against France for

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[5] https://www.mer.gouv.fr/protecting-cetaceans-annick-giradin-presents-7-commitments-made-french-state-fishermen-and

failing its obligations under the Habitats Directive, which lists the common dolphin as a species requiring full protection on its Annex IV. The same day, the Paris Administrative Court of Justice condemned the French government for failing to transpose and apply in a timely manner the dispositions of the Habitats Directive and Technical Measures regulating fisheries[6] (in French). Following the unprecedented number of strandings in 2017, a national working group with fishermen, their representatives, government officials, Non-Governmental Organizations, and academics was initiated to address the bycatch issue (Peltier et al., 2021). One recommended action was to improve estimates of bycatch due to high-risk métiers, and to develop adequate methodologies to analyse data from non-representative samples (Authier et al., 2021). The present work reports on a case study on PTM and operating for a large part in the Bay of Biscay, and to a lesser extent in the Celtic seas. The model-based estimates (i) can inform on pressures acting on common dolphins as required by the Marine Strategy Framework Directive (EU 2008/56) and (ii) heed ICES recommendation to develop estimation methods to make the best use of already collected data to inform management in a timely manner (ICES, 2020c).

Using a Potential Biological Removal (PBR) approach (Wade, 1998), ICES (2020d) estimated a removal limit of common dolphin for the whole North-East Atlantic of 4, 926 individuals. An annual bycatch no greater than PBR would allow the population of common dolphins to recover to or be maintained at or above 50% of carrying capacity with a probability of 0.95 (Wade et al., 2021). This conservation objective is, however, different from the ASCOBANS interim objective "to restore and/or maintain stocks/populations to 80% or more of the carrying capacity." Genu et al. (this issue) tuned a modified PBR to a quantitative interpretation of the ASCOBANS interim objective: "a population should be able to recover to or be maintained at 80% of carrying capacity, with probability 0.8, within a 100-year period." The removals limit computed using the modified PBR was down to 985 animals (that is, one fifth of PBR; Genu et al., this issue): in 2017, the estimated bycatch due to PTM and operating the Bay of Biscay amounted to more than 60% of this limit (**Table 5**). In recent years, the estimated contribution of this métier relative to the modified PBR remained large according to our results. Other fishing métiers could potentially impact the common dolphins in the Bay of Biscay resulting in mortality exceeding the threshold inferred by both modified and non-modified PBR. Regarding vessels flying the French flag, gill trammel netters (GTR), gillnetters (GNS), and pair trawlers were potentially associated with common dolphin mortality in ICES divisions 8.a and 8.b for different years (regarding the co-occurrence of mortality and fishing effort) (Peltier et al., 2021). Estimating the contribution of each métiers to overall mortality remains a difficult endeavor. Regarding the PBR removals limit used in WKEMBYC (ICES, 2020d), the overall mortality considering all the fishing métiers exceed PBR, notably from 2016 to 2019, years associated with the suspected highest contribution for the métiers listed above.

5. CONCLUSION

We have provided a case study on estimating bycatch of common dolphins by PTM and operating in the Bay of Biscay from a non-representative sample of bycatch events collected by non-dedicated onboard observers. Leveraging recent methodological developments in statistical modelling, we have illustrated how to use imperfect but currently available data to inform management. Our contribution thus heeds two recent recommendations: to use adequate estimation methods on existing data and to gauge the resulting estimates against threshold values for incidental bycatch, tuned to relevant conservation objectives. We evidenced a substantial contribution of PTM to common dolphin bycatch in the Bay of Biscay, especially in 2017. Considering the entire time series and the correlations with the estimates made from strandings, it is possible that other métiers than PTM were associated with bycatch, especially in recent years. Currently, the main mitigation measures recommended are spatio-temporal closures and the widespread use of acoustic deterrent devices on PTM/OTM and PTB to repel dolphins (ICES, 2020b). Spatio-temporal closures were not implemented in 2021 but systematic and mandatory deployment of pingers on trawls were[7]. Relevant to management in broadening the scope of potential measures is the evidenced correlation between bycatch risk and haul duration: further studies should investigate limiting haul duration (for example, below 5 h) as a complementary mitigation strategy, especially in winter.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because this study uses data that is collected as part of the Data Collection Framework under the Common Fishery Policy of the European Union.

AUTHOR CONTRIBUTIONS

ER and MA led the analyses, the conception, and writing of the paper. LD, TC, and SD curated and prepared the data. MG designed the shiny application. All authors support in analyses, paper conception, and writing, contributed to the article, and approved the submitted version.

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[6] http://paris.tribunal-administratif.fr/content/download/172866/1715763/version/1/file/1901535.pdf

[7] https://www.mer.gouv.fr/protecting-cetaceans-annick-giradin-presents-7-commitments-made-french-state-fishermen-and

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Conflict of Interest: MA and HP are employed by the commercial company ADERA which did not play any role in this study beyond that of employer.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Appendix 5: Tuna-Dolphin problem history

1959	Backdown first practiced by U.S. Captain Anton Meizetich
1961	Annual dolphin mortality estimated to be 550,000
1971	U.S. tuna purse-seine captains Harold and Joseph Medina report decrease in dolphin net entanglement and kill associated with use of the Medina panel
1972	Passage of the U.S. MMPA, including requirement for dolphin mortality levels to be reduced to "insignificant levels approaching zero"
1973	Medina panel used by 60–70% of the U.S. tuna purse-seine fleet
1975	95% of dolphins captured in dolphin sets estimated to be released through backdown
1979	IATTC begins dolphin conservation program modeled on U.S. effort
1981	U.S. embargoes Mexican tuna; MMPA amended to: (a) Reduce incidental mortality of marine mammals to levels approaching zero, (b) conduct research on locating and catching yellowfin tuna not associated with incidental take of dolphins
1984	U.S. proportion of total purse-seine fleet practicing dolphin sets drops to 42% (from 75% in mid 1970s); MMPA amended to: (a) prescribe dolphin mortality quotas for U.S. fleet, (b) require comparability in dolphin mortality between U.S. and foreign fleet, (c) direct research to assess dolphin abundance and trends
1986	Annual dolphin mortality estimated to be 133,000; U.S. lifts 1981 embargo against Mexican tuna; Use of high-intensity floodlights during dolphin sets made at night becomes mandatory for the U.S. fleet
1986–1990	U.S. NOAA Fisheries conducts annual research vessel surveys to estimate dolphin abundance and trends, clarify stock structure, and
1990	estimate dolphin abundance and trends, clarify stock structure, and characterize the ecosystem
1987	Undercover video footage from Panamanian yellowfin tuna purse-seine vessel depicting dolphin kill airs on U.S. national television
1988	MMPA amended to: (a) prohibit sundown sets; (b) require 100% observer coverage on U.S. vessels and comparable coverage for the foreign fleet; (c) place restrictions on use of explosives to herd dolphins; (d) establish vessel performance standards; (e) require research to identify alternative methods of catching tuna; (f) establish stock-specific dolphin mortality limits for foreign fleet and metrics for comparability between foreign and U.S. vessels
1990	Three largest tuna canners in U.S. announce they will no longer purchase tuna caught on dolphins; MMPA amended through Dolphin Protection Consumer Information Act thereby establishing the U.S. dolphin-safe label (defined as no sets made on dolphins during the entire trip for which tuna were captured, as verified by a certified observer)
1992	La Jolla Agreement reached thereby establishing the International Dolphin Conservation Program
1993	Eastern spinner and northeastern offshore spotted dolphins declared depleted under the MMPA
1995	U.S. fleet no longer setting on dolphins, thereby achieving zero dolphin mortality; Declaration of Panama established
1997	MMPA amended to establish International Dolphin Conservation Program Act
1998–2000	U.S. NOAA Fisheries conducts annual research vessel surveys to estimate dolphin abundance and trends, clarify stock structure, and characterize the ecosystem
1999	Agreement on the International Dolphin Conservation Program established
2001	Voluntary "AIDCP dolphin-safe label" created by the Parties to the Agreement on the International Dolphin Conservation Program for tuna caught in the eastern Pacific Ocean
2002	U.S. government scientists submit final report to Congress pertaining to research on "whether the intentional deployment on or encirclement of dolphins with purse seine nets is having a significant adverse impact on any depleted dolphin stock in the eastern tropical Pacific Ocean"; U.S. Secretary of Commerce makes "final finding" that the "intentional deployment on or encirclement of dolphins with purse seine nets is not having a significant adverse effect on any depleted dolphin stock in the Eastern Tropical Pacific ocean"; U.S. dolphin-safe definition changed to include tuna caught with dolphins if no dolphins were killed or seriously injured during those sets
2003	U.S. District Court issues hold on the 2002 change in definition of dolphin safe; U.S. NOAA Fisheries conducts research vessel surveys to estimate dolphin abundance and trends, clarify stock structure, and characterize the ecosystem
2004	U.S. District Court requires that the U.S. label definition remain unchanged from initial 1990 definition
2006	U.S. NOAA Fisheries conducts research vessel surveys to estimate dolphin abundance and trends, clarify stock structure, and characterize the ecosystem
2008	Mexico files formal complaint with World Trade Organization against U.S. claiming that the dolphin-safe label creates unfair trade discrimination
2017	Pacific Alliance for Sustainable Tuna (PAST) earns Marine Stewardship Council certification for tuna caught by setting on dolphins in the eastern tropical Pacific
2018	World Trade Organization Appeals Judges find the U.S. dolphin-safe label to be in compliance with international trade regulations
2019	Net canopies and collapses decrease from 22 and 29% of dolphin sets, respectively, in 1986–1.1% for both; Trial dolphin abundance survey conducted, funded by the government of Mexico and PAST

Figure 1: History of the Tuna-Dolphin problem in the North-East Pacific Ocean. Figure from Ballance et al. (2021).

Dynamique des populations d'espèces élusives :
Le cas du dauphin commun dans l'océan Atlantique Nord-Est

Résumé :

Les espèces élusives sont difficiles à suivre individuellement et il est difficile d'estimer leur mortalité ce qui freine la mise en place de politiques de gestion. En tant qu'espèce élusive, le dauphin commun, *Delphinus delphis* présente des enjeux de conservation importants. La population Atlantique Nord-Est est affectée par les captures accidentelles qui menacent sa viabilité. Les informations démographiques sur cette population sont insuffisantes et notre compréhension de la structure spatio-temporelle des captures ne permet pas de fixer des objectifs de gestion appropriés. Ce projet vise à déterminer le statut actuel de la population au regard des objectifs de conservation Européens. Premièrement, une approche flexible d'estimation des taux vitaux a été développée afin de mettre en évidence les variations temporelles et les effets de covariables en tenant compte de l'hétérogénéité individuelle. Ensuite, l'utilisation de cette méthode, combinée à un suivi transversal, nous a permis de mettre en évidence les variations temporelles des taux vitaux de la population et l'impact des captures sur sa démographie. La population n'est pas viable et son taux de croissance semble s'être détérioré depuis le milieu des années 2000. Troisièmement, en utilisant les données biaisées d'observateurs embarqués, le nombre de captures accidentelles a été quantifié sur une base hebdomadaire pour dix divisions CIEM sur seize ans. Quatrièmement, les taux vitaux obtenus combinés aux estimations de captures permettent de produire des seuils de captures soutenables. Cette évaluation a été effectué par une approche d'évaluation de stratégies de gestion en accord avec l'objectif de conservation européen.

Mots clés : démographie, mammifères marins, mégafaune, dynamique des populations, captures accidentelles, gestion, statistiques Bayésiennes, suivi transversal, âge à la mort, biologie de la conservation, échouages.

Population dynamics of elusive species:
The case of the common dolphin in the North-East Atlantic Ocean

Summary :

Elusive species are notoriously difficult to monitor individually and therefore it is difficult to estimate their anthropogenic mortality and to implement management policies. As an elusive species, the common dolphin, *Delphinus delphis* is a good example of these conservation challenges. The North-East Atlantic population is affected by bycatch that threatens its viability. However, demographic information on this population is very limited and our understanding of the spatio-temporal structure and dynamics of bycatch is insufficient to set appropriate management objectives. This project aims to determine the current status of this common dolphin population with regard to conservation objectives in European waters with a focus on the Bay of Biscay. First a flexible vital rates estimation approach has been developed in order to highlight variations in vital rates over time and the effects of covariates while taking into account individual heterogeneity. Second, using such a methodological approach through a cross-sectional monitoring, allowed us to highlight both the temporal variations of the population vital rates and the impact of bycatch on the common dolphin population demography. The population is not viable and the population growth rate seems to have deteriorated since the mid 2000's. Third, using biased data from on-board observers, the number of incidental catches on a weekly basis was quantified for ten ICES sub-area over sixteen years. Fourth, the resulting vital rates combined with bycatch estimates finally allowed the production of sustainable bycatch thresholds through a Management Strategy Evaluation approach in line with the European conservation objective.

Keywords: demography, marine mammals, megafauna, population dynamics, bycatch, management, Bayesian statistics, cross-sectional monitoring, age-at-death, conservation biology, strandings.

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Abstract

Elusive species are notoriously difficult to monitor individually and therefore it is difficult to estimate their anthropogenic mortality and to implement management policies. As an elusive species, the common dolphin, *Delphinus delphis* is a good example of these conservation challenges. The North-East Atlantic population is affected by bycatch that threatens its viability. However, demographic information on this population is very limited and our understanding of the spatio-temporal structure and dynamics of bycatch is insufficient to set appropriate management objectives. This project aims to determine the current status of this common dolphin population with regard to conservation objectives in European waters with a focus on the Bay of Biscay. First a flexible vital rates estimation approach has been developed in order to highlight variations in vital rates over time and the effects of covariates while taking into account individual heterogeneity. Second, using such a methodological approach through a cross-sectional monitoring, allowed us to highlight both the temporal variations of the population vital rates and the impact of bycatch on the common dolphin population demography. The population is not viable and the population growth rate seems to have deteriorated since the mid 2000's. Third, using biased data from on-board observers, the number of incidental catches on a weekly basis was quantified for ten ICES sub-area over sixteen years. Fourth, the resulting vital rates combined with bycatch estimates finally allowed the production of sustainable bycatch thresholds through a Management Strategy Evaluation approach in line with the European conservation objective.

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