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Ecological monitoring in Marine Protected Areas of the French Mediterranean Sea, an interdisciplinary approach about bottlenose dolphin

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Résumé

Les suivis écologiques permettent de collecter des données et d'acquérir des connaissances sur les espèces ou les écosystèmes. Les suivis écologiques constituent la base sur laquelle s'organise la gestion de la biodiversité. Aujourd'hui, ces suivis se font dans le contexte d'une diversification des échelles d'analyse des enjeux de conservation, et d'une complexification des dynamiques institutionnelles en lien avec la collecte de données écologiques. En Méditerranée française, une trentaine d'Aires Marines Protégées (AMP) forment un maillage de la façade maritime. Ces AMP collectent des données et œuvrent pour la protection de la biodiversité marine, chacune à son échelle et avec ses moyens. Pour de nombreux enjeux touchant à la protection de la biodiversité marine, l'échelle écologique pertinente est celle de la façade Méditerranéenne. C'est par exemple le cas pour les espèces mobiles comme les mammifères marins.

Dans ce contexte, acquérir des connaissances écologiques à large échelle à partir de données collectées par une multitude d'acteurs soulèvent deux grands enjeux. Premièrement, un enjeu opérationnel et politique consiste à impliquer et coordonner les institutions et les acteurs qui collectent les données écologiques. Deuxièmement, un enjeu méthodologique réside dans la capacité à proposer des outils statistiques pouvant produire des indicateurs écologiques robustes à partir de plusieurs protocoles de suivis écologiques. Durant cette thèse, j'ai souhaité proposer l'étude simultanée de ces deux enjeux, opérationnel et méthodologique, en mettant en place une approche interdisciplinaire mobilisant sciences sociales et écologie statistique. L'analyse est centrée sur les suivis écologiques du grand dauphin (*Tursiops truncatus*) réalisés en Méditerranée française.

En réalisant des entretiens semi-directifs avec les agents des AMP de Méditerranée française, j'ai développé une réflexion sur la place des données écologiques dans le fonctionnement des AMP et dans le quotidien des agents qui y travaillent. Les entretiens et la collaboration avec les professionnels de la biodiversité ont aussi permis d'identifier des besoins méthodologiques pour appuyer le suivi écologique du grand dauphin à l'échelle du réseau d'AMP de Méditerranée française. Ainsi, j'ai développé des outils de modélisation intégrée permettant l'analyse conjointe de plusieurs jeux de données pour estimer la distribution, les effectifs et la densité de grand dauphin à l'échelle de la Méditerranée française.

Mon travail aura permis i) de proposer des outils statistiques adaptés au contexte actuel du suivi écologique du grand dauphin en Méditerranée française, et ii) de mettre en évidence et décrire les enjeux opérationnels et politiques de coordination des suivis écologiques entre les différentes AMP de Méditerranée française. Plus largement, ma thèse constitue une illustration de la pertinence du dialogue entre sciences sociales et écologie statistique pour produire des propositions d'outils de conservation écologiquement efficaces et socialement pertinents.

Mots-clés : aires marines protégées, écologie statistique, grand dauphin, Mer Méditerranée, recherche interdisciplinaire

Abstract

Abstract:

Ecological monitoring allows to collect data and to gain knowledge on species or ecosystems. Thus, ecological monitoring is the basis on which biodiversity conservation is organized. Nowadays, the spatial scales of ecological monitoring and conservation issues diversify, as well as the increased complexity of institutional dynamics related to the collection of ecological data. In the French Mediterranean, a network of thirty Marine Protected Areas (MPA) is operating along the coastline. These MPA collect ecological data and work for the protection of marine biodiversity, each at its own scale and with its own means. For many issues related to the protection of marine biodiversity, the relevant ecological scale is that of the Mediterranean coastline embracing the entire MPA network around the same ecological context. This is the case for mobile species such as marine mammals.

In this context, acquiring ecological knowledge at large spatial scales from data collected by a multitude of actors raises two major issues. First, an operational and policy challenge that consists in involving and coordinating institutions and stakeholders that collect ecological data. Second, a methodological challenge that lies in the ability to propose statistical tools that can produce robust ecological indicators from several monitoring protocols. During this thesis, I wanted to jointly study both of these two issues, operational and methodological, by setting up an interdisciplinary approach mobilizing social sciences and statistical ecology. The analysis is focused on the ecological monitoring of bottlenose dolphins (*Tursiops truncatus*) in the French Mediterranean Sea.

By conducting semi-directive interviews with MPA managers in the French Mediterranean, I studied the place of ecological data in the functioning of MPA and in the working life of the MPA managers. The interviews and the collaboration with biodiversity managers also allowed to identify methodological requirements to support the ecological monitoring of bottlenose dolphins at the scale of the French Mediterranean MPA network. Thus, I developed integrated modeling tools allowing the joint analysis of multiple datasets to estimate the distribution, abundance and density of bottlenose dolphins at the scale of the French Mediterranean Sea.

My work will have allowed i) to propose statistical tools relevant to the current context of the ecological monitoring of bottlenose dolphins in the French Mediterranean Sea, and ii) to highlight and describe the operational and political issues of coordinating ecological monitoring between the different MPA of the French Mediterranean Sea. Overall, my thesis is an illustration of the relevancy of the dialogue between social sciences and statistical ecology to produce ecologically effective and socially relevant conservation tools.

Keywords: bottlenose dolphin, interdisciplinary research, Marine Protected Areas, Mediterranean Sea, statistical ecology

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Ecological monitoring in Marine Protected Areas of the French Mediterranean Sea

An interdisciplinary approach about bottlenose dolphin

1 GENERAL SCIENTIFIC CONTEXT

1.1 Ecological data as the cornerstone of biodiversity conservation

From naturalist observations to ecological monitoring

Historically, the observation of nature and environment have led successive human societies to collect information on what surrounded them. First, naturalist observations were limited to the inventory, description, observation and drawing of species. As early as 31,000 BC, the paintings in the Chauvet cave in Ardèche (Southern France) show a sharp sense of observation and knowledge of the anatomy of species. Later, naturalist observations were more sophisticated but the techniques for reporting them remained descriptive. In 1555 in Montpellier (France), the doctor Guillaume Rondelet delivered one of the first zoological book in which he described all the aquatic animals he knew, Universæ aquatilium historiæ pars altera (Rondelet, 1555). For a long time, macroscopic, charismatic, emblematic species were mainly observed, but gradually, techniques for collecting naturalist observations evolved (Troudet et al., 2017). Ecological data became more detailed and complex (Moussy et al., 2021). At the beginning of the 17th century, the development of the scientific method flooded the sciences at large (Glass & Hall, 2008). Sciences adopted conceptual frameworks linking hypotheses, predictions, observations and deduction (Glass & Hall, 2008; Platt, 1964). The hypothetico-deductive method is particularly widespread in the natural sciences (Betts et al., 2021; Platt, 1964;

Tosa et al., 2021). It proposes i) the formulation of multiple hypotheses, ii) the definition of an experimental protocol to discriminate the hypotheses, and iii) the realization of the experiment and the interpretation of the results. Natural scientists formulated hypotheses about the functioning of nature and designed strategies for collecting data about species, materializing the emergence of ecology as a scientific discipline (Betts et al., 2021; Moussy et al., 2021; Tosa et al., 2021). Since the early 20th century, scientific ecology has evolved from natural history and naturalistic field observations to an applied and quantitative multidisciplinary discipline (Anderson et al., 2021).

Ecological monitoring is the common term for data collection protocols in the natural environment. Ecological monitoring can be considered as the standardized and systematic collection of data in order to produce inferences about the ecology of one or more predefined taxa or taxonomic groups (Moussy et al., 2021). The objective of these protocols is to standardize the data collected for comparison purposes, hence permitting the reproducibility of the collection method in other contexts (Lindenmayer & Likens, 2010). Ecological monitoring protocols can take different forms: we refer to longitudinal monitoring when data collection is extended over time; on the contrary we refer to cross-sectional monitoring when data collection does not take into account the temporal dimension but sampling cover large spatial area; we refer to replication when a protocol is repeated identically multiple times. Step by step, the entire discipline of scientific ecology has been built around naturalist data (Besnard, 2013).

Ecological data highlighted the decline of biodiversity

Naturalist data collected have progressively changed the relationship between humans and other living creatures. In the 19th century, based on naturalist observations of Charles Darwin about finches in the Galapagos Islands (genus *Geospiza*), and those made by Alfred Russel Wallace in Southeast Asia, the two scientists revolutionized the conception of Nature theorizing the Evolution of species (Darwin, 1862). During the 20th century, knowledge accumulated on biodiversity revealed the impacts of human activities on the environment (Dirzo et al., 2014; McCauley et al., 2015; Payne et al., 2016). Facing the alarming evidence of biodiversity erosion that is mainly due to the practices of Western countries, efforts are being made to try to halt the declines and to limit the casualties (Godet & Devictor, 2018). Since the 1980s and along with the rising awareness about protecting nature, ecological data have been taken out of their fundamental knowledge position and applied to the preservation of biological diversity (Godet & Devictor, 2018; Mauz & Granjou, 2010). Using ecological data to address the problems of threatened species and ecosystems led to the emergence of an applied science, conservation biology, whose goal is to provide principles and tools for biodiversity preservation (Besnard, 2013; Soulé, 1985).

Conservation sciences, a mandatory multidisciplinarity

The obvious societal dimension of conservation biology involves linking ecological information to public policy for biodiversity protection (Bennett et al., 2017). However, converting ecological information into conservation measures requires engaging human and political dimensions that are beyond the natural sciences (Bennett et al., 2017; Christie et al., 2017; Mathevet & Mauchamp, 2005). During the 2015 International Congress for Conservation Biology in Montpellier, the president of the Society for Conservation Biology noted that *"Conservation science is evolving. Both natural and social sciences are crucial to solving conservation problems"*. Conservation science is not just ecology and biology. Conservation science is highly multidisciplinary in its goal to provide ecologically effective and socially fair conservation tools (Bennett et al., 2017; Besnard, 2013). Thus, humanities and social sciences emerged as a vital complement to the natural sciences to understand and describe the sometimes antagonistic human interests around nature-related problems (Redpath et al., 2013), to study the acceptability of conservation measures (Gall & Rodwell, 2016), or to grasp local knowledge and to inform the policy-making process (Huntington, 2000; Nuno et al., 2014; Vimal & Mathevet, 2011). Despite the impediments of interdisciplinary approaches, the integration of humanities and social sciences to biodiversity conservation issues is still in progress (Chassé et al., 2020; Martin et al., 2009; Redpath et al., 2017).

Which role for ecological data in the political arena of decision making?

Conservation sciences are crucial important because ecological knowledge and scientific results underpin biodiversity management and protection (Sutherland et al., 2004). Ecological information obtained from monitoring protocols can be used to identify biodiversity issues, to understand ecosystem functioning and ecological mechanisms that explain biodiversity declines (Moussy et al., 2021; Nichols & Williams, 2006). Ecological information also allows to propose mitigation measures for effective conservation, and to assess the effect of management (Besnard, 2013; Dunham et al., 2020; Nichols & Williams, 2006). Furthermore, ecological monitoring can also drive positive conservation outcomes by structuring the functioning of protected areas and by motivating managers and people involved in data collection (Danielsen et al., 2005; Vimal et al., 2018). Because it encompasses these multiple dimensions, ecological monitoring is considered a vital component of biodiversity management (Moussy et al., 2021).

Professionalization of biodiversity management and the emergence of ecological indicators

The addition of biodiversity conservation in the international agenda of public policies led to the increasing professionalization of the sector and transformed the use of ecological knowledge (Besnard, 2013; Granjou, 2013). Whereas 50 years ago, people working for nature protection were essentially volunteer and activists, today in France this protection is provided by civil servants (Arpin, 2020; Besnard, 2013). There has been a transition from environmental activism toward rigorous needs of expertise and the institutionalization of nature protection (Granjou, 2013). Gradually, aesthetic and passionate considerations had been forgotten to move from nature protection to biodiversity management (Blandin, 2009). Empirical knowledge or "expert opinion" is not sufficient anymore to justify environmental policies. On the contrary, indicators obtained from precise and rigorous ecological monitoring permit more objective decision-making (Alphandéry & Fortier, 2015; Besnard, 2013; Granjou et al., 2010). An ecological indicator can be defined as a metric reflecting one or more components of the state of ecological systems. An ecological indicator can either be measured directly or result from the simplification of several field-estimated values (Niemi & McDonald, 2004). The use of indicators in conservation stems from the requirements to assess the ecological status of species and ecosystems for biodiversity management decisions (Buckland et al., 2005; Nichols & Williams, 2006). As there is a great quantity of ecological information possible to describe the state of an ecosystem, ecological indicators also aim to reduce the amount of information to isolate key aspects of ecosystem status and help determine appropriate measures (Buckland et al., 2005; Niemi & McDonald, 2004). For example, the number of individuals belonging to a given population and the trend over time are parameters perceived as objective, which can lead to judge the situation of a declining population and call for the implementation of conservation actions (Buckland et al., 2005; Magurran et al., 2010). To justify environmental decisions and evaluating public policies, the introduction of ecological indicators becomes a scientific imperative on which policies are based. Thus, ecological indicators ensure a gain in legitimacy but also transparency of public action (Ferraro & Pattanayak, 2006; Granjou et al., 2010). Mainly developed since the Convention on Biological Diversity in 2004, the number and the use of ecological indicators have flourished at the international scale and at the national and local scales (Arpin, 2020; Granjou, 2013). At the international scale, ecological data with aim at assisting governments on biodiversity issues. One can cite for example endangered species lists such as the International Union for Conservation of Nature (IUCN) red list, or the establishment of global syntheses about the state of biodiversity such as the reports of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) (Mauz & Granjou, 2010). At the local scale, the government implements regulations prohibiting the anchoring of recreational boats on the basis of local ecological indicators attesting to conservation status of Mediterranean seagrass beds (ANDROMEDE, 2020). The scientific results inform and justify political decisions to protect biodiversity. The reliability of ecological results is therefore of primary importance to effectively inform decision making. Indeed, the study of plant and animal populations is marked by a high demand for scientific expertise (Granjou et al., 2010; Granjou & Mauz, 2007). However, the exigence of reliability requires methodological developments to obtain precise ecological indicators while taking into account the uncertainties associated with the study of populations in their natural environment (Buckland et al., 2005; Callon et al., 2001; Stephenson et al., 2021; Yoccoz et al., 2001).

1.2 The contribution of statistics to applied ecology and management

Complex ecological questions related to the uncertainties of ecological monitoring in natural environments

Providing answers to basic ecological questions such as “how many?” or “where?”, population ecology makes it possible to understand the biology of threatened species and to determine the conditions for their restoration or conservation (Besnard, 2013). Answering the question “how many?” or in other words, what are the abundance and the trend of a population, consists in estimating the number of individuals in a given space. Answering the question “where” consists in estimating the geographic distribution of a given group of individuals and describing the mechanisms that influence it. In addition to estimating “static” ecological patterns such as the distribution or abundance of a population, other more complex questions may involve inferring the ecological mechanisms underlying the spatial and temporal dynamics of the population (Williams et al., 2002). Inferring ecological mechanisms such as survival rate, reproductive rate, colonization, or extinction of a population requires data spread in time. For example, more qualitative and quantitative ecological data are needed to determine the reasons for a decline in population abundance than to “only” document a declining trend in abundance, hence underlining the importance of long-term datasets in population ecology (Lindenmayer & Likens, 2009; Magurran et al., 2010). Answering these two questions about population distribution and abundance may seem straightforward, yet in many cases when studying populations in their natural environment, these questions are complex (Besnard, 2013). This is the case when it comes to mobile, elusive species with large home ranges such as marine mammals, large terrestrial carnivores, or certain bird species for which monitoring protocols do not allow for coverage of the entire population range or for the enumeration of all individuals (Louvrier, 2018; Williams et al., 2002). Moreover, ecological data collected in natural environments are generally contaminated by errors such as false negatives (an individual or species is not detected despite being present) and false positives (an individual or species that is not present is falsely detected due to misidentification, for example), whether in counts or in detection/non-detection data (Kéry & Royle, 2020; Yoccoz et al., 2001). Thus, ecological analyzes require accounting for imperfections in data collection and mobilizing statistical methods to accommodate these uncertainties.

The example of imperfect detection

Let us have an example, counting all individuals present in a study area is often impossible, even for species that are not mobile, which generates "false negative" errors. For example, it is impossible to count all wolves (*Canis lupus*) present in the Alps to obtain the exact population size. Wolves are too difficult to detect and the sampling area is too large (Louvrier, 2018). Indeed, accounting for imperfect detection of individuals represents one of the main challenges when monitoring populations in the wild (Guillera-Arroita et al., 2010; Yoccoz et al., 2001). Imperfect detection may originate from the ecology of the species that makes it difficult to detect, from habitat characteristics, or from the observation process (e.g. bad weather, inexperienced observer,Guillera-Arroita et al. (2010); Besnard (2013); Louvrier (2018)). Imperfect detection can also vary in time and space. Failure to account for these detectability issues results in underestimating population size (Cubaynes et al., 2010), or species distribution (Comte & Grenouillet, 2013; Lahoz-Monfort et al., 2014).

To make inferences about ecological processes and to quantify the error generated during their observation, we need additional information, which most of the time comes from repeated observations, or from knowledge of the identity of individuals (Kéry & Royle, 2020). Thus, some ecological monitoring protocols are repeated multiple times under similar conditions and enable the estimation of imperfect detection with statistical models that jointly estimate the ecological process studied and the observation process (Kéry & Royle, 2020; Kéry & Royle, 2016; Williams et al., 2002).

Beyond this example on imperfect detection, the variability of natural populations is a major challenge in ecology. Variability when monitoring wild populations results from both the ecological processes (e.g., animal movement, or ecology) and the sampling process (e.g., spatially biased sampling, presence-only data, species identification errors related to an observer effect). In order to account for these uncertainties, one can obtain ecological inferences through calculations and extrapolation from the data. Statistical methods are used to extract information from data to describe, interpret, and infer ecological mechanisms, while taking into account the uncertainties associated with studies in natural environments. Thus, statistical ecology emerges as a scientific discipline that contribute to the developments of tools for analyzing ecological data in order to answer questions about population dynamics and species distribution, in particular (Gimenez et al., 2014).

Statistical methods to estimate species distribution and abundance

To estimate the distribution of a species or population, ecologists use statistical tools known as species distribution models (Franklin, 2010; Guisan et al., 2017). Most of these models are based on correlative approaches between spatial patterns of observations and environmental variables (Guillera□ Arroita, 2017; Guisan et al., 2013). Statistical tools for modeling species distribution differ in the type of ecological data they analyzed: presence-only or presence-absence (Elith & Leathwick, 2009). MaxEnt models are widely used in conservation to analyze presence-only data (Bradie & Leung, 2017; Elith et al., 2011). The flexibility of MaxEnt models, however, requires to account for biases related to spatially irregular sampling effort, and to the absence of real absence data (Kramer-Schadt et al., 2013). Using presence-absence data collected repeatedly at fixed geographic sites, occupancy models explicitly estimate the probability of detection and infer the spatial distribution of a species while correcting for imperfect detection (Mackenzie et al., 2002; Williams et al., 2002).

About the tools to estimate population abundance, two main classes of methods coexist depending on whether animals are marked or individually identified. From count data, "*distance sampling*" consists in measuring observation distances between target and observer during the course of a linear transect or during an observation session of fixed duration on a point. Assuming that the probabilitý of detecting individuals decreases with the distance to the observer, distances measure provides the information to estimate densities by modeling the function linking detection probability and distance to the observer [Buckland et al. (2005). Once the function is correctly modeled, the abundance or density of the species under study is obtained. Another approach is based on substantially different data type but very common among biodiversity managers. Using counts repeated over time and across multiple, so-called "*N-mixture*" models use data from unmarked animals and allow estimating relative abundances or densities of individuals at monitored sites (Besnard, 2013; Royle et al., 2004). In contrast to methods derived from count data, capture-recapture methods are based on successive detections of marked or identified individuals, which involve several field sessions to build capture histories for each individual observed (Williams et al., 2002). Repeated captures allow estimating the probability of capture of an individual and therefore provide unbiased abundance estimates. Extending to spatially explicit capture-recapture models provides a way to jointly estimate abundance and the spatial distribution of individuals (Kéry & Royle, 2016; Royle et al., 2014).

Optimization of ecological monitoring programs

Some statistical developments focus on the optimization of ecological monitoring programs (Field et al., 2005; Hooten et al., 2009; Morán-Ordóñez et al., 2018). Many parameters such as the frequency or the spatial design of the monitoring protocols influence the data collected and ecological estimates. Ecological monitoring being time and budget consuming, thinking ahead about the spatio-temporal optimization maximizes the chances of obtaining the desired ecological information while being cost effective (Besnard, 2013; Grant et al., 2013; Pacifici et al., 2016). Structured decision-making methods formalize monitoring objectives and, through statistical optimization, iteratively evaluate and reallocate the sampling design results according to the collected data to reach the defined monitoring objectives (Gregory et al., 2013; Martin et al., 2009). These statistical methods, known as adaptive monitoring, are similar to those of adaptive management and aim to iteratively reduce uncertainty around the modeling of the ecological system to improve the efficiency of the ecological monitoring protocol (Lindenmayer & Likens, 2009).

Data integration

In many situations when analyzing ecological data, we have multiple types of observations or datasets available (Kéry & Royle, 2020; Zipkin et al., 2019). For example, we may have counts and detection/non-detection data, and both of them contain information about species' distribution. Alternatively, we may have counts data that provide information on abundance, and we may also have access to capture-recapture data that provide information on population dynamics and survival. In these cases where multiple datasets coexist, it is tempting to combine the available datasets to make the most of all the information they contain (Besbeas et al., 2002;

Miller et al., 2019; Schaub & Abadi, 2011; Zipkin & Saunders, 2018). The development of integrated models has been an important research avenue in statistical ecology over the past 20 years, with the emergence of various approaches to combine information from multiple datasets (Amundson et al., 2014; Fletcher et al., 2019; Kéry & Royle, 2020; Miller et al., 2019; Pacifici et al., 2019). The root principle of most integrated models is that multiple datasets are described with the same underlying ecological process. This ecological process is formulated at the resolution corresponding to the most detailed dataset. A common approach is to specify a joint likelihood, where at least one parameter is shared between several datasets. The joint likelihood of most integrated models incorporates an ecological process common to all involved datasets, and a different observational process corresponding to each monitoring protocol (Fletcher et al., 2019; Kéry & Royle, 2020; Miller et al., 2019). The two main advantages of integrated models are i) increased accuracy of ecological estimates, and ii) the ability to sometimes estimate additional parameters that could not be inferred from each data source alone (Kéry & Royle, 2020; Zipkin et al., 2019). Methodological developments on data integration have made it possible to combine many different data types (see Kéry & Royle (2020) for a review).

Being applicable to many situations, the use of integrated models in ecology and conservation has increased greatly in recent years. Often, one can combine a large dataset that is relatively cheap or easy to collect, but that contains little information (e.g., large-scale counts, opportunistic data), with a smaller dataset that is more difficult to obtain, but contains more information. On the one hand, the detailed data can mitigate the weaknesses of the larger dataset (Dorazio, 2014). On the other hand, the detailed dataset is often collected within a more limited spatial or temporal scale, while the less expensive dataset may extend over a larger spatio-temporal scale. The combination of the two can then increase the scope of ecological inference for both the former and the latter (Kéry & Royle, 2020). Integrated analyses offer promising perspectives when planning ecological monitoring protocols in conservation contexts (Zipkin & Saunders, 2018). Methodological developments on integrated models are still ongoing as evidenced by the large number of scientific publications in the field, or the setting of specific sessions dedicated to data integration during international conferences on statistical methods applied to ecology. However, handling of integrated models can be complex and their application to conservation case studies requires the help of statisticians to transfer these methods to the world of biodiversity managers.

1.3 Biodiversity conservation policies, a focus on protected areas

Awareness of the importance of biodiversity conservation has led to the emergence of different forms of policies aimed at protecting biodiversity and ecosystems. In addition to policies oriented towards mitigation of anthropic pressures ("*threat-based conservation*"), which result in the regulation of dangerous or harmful practices to biodiversity (e.g. the listing of protected species for which hunting or fishing is prohibited), the active protection of nature has mainly focuses on the creation of protected areas since the 1970s ("*area-based conservation*", Maxwell et al. (2020)). In these limited geographical areas, human practices and pressures are more or less controlled and regulated. Along with the emergency of protecting wildlife, the agenda of international institutions accelerated and set ambitious protected areas targets. The Convention on Biological Diversity stated that 17% of the continental land and 10% of the oceans should be effectively protected by 2020 (decision, 2010; Maxwell et al., 2020). Despite an increase in the coverage of protected areas in recent years, protected areas covered only 15.3% of the land and 7.5% of the oceans in 2019, falling behind the announced targets (Maxwell et al., 2020). More than a problem of area coverage, the quality of protected areas is often blamed (Coad et al., 2019; Maxwell et al., 2020; Mazaris et al., 2019; Rife et al., 2013). Less than a quarter of the world's protected areas report sufficient budgetary resources to meet their objectives, with only 4-9% of terrestrial vertebrate species sufficiently included in the global protected area network (Coad et al., 2019). Surface covered by protected areas provides no guarantee of protection effectiveness and is sometimes criticized as being a bad policy target (Costello & Ballantine, 2015; Maxwell et al., 2020). Despite these criticisms, protected areas are the primary tool for managing biodiversity around the world. Hence, protected areas have a political dimension as they regulate a public domain and comply with international geopolitical objectives. Management approaches of protected areas mobilize various fields of action since they produce scientific knowledge via ecological studies (Granjou et al., 2010), and they also have a social role via the controlled opening to the public and the transmission of nature experiences (Cosquer et al., 2019; Mazurek et al., 2019; NRC, 2001). Overall, the main objective remains to ensure efficient protection of biodiversity and landscapes.

1.4 Marine conservation

The specific nature of marine environments

Most conservation science focused on developing strategies to protect terrestrial biodiversity (Agardy et al., 2011; Boonzaier & Pauly, 2016). Because of the difficult accessibility of oceans and seas, knowledge of marine ecology is less advanced than terrestrial ecology. Only a small fraction of the biological diversity of the oceans has been described (Dayton, 2003). Nevertheless, marine ecosystems are more open than terrestrial ecosystems that exhibit clearer boundaries. Then, marine species have more important dispersal and migration than on land (NRC, 2001). Terrestrial ecology of species is particularly linked to the concept of habitat, which facilitates the identification of protected areas. However, in water, mobile species move in three dimensions and are likely to migrate long distances, which makes it difficult to identify distinct populations and blurs apparent boundaries of marine ecosystems (NRC, 2001). In fact, the openness of marine world increases sensitivity to threats such as pollution from surrounding land and water (Coll et al., 2012). Although human populations might have less impact on marine ecosystems than on terrestrial ones, marine habitat loss has been rarely documented. Population declines and extinctions of marine species are more often imputed to overexploitation or direct harvest (Dayton, 2003; McCauley et al., 2015; NRC, 2001).

A major distinction between the use of marine and land resources derives from historical perceptions of ownership and laws that govern the oceans. At the international level, nations undertook measures only recently to establish ownership of the seabed and subjacent waters by declaring territorial seas and exclusive economic zones (EEZs) during the 1982 United Nations Convention on the Law of the Sea. Degrees of ownership are much more limited than the standards applied to most land areas. Perception of the sea as a common good that is accessible to all is ubiquitous in the discourses of marine users. "*The sea is everyone's*" notes an agent working in a marine protected area (personal communication). Despite these legal and cultural differences, marine conservation is also based on the creation of regulated territories, marine protected areas (MPAs) being the primary tool for marine conservation (Agardy, 1994).

Marine Protected Areas

Objectives of MPAs are similar to terrestrial protected areas and include maintaining ecosystem health, protecting biodiversity, achieving sustainable use of marine resources, and conserving cultural heritage sites (Mazurek et al., 2019; NRC, 2001). Attempts to develop definitions for the term MPA led to the most accepted classification system, that of the IUCN, which includes six categories to assess the status of protected areas worldwide. However, due to a lack of consensus, we defined an MPA as a geographical area with clear boundaries that aimed to achieve the conservation of marine resources (NRC, 2001). One can note that this wide definition of

MPA does not include any reference to the degree of protection. Several critics argue that MPA label creates an illusion of marine biodiversity conservation (Costello & Ballantine, 2015; Rife et al., 2013). The objective of 10% ocean coverage by MPAs by 2020 (see Section 1.3) will have yielded a rush to create MPAs without the appropriate resources, which does not resolve conservation issues (Agardy et al., 2003; Maxwell et al., 2020). The percentage of sea surface labeled as MPAs is not a good indicator of protection effectiveness (Boonzaier & Pauly, 2016). In spite of these critics, MPAs cover large areas without appropriate resources to ensure effective protection. One may cite examples of large MPAs in Brazil (Magris & Pressey, 2018), in the USA (Rife et al., 2013), or in Europe with the Natura 2000 marine network (Mazaris et al., 2019) and in the Mediterranean Sea (Amengual & Alvarez-Berastegui, 2018; Giakoumi et al., 2017). Several studies also highlighted the major benefits of establishing MPAs to protect marine biodiversity (Blowes et al., 2020; Evans, 2018).

1.5 Producing ecological indicators in an MPA network

High mobility of marine species raises issues about protected areas connectivity in the marine environment (Agardy et al., 2011; NRC, 2001). Often, a single MPA will not be enough to meet the multiple needs of an eco-region where an MPA network can ensure a better connectivity between protected reserves NRC (2001); Green et al. (2009); Pajaro et al. (2010); Roberts et al. (2018); García-Barón et al. (2019)]. Implementing multiple MPA networks can theoretically outperform individual MPAs for various ecological, economic, and social reasons (Grorud-Colvert et al., 2014). On the one hand, MPA networks can minimize the potential negative economic, social, and cultural impacts of a large single reserve. On the other hand, MPA networks exhibit ecological benefits in terms of connectivity between different populations (Grorud-Colvert et al., 2014; NRC, 2001). Indeed, the relevant ecological scale in the marine environment often turns out to be that of the MPA network. Working in marine conservation at the large-scale of MPA networks requires producing wide ecological indicators (Roberts et al., 2018), which raises methodological challenges related to the integration of different datasets collected at multiple locations with multiple protocols. Furthermore, complex institutional settings such as an MPA network emphasize the need to study and evaluate governance frameworks for effective conservation (Agardy et al., 2011; Nuno et al., 2014). **Establishing large-scale ecological indicators from data collected by a multitude of actors raises two main challenges. First, an operational and political challenge lies in involving and coordinating institutions and actors who collect ecological data. Second, a methodological issue lies in the development of statistical tools that can produce robust ecological indica-**

tors from multiple monitoring programs and existing datasets. During this thesis, I proposed to study these two challenges, operational and methodological, by setting up an interdisciplinary approach mobilizing social sciences and statistical ecology. The crossing of several scientific disciplines can facilitate the study of increasingly complex and multi-faceted conservation problems (Braunisch et al., 2012). Interdisciplinarity work between social and natural sciences makes possible to anchor in a territory and to respond directly to the problems faced by stakeholders (Chassé et al., 2020). In this thesis, I have tried to illustrate that interdisciplinary approaches facilitate the link between the world of biodiversity managers and the world of academic research, hence allowing to combine social significance and scholar outcomes (Arlettaz et al., 2010; Chassé et al., 2020).

2 MARINE CONSERVATION IN FRANCE AND THE BOTTLENOSE DOLPHIN CASE STUDY IN THE MEDITERRANEAN SEA

2.1 French MPAs and marine conservation policies

Holding the second largest maritime territory in the world after the United States of America with more than 10 million km2, France plays a leading role in the conservation of seas and oceans. To protect and manage the maritime world, the Marine Strategy Framework Directive (MSFD) adopted in 2008 by the European Union contains a set of regulations concerning the marine environment, including in France. MSFD provides a legal framework that aims to "*maintain or restore the functioning of marine ecosystems while allowing sustainability of human activities*". At the national scale, MSFD implementation is divided by maritime coastline or sub-region via specific management plan renewed every 6 years, which requires i) the definition of the good ecological status of sub-region French waters as a conservation objective to be achieved, ii) the establishment of ecological indicators associated with the good ecological status iii) the establishment of a monitoring program for assessment and regular update of ecological indicators, iv) the development of a program of measures designed to achieve or maintain the good environmental status. Since the adoption of the MSFD in the political agenda in 2008, many French MPAs have been created to support its application. In 2019, 23.5% of French seas were covered by at least one MPA, compared to 0.8% in 2009 (Figure 2). French MPAs have various protection statuses and governance models. The French law recognizes more than 15 different types of MPAs (Labach et al., 2021). In France, the Office Français de la Biodiversité (OFB – French Biodiversity Office) is the public institution that centralizes biodiversity management policies. OFB is in charge of coordinating the MPA network and managing some MPAs, mainly the Marine Natural Parks, as well as marine Natura 2000 areas. Besides MPAs managed by OFB, other MPAs are managed by local authorities: Regional Natural Parks, some Natura 2000 areas, and Natural Reserves. The administrative status of MPAs can be difficult to understand with clarity due to the institutional mosaic involved. National Parks and Marine Natural Parks are exclusively attached to or managed by OFB. However, Natura 2000 areas can be managed by OFB or by local authorities. For example, the Natura 2000 area of the Posidonia of the Cap d'Agde is managed by the city of Agde, whereas the Natura 2000 area of the Posidonia of the Palavasian coast is managed by OFB. In addition to these official administrative statuses, there are international labels por MPAs such as Specially Protected Areas of Mediterranean Importance (ASPIM, 2014), Biosphere Reserves, or IUCN Green List status (https://iucngreenlist.org/explore/). The recent national strategy for MPAs plans to protect, 30% of French waters by 2030, with one third under strong protection (OFB, 2021). As such, the strategy not only aims to create additional protected areas but also to ensure that these are representative of ecosystems diversity, well-managed, interconnected, with sufficient resources to create a robust network of protected areas resilient to global changes (Labach et al., 2021). The French Mediterranean coastline had more than 60 MPAs in 2016 (including 2 Marine Natural Parks, 2 National Parks, 3 Natural Reserves, 3 biotope protection areas, 49 Natura 2000 areas) covering nearly 34% of the French EEZ. Five MPAs have the SPAMI label, 2 are biosphere reserves, and 2 are on the IUCN Green List. In Figure 1, we show the main MPAs in the French Mediterranean Sea, including the Pelagos Sanctuary, an 87,500 km SPAMI that results from an international agreement between Italy, Monaco and France for the protection of marine mammals. Mediterranean MPAs are regularly consulted to collect data to inform ecological indicators for the MSFD monitoring program.

The administrative context of biodiversity conservation in France is complex. In the marine environment, production of ecological indicators is synthesized at the scale of maritime coastlines to inform national or international laws such as MSFD. OFB centralizes biodiversity management, and relies on a wide variety of local structures to collect data and apply management policies involving municipalities, associative and private partners. Given the diversity of institutional forms of MPAs, ensuring the coordination and compatibility of ecological monitoring programs at the scale of the Mediterranean coastline is a major challenge to obtain sound ecological indicators.

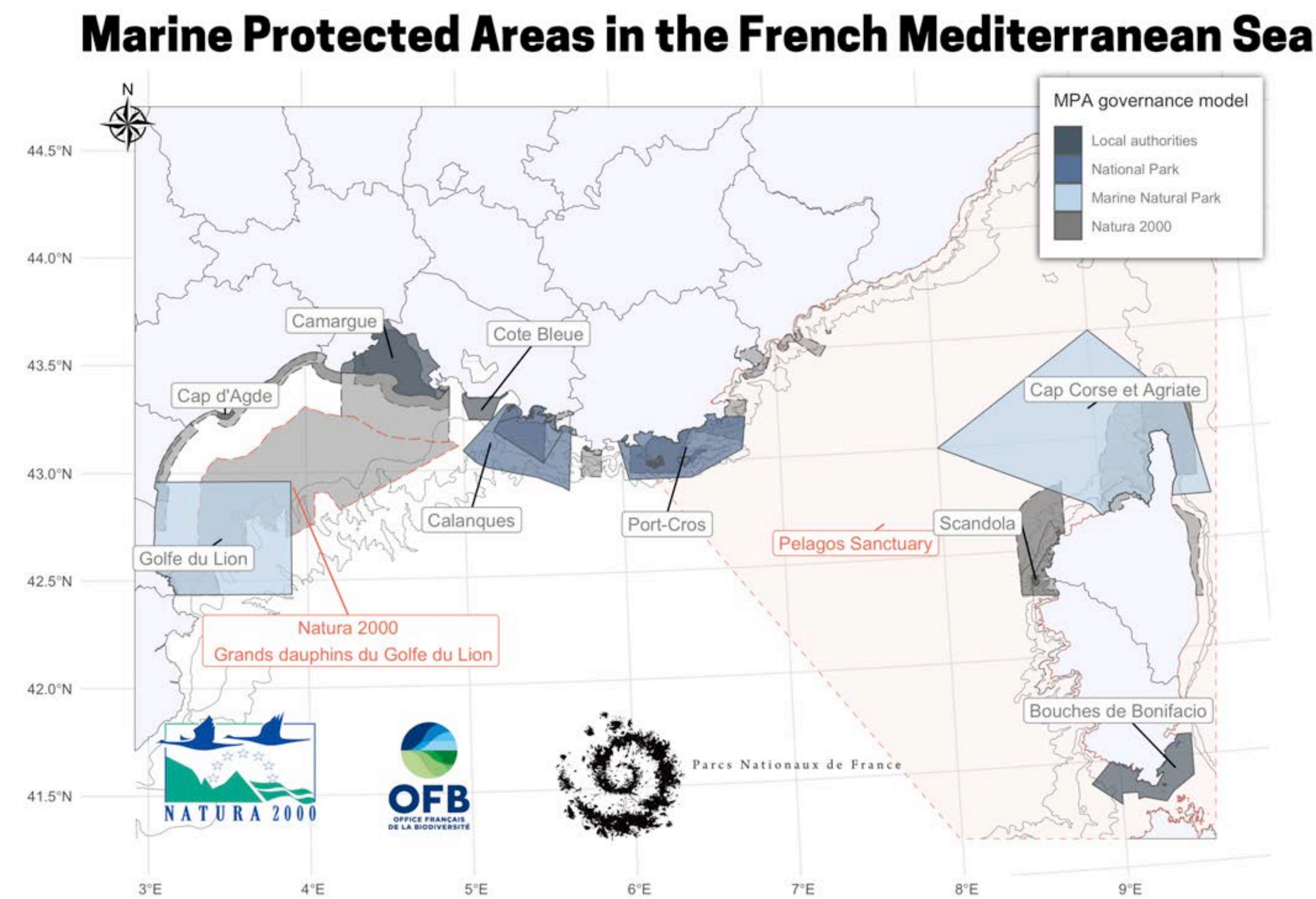

Figure 1: Main Marine Protected Areas of the French Mediterranean Sea classified by governance mode. MPA fill color corresponds to governance mode, distinguishing between MPAs managed i) by local authorities: Blue Coast Marine Park, Camargue Regional Natural Park, Natura 2000 area of the Posidonia of Cap d'Agde, Scandola and Bouches de Bonifacio Natural Reserves, ii) in the form of a National Park with state governance for the Port-Cros and Calanques National Parks, iii) in the form of a mixed governance between the French Office for Biodiversity and a management council made up of local stakeholders, as in the case of the Gulf of Lion and Cap Corse and Agriate Natural Marine Parks. Marine Natura 2000 network is shown in dotted line by transparency. In orange, there are two large MPAs designated for the protection of bottlenose dolphins: the recently created Natura 2000 area of the Gulf of Lion bottlenose dolphins, and the Pelagos Sanctuary. Source: https://inpn.mnhn.fr/telechargement/cartes-et-information-geographique

2.2 Bottlenose dolphin in the French Mediterranean Sea, ecology and conservation status

Bottlenose dolphin (*Tursiops truncatus*) is a common species in the Mediterranean Sea that occurs along most Mediterranean coasts, most on the continental shelf (Bearzi et al., 2009; Gnone et al., 2011; Labach et al., 2021), although groups are also observed offshore (Laran et al., 2017). Based on genetic analyses, two populations are identified in the Mediterranean Sea: one population in the western Mediterranean Sea from Gibraltar to a boundary found south to the Italian peninsula, one population in the eastern Mediterranean (Louis et al., 2014; Natoli et al., 2005). The genetic isolation of these two bottlenose dolphin populations is marked, indicating little to no exchange between individuals, whereas the isolation between the western Mediterranean and Atlantic populations is weakly marked indicating a high rate of exchange between individuals.

Bottlenose dolphins are social animals that exhibit a fission-fusion social structure characterized by a high degree of spatio-temporal variation in group size and members composition (Labach, 2021). In the Mediterranean Sea, bottlenose dolphin groups are generally smaller than 10 individuals s (Bearzi et al., 2009) although groups of more than 50 dolphins have been observed. Bottlenose dolphins show a great variability in their migratory behavior. Some individuals follow seasonal migrations while others can be considered as resident in an area. Home range size can vary between regions and social groups (Wells & Scott, 2009). The total population size of bottlenose dolphins in the entire Mediterranean Sea was recently estimated to be at 75,000 individuals (95% confidence interval - 95% CI 50,116-114,903) by a large-scale aerial survey (ACCOBAMS, 2021). The Mediterranean subpopulation of bottlenose dolphin is listed as "vulnerable" in the IUCN red list (IUCN, 2009). At the national level, the bottlenose dolphin is strictly protected by a French ministerial legislation.

Studying bottlenose dolphins is complex because of the mobile behavior, and because dolphins are not easily accessible to both observation and management measures (Labach, 2021). As a consequence, the effectiveness of MPA management measures for the conservation of mobile species such as bottlenose dolphins is controversial. However, bottlenose dolphin is the most prevalent cetacean species in the French Mediterranean MPAs and is included in the list of species of concern in several MPAs. Therefore, MPAs can play a key role to lead actions of knowledge acquisition, to carry out ecological monitoring, and to identify possible threats on bottlenose dolphin populations (Dunham et al., 2020; Labach, 2021).

2.3 Existing ecological datasets in the French Mediterranean Sea

Knowledge on bottlenose dolphin populations in the French Mediterranean Sea comes mainly from two recent large-scale monitoring programs. First, Aerial Surveys of Marine Megafauna (SAMM in French) conducted in 2011 and 2012 estimated bottlenose dolphin abundances in the French Mediterranean and Italian waters of the Pelagos Sanctuary at 13,400 individuals (95% CI: 5,500- 32,600) in winter and 3,900 individuals (95% CI: 1,000-15,000) in summer (Laran et al., 2017). These aerial surveys are operated by Pelagis, a French research laboratory, and aimed to collect data on human activities, seabirds, fish, and marine mammals (Baudrier et al., 2018; Lambert et al., 2020). SAMM aerial surveys are planned to be conducted every 6 years. The first campaign took place in 2011-2012, and the second in 2018-2019. The sampling design follows an aerial line transect protocol that covers 24.624 km with between 1 and 4 flights per transect (Laran et al., 2017). Two observers collect data following a distance sampling protocol, recording species name observed, group size, and declination angle.

The second monitoring program on bottlenose dolphin in the French Mediterranean Sea was led by French Non-Governmental Organizations (GDEGeM project, Labach et al. (2021); Labach (2021)). The goal was to monitor bottlenose dolphin habitats in the French Mediterranean Sea using a photo-identification protocol. Taking a photograph of the dorsal fin allows individual identification from the depigmentation marks (Figure 2). The study area covered the French Mediterranean continental shelf between the coast and the 500 m isobath, delimited by the Spanish border on the west, the Italian border on the east and includes the entire Corsican coastline. Survey routes were defined randomly according to weather conditions to maximize the encounter rate of dolphin groups and to cover the largest area possible (Labach, 2021).

Additional datasets exist on bottlenose dolphins in the Mediterranean Sea. Conducted by IFREMER (French Research Institute for the Exploitation of the Sea), scientific fishing programs assess the status of pelagic fish stocks annually and collect data on bottlenose dolphins in the Gulf of Lion following a boat line transect protocol (Baudrier et al., 2018). Also conducted by the IFREMER, aerial surveys aimed at estimating trends in bluefin tuna abundance in the Mediterranean Sea and collect bottlenose dolphin data in the Gulf of Lion (Ifremer, 2015). In addition, several Mediterranean MPAs have developed monitoring programs targeting bottlenose dolphins, such as the Calanques National Park (PNC, 2020), the Port-Cros National Park, or the Bouches de Bonifacio marine Reserve. In parallel, the development of citizen science through ObsenMer, a smartphone application, (https://www.obsenmer.org/)

provides more and more opportunistic observations of bottlenose dolphins by sea users. For now, only data from SAMM and GDEGeM programs have been used to estimate bottlenose dolphin abundance (Labach et al., 2021; Laran et al., 2017), while other scientific or opportunistic datasets remain unused.

Figure 2: Dorsal fin of bottlenose dolphin (Trusiops truncatus) with marks of depigmentation useful to individual identification

2.4 Monitoring objectives of bottlenose dolphin

Bottlenose dolphin is a sensitive species and is the object of conservation priorities throughout the Mediterranean coast. Bottlenose dolphin is the target of monitoring programs in some MPAs, and of a dedicated monitoring objective in MSFD (DCSMM, 2008; Labach, 2021). During the first MSFD cycle, only data from aerial surveys performed in 2011-2012 were used to establish ecological indicators of abundance and distribution for bottlenose dolphin. However, MFSD monitoring objectives for bottlenose dolphins include the development of a monitoring program targeting coastal populations via photo-identification. Regular monitoring by photo-id would provide more detailed ecological indicators than aerial surveys that are done once every six years (Labach, 2021). For this purpose, OFB intends to work with the MPA network, while continuing large-scale aerial surveys that provide information on many other species. We have seen that the MPA network in the French Mediterranean Sea is quite recent (Section 2.1), and construction of ecological monitoring programs is still in progress in the MPAs. To strengthen bottlenose dolphin monitoring by the MPA network, OFB funds photo-identification teaching programs for MPA agents and helps to define ecological monitoring protocols in MPAs (MIRACETI, 2019). Therefore, multiple complementary datasets coexist around bottlenose dolphins in the Mediterranean Sea. SAMM aerial surveys are performed at low frequency but are the only program to sample pelagic seas. Coastal photo-id monitoring performed in MPAs or by associative partners provide more detailed and frequent information because MPAs monitoring programs are usually repeated yearly or monthly. For now, each dataset has been analyzed independently, producing ecological indicators with limited precision and sometimes even contradictory results. While the joint analysis of datasets can help to get more precise ecological estimates (Section 1.2), the development of integrated modelling tools is a promising perspective for future assessments of bottlenose dolphin populations in the French Mediterranean Sea. Centralizing the production of bottlenose dolphin ecological indicators at the scale of the Mediterranean Sea remains ambitious given i) the multitude of actors and institutions involved in monitoring programs, ii) the diverse objectives of each partner, and iii) the methodological and logistic challenges. Regarding bottlenose dolphin in the French Mediterranean Sea, the methodological and operational challenges detailed in Section 1 are i) the coordination of numerous associative, professional, and scientific actors who actively participate in data collection, ii) the coexistence of several ecological monitoring programs which implies to jointly analyze collected data to establish robust indicators.

3 AIM AND PROGRESS OF THE THESIS

3.1 Aim and collaborative context of the thesis

The thesis project started in early 2018. We had discussions with Hélène Labach, director of MIRACETI (ex Groupement d'Intérêt Scientifique pour les Mammifères Marins de Méditerranée et leur environnement - GIS3M) who motivated the project around the ecological monitoring of bottlenose dolphins. At that time, several meetings were being held between MIRACETI and the Mediterranean branch of OFB (French Agency for Biodiversity - AFB at the time) to promote integrated and sustainable bottlenose dolphin management in the French Mediterranean Sea through MPA network empowering (Labach, 2021). During these meetings, several objectives were addressed, including: i) to standardize bottlenose dolphin monitoring performed in MPAs, ii) to centralize, analyze, and value data collected by MPAs, iii) to train and support MPA agents for monitoring protocols, and iv) to develop research on cetacean management in France, by starting collaborations between MIRACETI, OFB, and academic actors. In this context, my thesis project was born, which aims to identify the issues related to bottlenose dolphins monitoring in the French Mediterranean Sea and to provide statistical tools relevant to the study and species management.

3.2 Choosing an interdisciplinary approach and thought process

From the very beginning, we tried to work in close collaboration with MIRACETI and OFB to provide methodological tools useful to stakeholders and to bottlenose dolphin managers. Although the worlds of biodiversity management and academic scientists can have trouble to interact (Arpin et al., 2019; Besnard, 2013), we wished to have MPA managers involved from the very beginning of the process. We decided to develop a social sciences study that aimed at characterizing methodological needs and limitations associated with ecological monitoring in MPAs, and also to understand the context of data collection and perceptions of MPA agents. Motivations for embarking in this social science study stem, on the one hand, from my interest in the study of human dimensions of conservation conflicts developed during a previous internship (Lauret et al., 2020), and on the other hand, from the scientific context at CEFE in Montpellier with the creation of a new multidisciplinary team bringing together statisticians, ecologists, ethnologists and geographers, which constituted a favorable working ground for the emergence of interdisciplinary approach. The social science study initiated with the help of Nicolas Lescureux for the methodological supervision in social sciences and thanks to the financial support of the French Society of Ecology and Evolution (SFE2) for travel expenses. I conducted semi-directive interviews of agents from the main MPAs in the French Mediterranean (see Section 4) to study implementation of ecological monitoring programs and their role in the functioning of MPAs. A total of 21 MPA agents were interviewed: 9 were field-work agents, 9 were scientific managers, and 3 were MPA directors. I interviewed people from 8 different MPAs along the French Mediterranean coast (see Section 4). In addition to the social science study, we held several meetings and field missions with agents of the Mediterranean OFB branch and with MPA managers. Meetings aimed at identifying challenges and possible work trajectories to propose more adapted tools for the monitoring of bottlenose dolphins in the French Mediterranean MPAs.

The social science study, as well as the meetings and discussions with biodiversity workers, contributed to the redirection of the thesis project during the first months. Before the beginning of the collaborative process, we held informal discussions with Olivier Gimenez and Hélène Labach about the challenges of bottlenose dolphin monitoring. During this brainstorming process, we targeted methodological development avenues towards the spatio-temporal optimization of ecological monitoring protocols. Initially, we started to explore adaptive monitoring models through simulation studies (Appendix 2). Managers opinions collected during the social science study and the collaboration with the Mediterranean OFB branch clearly showed us that the main challenge around ecological monitoring of bottlenose dolphins was data integration. Our idea of temporal optimization of ecological monitoring programs was far from being on the agenda of MPAs due to the current coordination issues of the French Mediterranean MPA network. This was confirmed in a meeting with managers of the Gulf of Lion Marine Natural Park, during which they underlined the challenges to deal with the different protocols that coexist within their MPA. They developed coastal monitoring by photo-identification in parallel with linear transects targeting several species and monitoring coastal and pelagic areas. The most needed statistical tools in the Gulf of Lion MPA are expected to allow the combination of the two datasets to extract the ecological information on bottlenose dolphins. In this case, we had an illustration at the scale of an MPA of the biggest challenge identified at the scale of the French Mediterranean coastline: data integration.

In passing, I would like to emphasize that the social science study outcomes went beyond the identification of the needs in statistical tools. We also addressed opinions and perceptions of MPA agents about ecological data, as presented in Section 4. All discussions held with biodiversity professionals underlined benefits in the dialogue between managers and scientists, and embracing social sciences contributed to correctly identify the methodological challenges at stakes and to understand institutional drivers of conservation policies.

3.3 Goal of statistical developments

Starting with the social science study and together with MPA managers, we identified the main challenge with bottlenose dolphin monitoring in the French Mediterranean Sea, namely the development of statistical tools allowing the integration of multiple datasets of different nature to feed both the MSFD and MPA indicators. Two ecological indicators were reported by professionals: distribution and abundance/density. To work on the methodological objectives identified, we relied on data from SAMM aerial surveys and GDEGeM photo-id program presented in Section 2 because they represent the most comprehensive datasets on bottlenose dolphins in the French Mediterranean Sea. We designed statistical tools to integrate datasets collected by MPAs and OFB, which corresponds to what is needed by Mediterranean conservation institutions. Our main interest was to make available data integration to inform ecological indicators. The downside is that we did not focus much on inference about bottlenose dolphin ecology, and we just superficially investigated the ecological drivers of dolphin abundance and distribution; we come back to this issue in the Discussion (Section 7).

In Section 4, we present the results of our social science approach to study MPA agents' perception of ecological monitoring in the French Mediterranean Sea. The first objective was to reflect on the place of ecological data in the functioning of protected areas and in the everyday life of the agents who work there. The second objective was to identify relevant methodological developments to support the monitoring of bottlenose dolphins at the scale of the French Mediterranean MPA network.

In Section 5, we propose an occupancy model that integrates several datasets to estimate bottlenose dolphin distribution. We developed an integrated occupancy model for combining SAMM aerial surveys and GDEGeM photo-id datasets. In parallel, we explored the possibility of building occupancy models without repeated visits to sampling sites, i.e. single-visit models. From simulations and based on the analysis of bottlenose dolphin data, we highlighted that integrated occupancy models and single-visit models allowed a flexible use of existing bottlenose dolphin datasets to produce robust estimates of its distribution.

In Section 6, we used SAMM aerial surveys and GDEGeM photo-id datasets to estimate bottlenose dolphin abundances and densities in the French Mediterranean Sea. We built: i) a spatial distance sampling model to analyze the SAMM line transects, ii) a spatial capture-recapture model to analyze the GDEGeM photo-identification data, and iii) a spatial integrated model combining both the distance sampling and capture-recapture parts, using the two datasets. The integrated model opens promising perspectives for efficient use of available data to estimate bottlenose dolphin abundance in the French Mediterranean Sea.

In Section 7, we discuss the benefits of the statistical tools we developed for the monitoring of bottlenose dolphins in the French Mediterranean Sea. We also discuss their potential applications for other ecological contexts and list some perspectives of statistical developments. We also adopt a broader reading of the role of ecological monitoring French in biodiversity policies and of the functioning of MPAs network. Last, we quickly review the interdisciplinary dimension of our research and the scope of this type of approach.

Section 4

Ecological monitoring in Marine Protected Areas

Section 4

Article 1: The construction of ecological expertise and its implications – Biodiversity workers viewpoint on the role of ecological monitoring in the French Mediterranean Marine Protected Areas

French abstract and keywords

Résumé : A l'heure où les motivations pour constituer une solide expertise écologique sont importantes dans le monde de la gestion de la biodiversité, nous étudions ici les réactions des professionnels de la biodiversité à la place des données écologiques dans le fonctionnement des aires marines protégées et dans leur quotidien. Disposer d'une expertise écologique permet aux aires marines protégées et à leurs agents de s'imposer localement comme des institutions incontournables de la gestion de la biodiversité. Cependant, le sous-financement des politiques de la biodiversité induit un double risque car les objectifs affichés en termes d'expertise écologique deviennent difficilement réalisables. Le manque de moyens humains, principal marqueur de ces budgets insuffisants, fait craindre un risque d'une part pour la qualité et la quantité des expertises écologiques produites, et d'autre part pour la qualité des conditions de travail des agents. Ce travail constitue une première enquête qualitative réalisée auprès des professionnels de la biodiversité marine et prolonge les travaux menés en milieu terrestre. Nous montrons que la collecte de données écologiques dans les aires protégées revêt de multiples dimensions et remplit plusieurs fonctions d'ordre scientifique, économique, psychologique, et politique qui peuvent être altérées par le tournant actuel des politiques de la biodiversité en France.

Mots-clés : biodiversité, données, espaces naturels protégés, expertise, professionnels

Contribution: I motivated and defined the research subject on ecological monitoring. I thank Ruppert Vimal who provided a literature corpus to familiarize myself with the field of sociology of expertise and of biodiversity micropolitics. I identified the relevant methods to adopt and wrote the interview guide with the help of Nicolas Lescureux. I conducted all semi-structured interviews by travelling to the marine protected areas (except for two interviews that were conducted remotely due to the health situation). All interviews were recorded and I transcribed them manually. I codified and analyzed all discussions. I wrote the scientific article with the help of Nicolas Lescureux and Olivier Gimenez. Fieldwork was funded thanks to the French Society of Ecology and Evolution from which I received a field grant in 2019, and with the logistic help of Hélène Labach and MIRACETI.

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The construction of ecological expertise and its implications – Biodiversity workers viewpoint on the role of ecological monitoring in the French Mediterranean Marine Protected Areas

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Abstract: At a time when motivations to build strong ecological expertise are important to implement efficient biodiversity conservation policies, we study the viewpoints of biodiversity professionals on the place of ecological data in the functioning of marine protected areas and in their everyday work. Having ecological expertise allows marine protected areas and their agents to establish themselves locally as essential institutions for biodiversity management. However, the chronic under-funding of biodiversity policies leads to a double risk because the stated objectives in terms of ecological expertise become difficult to achieve. The lack of human resources, which is the main reason for these insufficient budgets, poses a risk to the quality and quantity of the ecological expertise produced, as well as to the quality of the agents' working conditions. This work is the first qualitative survey of French marine biodiversity professionals and echoes the work carried out in terrestrial environments. We found that the collection of ecological data in protected areas encompasses multiple dimensions and fulfills several scientific, economic, psychological and political functions that may be affected by current trajectories of biodiversity policies in France.

Keywords: *biodiversity, data, ecological monitoring, protected areas, Mediterranean Sea*

1 Introduction

With the awareness of the need to protect nature since the 1980s, naturalist observations and ecological data have gone beyond their fundamental knowledge framework to endorse a political dimension in the preservation of biological diversity (Godet & Devictor, 2018; Mauz & Granjou, 2010). Ecological knowledge about natural environment, species, or populations is a crucial element for biodiversity protection and management (Martin et al., 2009; Nichols & Williams, 2006). Conservation policies generally rely on ecological knowledge and data to establish legislations (e.g., the IUCN Red List classify as protected). However, during the last decades, two major changes have impacted the world of nature conservation in its relationship with ecological data. First, technological and scientific transformations allowed for the observation of new species, and access to complex ecological systems (Moussy et al., 2021). While ecological monitoring in national parks used to focus on large wildlife species, the fraction of studies dedicated to insects, flora, and other taxa that may be poorly known has greatly increased in recent decades (Jailloux, 2010). Second, there has been a political and institutional shift in the world of biodiversity management since the 1990s. The inclusion of biodiversity conservation in the international public policy agenda led to the increasing professionalization of the sector and reshaped the role of ecological knowledge (Granjou, 2013). Empirical knowledge or expert subjective judgements are no longer sufficient to motivate environmental management policies, while at the same time, quantitative ecological indicators obtained from precise and rigorous scientific protocols allow for objective decision-making (Alphandéry & Fortier, 2015; Granjou et al., 2010).

These two important changes have led to the emergence of new demands for "scientific" or "objective" ecological knowledge in the field of biodiversity conservation. In protected areas, collection of ecological data is increasingly performed through the implementation of advanced scientific protocols and sets aside more qualitative expert judgements (Jailloux, 2010). To name to these protocols for collecting ecological data, we commonly refer to ecological monitoring. Ecological monitoring can be defined as the standardized and systematic collection of data to produce inferences about the ecology of one or more predefined taxa or taxonomic groups (Moussy et al., 2021). In this article, we will adopt a broad definition of ecological monitoring to include any protocolized operations for collecting ecological data. We can distinguish *scientific expertise*, which results from the implementation of a scientific approach to the acquisition of ecological knowledge (e.g., robust sampling protocol, statistical analysis method), from *ecological expertise*, which results from the acquisition of ecological knowledge, regardless whether this knowledge emerges from a scientific approach or not (e.g., expert opinion).

Having ecological expertise allows biodiversity management stakeholders to participate in the decision-making process of environmental policies (Arpin et al., 2015). Ecological expertise ensures a gain in legitimacy for those who hold it and acts as an access condition to decision-making and deliberative mechanisms (Alphandéry & Fortier, 2015; Granjou, 2013). Mainly developed since the Convention on Biological Diversity in 2004, the increasing demand for ecological expertise took place at the international scale (e.g. IUCN, IPBES) as well as at the national or local scale (e.g. health indicators of Mediterranean seagrass beds, ANDROMEDE (2020)) to assess and protect biodiversity. The almost ubiquitous requirements for environmental impact assessment before a construction project, or prior to the designation of sites of ecological interest increase the demand for environmental data required for conducting these procedures. With the growing need for robust ecological expertise to assess and understand the status of ecosystems and species, scientific data collection and analysis became an imperative in the acquisition of ecological knowledge. Public institutions fund ecological data collection programs to contribute to what Céline Granjou calls the "ecological expertise market" on which biodiversity stakeholders are expected to participate. Among the stakeholders of biodiversity conservation, we broadly include nature protection associations, managers of protected areas, private consulting firms, and specialized public administrations such as the French Office for Biodiversity (OFB). Recently, other sectoral structures such as agricultural unions, fishing and hunting federations have presented themselves as holders of ecological expertise. Holding ecological expertise responds to an economic necessity but has also a political purpose to be perceived as a credible actor. Having an expertise allows one to obtain funding and to present oneself as a relevant party (Granjou, 2013). As a consequence, the growing expectations in terms of ecological expertise are transforming the professions of nature protection in France. The two main paths taken by biodiversity management institutions to comply with analysis and technical requirements are the incorporation of new monitoring technologies and the increasing specialization of agents (Granjou, 2013).

Currently, public environmental policies rely on protected areas as a preferred tool for managing natural resources (Blandin, 2009). Ecological monitoring has a central role in the functioning of protected areas and structures the working life of the agents who work there (Granjou, 2013; Vimal et al., 2018). Among the studies on biodiversity policies and workers in France, the marine environment has received little attention. The French maritime coastlines are mapped by a network of Marine Protected Areas (MPAs) that constitute the institutional tool for the protection of the seas and oceans (Agardy, 1994), in which biodiversity policies are implemented. Similar to "terrestrial" environments, MPAs are administrative institutions that produce and use ecological data to set up indicators and local legislations (Dunham et al., 2020). MPAs form a network whose contribution to the production of ecological data on the marine environment is important, particularly because they are permanent institutional structures like the scientific research centers and universities (e.g. French Research Institute for the Exploitation of the Sea), but in contrast to private actors or associations.

Collecting ecological data in the French seas is embedded in a well-defined legislative framework. To provide a common basis for national policies protecting European seas, the European Union recently voted the Marine Strategy Framework Directive (MSFD) that is now included in the international biodiversity protection agenda of European states (*La Directive Cadre Stratégie Pour Le Milieu Marin (DCSMM)*, 2008). Each member state must conduct monitoring programs to assess usages, threats, and the conservation status of marine ecosystems through the production of indicators (e.g. for marine litter, fisheries stocks, conservation status of seabird populations, marine mammals, Baudrier et al. (2018); Lambert et al. (2020); Laran et al. (2017); Pettex et al. (2017)). MSFD objective is to implement a measures program to reach or to maintain the good ecological status of the marine environment (e.g. prohibition of anchoring in Posidonia meadows, ministerial decree on grouper fishing). MPAs are deeply involved to apply and develop the numerous ecological monitoring programs required by MSFD. Since 2010, ten Marine Natural Parks have been funded and created in the French seas, while at the same time, MSFD has been implemented with the associated requirements in terms of ecological data. The increase in number of MPAs has led to scientific and administrative emulation in biodiversity institutions in France. In the French Mediterranean Sea, MPAs take different institutional forms, but they constitute a dense network where many ecological issues and some monitoring protocols are shared by multiple MPAs (Figure 1).

On the one hand, the culture of ecological expertise is flooding the world of biodiversity management, hence logically impacting the marine environment. On the other hand, the synchrony between the recent MSFD implementation and the strengthening of the MPA network led to a significant increase in the need for marine ecological expertise. Marine conservation is undergoing rapid development in France and MPA agents are the main actors. Therefore, marine conservation in France provides a relevant context to study the construction of ecological expertise in the marine environment, and its implications for the MPA network and for the workers. In this context, which has been little studied to date, we aimed to analyze the role of ecological expertise in the functioning of protected areas through the perception of MPA agents in the French Mediterranean Sea. First, we present how ecological monitoring structures the organization of MPAs through the production of ecological expertise, which is of critical importance for MPAs.

Holding a precise knowledge of their territory allows the MPA agents to be accepted as biodiversity actors in the eyes of local and national stakeholders. Second, we argue that the multiplication of ecological monitoring protocols in the MPA to meet the requirements of expertise poses a risk to the quality of the ecological expertise and raises concerns about the working conditions of the agents. Finally, we discuss the role of ecological expertise in the decision-making process of marine conservation policies.

2 Methods

2.1 Study area

The institutional framework of French Mediterranean MPAs is complex and several governance models coexist. Some MPAs are managed by local authorities (e.g. Regional Natural Park - PNR - of the Camargue, or by municipalities). Other MPAs are under the authority of the French Office of Biodiversity (OFB), such as Marine Natural Parks and National Parks. The internal organization of MPAs is distinct depending whether the MPA is managed by OFB which provide recurrent funding allocated by the government, or whether the MPA governance comes from local and regional authorities that goes with more precarious funding. Hereafter, we discuss this distinction about the MPAs governance for comparative purposes of the institutional framework.

2.2 Semi-structured interviews

For two years, we conducted qualitative interviews with agents of 8 MPAs of the French Mediterranean Sea and OFB agents. We performed individual semi-directive interviews to explore the perceptions of marine biodiversity professionals concerning ecological monitoring and their role in the marine protection policies. The interview guide included 31 questions structured in three sections (Appendix 1).

The first section dealt with the current and past professional activity of the MPA agent. We discussed his current missions within the MPA as well as his educational and professional background. The second part of the interview aimed at exploring how is performed the ecological monitoring programs in which he/she takes part. Questions focused on the different stages of the monitoring process, from the definition of the scientific question, to the reporting and the analysis of the results, including the data collection through a field protocol. In the third section, we explored the role of ecological monitoring in the MPA functioning, and in relation to national policies for the protection of the marine environment.
During the interview, we ensured to address each topic in the interview guide, even if some answers went beyond the scope of the question. We targeted eight Mediterranean MPAs among the most important in terms of surface area and resources (see figure1 describing the study area). A standard interview lasted about 45 minutes. In total, 22 people answered to the interview. Interviews took place directly in the MPA offices, or in the field. Due to health restrictions related to the Covid-19 epidemic, we conducted 4 interviews via videoconference, two of them were performed with individuals already met in the field at their MPA.

Along with qualitative interviews, this study is also based on the involvement of one of the authors during his work on ecological monitoring of marine mammals by the French Mediterranean MPAs. Over the last three years, several field missions and meetings have been carried out jointly with MPA agents, and have nourished some of the discussions presented here.

3 Results

Among the 22 MPA agents we interviewed, 12 belonged to governmental civil service and work for Marine Natural Parks or National Parks, while 10 were employed by local authorities (municipalities, Regional Natural Park, Corsican community). Nine were field-work agents, 9 scientific managers, and 3 MPA directors. There were 7 women and 15 men.

##The race for ecological expertise in MPAs

Ecological monitoring and collected data allow MPAs to build up ecological expertise, which informs government services, MSFD indicators, and enables the implementation of legislations. *"The role of monitoring is to provide clues for setting up protection tools" #7* emphasizes one agent. MPA agents claim to have a high level of ecological expertise, which is based on a detailed knowledge of the local context. Local management is their asset, because MPA know their territories. They also perceive their knowledge as more legitimate than large-scale indicators. For the agents, ecological expertise comes from *"the manager's initiative because she/he is directly concerned by management issues. The field-work expertise, history of monitoring design, are only known by the manager" #15*. MPA managers know how to justify the reliability of their data. Because of their in-depth knowledge of their territory and their close relationships with local stakeholders, MPA agents explicitly integrate the needs of their area, unlike national or European policies such as the MSFD. Legislation resulting from national monitoring programs are sometimes perceived as not very precise, and the adequacy of legislations is sometimes contested by MPAs. *"We would like to be listened to upstream rather than downstream, but that is where we come in, when the measure is set, just before it is applied, we bring our data and we contest everything." #2*

Thus, MPA agents assume a responsibility for the detailed knowledge of their territory, which asks for re-

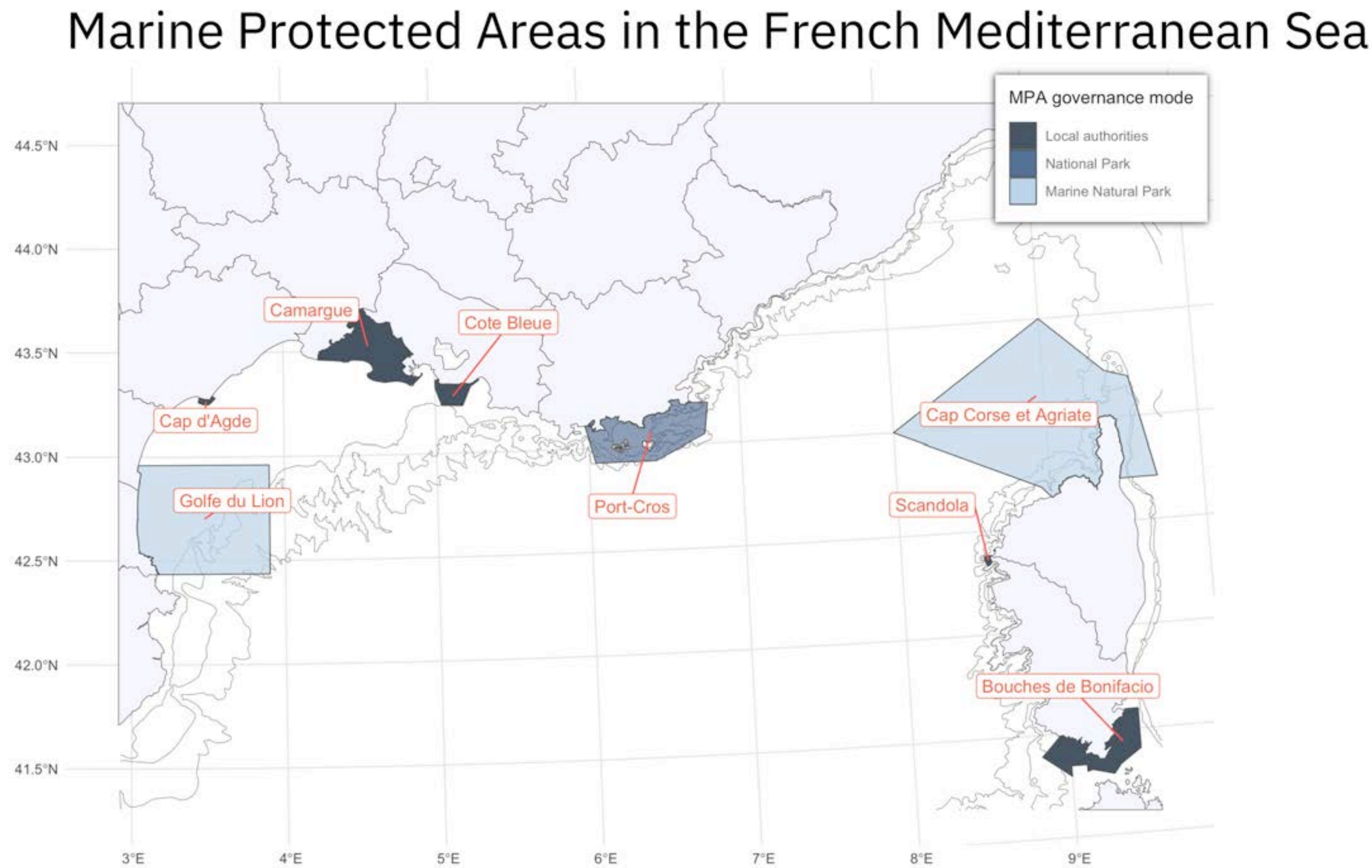

Figure 1: **Location of the Marine Protected Areas (MPAs) visited during the study.** Filled color of the MPA corresponds to governance mode, which distinguish between MPAs managed i) by local authorities: Blue Coast Marine Park, Natura 2000 area of the Posidonia of Cap d'Agde, Camargue Regional Natural Park, Scandola and Bouches de Bonifacio Natural Reserves), ii) with public governance as the Port-Cros National Park, iii) with a mixed governance between the French Office for Biodiversity and a management council made up of local stakeholders, as the Marine Natural Parks of the Gulf of Lion and Cape Corse and the Agriate.

quirements in terms of the ecological expertise to be produced. Ecological expertise is a guarantee of credibility for MPAs and their agents, both regarding local stakeholders and governmental services. Knowing the ecological stakes of the territory makes it possible to legitimate MPA in the arena of biodiversity decision-making.

3.1 MPA with limited resources

Although all MPAs are affected by this imperative to produce ecological expertise, public institutions such as Marine Natural Parks and National Parks are not impacted the same way as MPAs managed by local authorities. In MPAs managed by OFB, the management dashboard summarizing all ecological indicators to be filled out is quite rigid, and ecological monitoring programs take a predominant place in the agents' schedules compared to police oversights. *"Usually, it is 80% of our time for knowledge and 20% for police"* reports an agent of the Gulf of Lion Marine Natural Park. Besides, MPAs managed on a smaller scale (e.g. Regional Natural Park, Blue Coast Marine Park) have more flexibility defining their monitoring objectives and when organizing their missions. Teams are usually smaller and for these agents, police surveillance can take a more important role, even though they are not authorized in to issue fines.
Nevertheless, global trends of underfunding exist in MPAs. The main problem is insufficient human resources, while equipment requirements are often satisfied, with rare exceptions. *"We are fine. In terms of investment, it's not open bar but close. We have good equipment. It's more the number of agents that raise concerns. We're not enough." #10*. MPAs agents point out the dissociation between stated objectives and decline in recruitment. *"Maybe we wanted to do things too big. But we are fewer and fewer" #19*.
Producing a complete and qualitative ecological expertise places a significant burden in terms of quantity of data to be collected for the MPA. When human resources lack, it can be complicated to perform all ecological monitoring protocols. An agent testifies that the financial resources are too limited to meet the objectives set when the MPA was created:

"The main concern is that we are not geared adequately. When they created the status of Marine Natural Parks in 2011, the financial conditions were different, there announced money. Parks were supposed to hold 30-40 people. So indeed, with 30-40 people and significant budget, we could consider many things. Except that today, the reality is that a park with 10 people is quite good. And the budgets, we see everywhere else that they are decreasing. The Marine Natural Park of Iroise used to do a lot of monitoring programs because they were involved in a lot of initiatives in the good old days. Now, they had to stop a lot of monitoring activities. Because there are no more funding and no more human resources" #6

The overestimation of the number of ecological monitoring programs to perform regarding capacities of the MPA has scientific implications on both the quality of the collected data and the human conditions for the MPA workers.

3.2 The race for ecological expertise affects the quality of the ecological data collected

Limited human resources regarding ecological monitoring objectives requires some adaptation form MPA agents. When the planning of all protocols is impaired, MPA agents can be forced to choose between several ecological monitoring programs:

"In times of high attendance, it is too hard. Then in summer, it is too difficult to ensure monitoring. This is a crucial period for the western Mediterranean." #19

Within an MPA, communication between agents can suffer from this excessive workload, which deteriorates the quality of the monitoring that is performed. The agents who plan and analyze monitoring do not necessarily have enough time to ensure that field-work agents correctly collect data:

"Scientific managers do not have enough time to go out on the field. Then, on some protocols we realize that there is a misunderstanding between data collection in the field and data processing afterwards" #10

In addition, MPA agents may not have enough time to define the protocols: *"We have identified the ecological indicators but we haven't thought about the protocol. And we don't have the time to do that." #6*. Lack of resources also impacts other MPA missions. As one agent testified, the recent Marine Natural Parks are very large MPAs and agents almost never go to the pelagic seas because the human and nautical resources are not available to go and work in these pelagic zones. Despite their MPA label, these very large pelagic areas are not monitored, not regulated, and poorly studied.

3.3 The race for ecological expertise also impacts working conditions

The lack of human resources also impacts working conditions in MPAs. Important needs in terms of monitoring protocols and police surveillance imply that MPA agents are often engaged in field-work while being dependent on the weather conditions at sea. Several MPA agents are concerned about their workload, which they consider difficult to sustain. Some deplore this "just-in-time" workload that is difficult to balance with their personal lives (e.g. working on weekends, dependence on weather conditions). Besides, one agent expressed his fear of a work accident due to the intense schedule of the field work. Despite the increasingly complicated working conditions, MPA agents report a strong commitment to their job that some of them describe as a "passion":

"As I already said, we are pointed out as being very efficient but at the expense of the conditions of the staff. I'm happy with that and I'll continue, but we're among the worst off." #2

MPA agents emphasized their commitment to field work. However, under-staffing conditions lead some of them away from field work and towards more administrative tasks: *We were much more in the field before. And even for us, being bookworms is not..." #13*. In addition, some MPA agents fear that the increase in technical protocols will decrease their field work: *"A wish for the future? To be able to continue diving, not to be replaced by robots" #3*.
Overall, deterioration of working conditions is not subject to internal complaints within the MPA and the working atmosphere is perceived as quite good by the agents interviewed. The problem is viewed as being structural and affecting all biodiversity policies: *"There is no conflict internally because everyone is aware of the lack of funding, it is not the directors who do not support us" #2*. Structural problems of underfunding threaten the missions of MPA agents and their working conditions. Furthermore, the underfunding of MPAs could affect the efficiency of marine protection: *"[An MPA is] a team and funding resources. If there isn't that, it doesn't work as well, it's paper parks." #3*. The reference to "paper parks" targets purely administrative protected areas where insufficient resources allocated do not allow for the effective fulfillment of biodiversity protection (Rife et al., 2013). In some MPAs, budgetary constraints have forced a reduction or even a halt in the recruitment of permanent jobs and have pushed structures to turn to Voluntary Civic Service procedures, through which qualified staff is hired at a lower cost and under advantageous conditions due to the flexibility and precariousness of the contract. Very recently, in order to mitigate the lack of human resources, other fixed-term recruitment have been contracted through calls for proposals (e.g. financing of contracts with NGOs), including in MPAs where the vast majority of permanent positions are held by civil servants. MPAs managed by local authorities do not receive enough recurrent funding to ensure their functioning. In order to "balance the budget",

applications to calls for proposal are part of the daily routine of MPA agents to respond to the precariousness of the funding.

3.4 Ecological expertise faces the deliberative imperative

Despite the pressure to hold ecological expertise, some MPA agents point out that regulatory decisions are not motivated by ecological data and scientific evidence but are instead based on political considerations. Regarding some topics, such as marine mammals, MPA agents underlined the impossibility of implementing protection measures because these are mobile species on which no regulation has any effect, hence questioning the relevance of data collection:

> *"Yes, we should not question knowledge acquisition, but today I have the feeling that we never know enough... we perform ambitious monitoring programs, monitoring strategies, but we still don't have any plan for action." #1*

More generally, MPAs would not guarantee effective protection:

> *"We are a MPA, so yes, we perform monitoring, but for now there is no place more protected than Calvi where there is no MPA. Then, strict protection measures are good, they are necessary. But we need a little more in MPAs." #10*

MPA agents highlight the lack of political will to implement protection measures and the low value given to ecological evidence:

> *"For sea urchins, we keep the decree. But given the urchin report, it's not a critical argument to maintain the bylaw. It's just that no one asked to have the order removed." #8*
> *"There are not enough regulations or legislation resulting from monitoring programs. At first glance, it is obvious. There is a lack of actions." #7.*

Besides, some MPAs such as marine Natura 2000 areas are simply not funded:

> *"Marine part of Natura 2000 areas is not funded. But it is completely aberrant because the OFB is supposed to manage the sites but it can't because one person has to deal with 4 or 5 Natura 2000 areas." #17*

Aware of the shortcomings of ecological expertise to establish conservation policies, MPA agents underline that MPA range of action extend beyond the scientific domain to include a deliberative role. MPA agents emphasize their trust relationships with stakeholders to encourage practices changes:

> *"We are encouraging better practices. Monitoring results will produce ecological evidences that we will present to the stakeholders concerned and to the management board, trying to encourage them to change their practices. By considering another way of doing things according to the data so that it is a win-win." #7*

Despite numerous ecological monitoring protocols that put under pressure the functioning of MPAs, the key piece of marine management policies lies in the interplay of stakeholders within which MPAs and their agents advance their ecological expertise to hold their position.

4 Discussion

Our work provides the first qualitative social research on French marine biodiversity professionals and echoes the work conducted in terrestrial environments (Arpin et al., 2015; Arpin, 2020; Jailloux, 2010). The interviews we conducted provide an overview of field conditions in MPAs, in relation with national policies the marine conservation and their funding. This research also contributes to the field of sociology of expertise and illustrates the consequences and contradictions related to the requirements to produce ecological expertise that spans biodiversity actors. More broadly, implications raised here are likely to be found in many biodiversity management institutions, associations, and NGOs.

4.1 The imperative of ecological expertise and its implications

The institutional context of marine conservation is not exempt from the influence of the "market of expertise" on which biodiversity professionals are expected to compete to claim credibility (Granjou, 2013). Legitimacy and acceptance of MPAs in the eyes of local stakeholders relies on a detailed knowledge of the territories and a high level of ecological expertise. Acceptance and commitment of stakeholders favor the sustainable implementation of a biodiversity management tool on a territory (Danielsen et al., 2005; Garcia & Lescuyer, 2008). Ecological knowledge acquired makes possible to engage in a dialogue with local populations who are interested in the detailed information available by the MPA. While the primary motivations for holding ecological expertise are operational (e.g., inform the indicators of the MPA dashboard), MPA agents also value their ecological knowledge in an informal setting, notably by facilitating dialogue with stakeholders outside the MPA. Cooperation between managers and local stakeholders has been identified as one of the main factors beneficial to the efficiency of MPAs (Giakoumi et al., 2018). On this subject, MPA have departments and services that go beyond ecological expertise and that aim to develop cultural heritage, or to support economic activities (Mazurek et al., 2019). Hence, ecological expertise contributes to MPA acceptability, which gains credibility in the eyes of local stakeholders. Because of their involvement in the local socio-economic world, MPAs build their actions and missions according to the challenges of the territory.

In parallel, holding "proximity expertise" is sometimes claimed as a counterbalance to national legislations judged with mistrust because they distance the decision-making process from the place of data collection (Arpin, 2020). This conception of local expertise echoes the tensions in which the world of naturalist associations finds itself between a perspective of territorial and social proximity with the data, and a perspective of professionalization and large-scale standardization via the centralized databases of the French National History Museum (Alphandéry & Fortier, 2015). MPAs are committed to producing advanced ecological expertise on their territory to assume responsibility as a legitimate local biodiversity actor. Our study reinforces the idea that monitoring programs shape the actions of protected areas by mobilizing financial, logistical, and human resources (Vimal et al., 2018). Holding ecological expertise also has a symbolic utility by shaping MPA actions. Instead of playing an important role in decision-making, human dimensions of ecological expertise tend to prevail by strengthening the relationships between the MPA agents and the local populations (Vimal et al., 2018).

However, requirements to produce ambitious ecological expertise is hampered by MPAs budgetary constraints. Widespread among biodiversity protection institutions, underfunding leads to scientific and operational dysfunction in protected areas (Balmford & Whitten, 2003; Coad et al., 2019). French Mediterranean MPAs are no exception to this scheme and also suffer from limited human resources according to stated objectives. When all ecological monitoring programs cannot be performed under adequate conditions, MPA agents are not blind to the difficulties they encounter and try to improve working conditions of production of ecological information. Underfunding can lead staff to rank MPA missions to focus on the highest priority actions (Gardner et al., 2008), or to collect lower quality data *"data rich but information poor"* (Gardner et al., 2008; Vimal et al., 2018). Then, limiting MPA actions leads to deterioration of the quality of ecological expertise produced, and hence of the information needed to protect biodiversity. While one goal of ecological monitoring is to reduce uncertainty about biodiversity decision-making (Callon et al., 2001), MPA underfunding can increase this uncertainty by limiting the quantity and quality of the information available. Consequently, degradation of working conditions for performing ecological monitoring has deleterious implications for the effectiveness of biodiversity protection (Coad et al., 2019).

Along with the risk of deterioration of ecological information, MPA underfunding sometimes compromises MPA agents working conditions. However, most MPA agents report a high level of motivation to do their job, which is seen as a "passion" as it is the case for many biodiversity professionals (Granjou, 2013). MPA agents see multiple psychological dimensions in their relationship to their job. Working in an MPA mobilizes technical knowledge during when performing monitoring protocols, relational/social knowledge during exchanges with local populations or during police missions for certain agents, but also involves the identity of MPA agents and the perception they have of the meaning of their jobs (Dejours, 2009). The subjective relationship of MPA agents to their missions is disrupted by MPA underfunding that affects work conditions. Their "social world", which includes interpersonal relations, is degraded by work overload, and to a larger extent the "subjective world" is affected (Fiorelli et al., 2012). Indeed, MPA agents commit their personality and their convictions in a sometimes passionate relationship with their work. Holding a high-quality ecological expertise is rewarding for the agent and constitutes a symbolic reward of the accomplishment of her/his work. This subjective dimension can be affected when the ecological knowledge produced is no longer of satisfying quality or loses its usefulness. Thus, while the agents invest strongly their personality in the collection of ecological data, understaffed conditions could affect the symbolic reward of the agents for their work within the MPA. Nevertheless, MPA agents interviewed emphasized that their missions contribute to the protection of a common good which is nature, or biodiversity (Granjou, 2013). Symbolic and personal recognition that MPA agents derive from their missions remains important despite the work pressure. Attachment of MPA agents to their role of biodiversity protectors compensates for the harsh working conditions they experience sometimes.

Moreover, progressing technologies of ecological monitoring, growing use of external service providers, and lack of human resources have led to fears that some agents will be confined to their offices, as Céline Granjou (Granjou, 2013) has also shown, stressing their attachment to field work. Technical rise of monitoring programs transformed the relationship of agents to nature; some aesthetic and physical dimensions have been discarded. Job modernization accelerated the implementation of operational and technical dimensions, linked to the production of ecological expertise (Granjou, 2013). On the one hand, repetitive and standardized protocols are sometimes difficult to accept for MPA agents who do not feel that knowledge and personal expertise are valued by these practices. On the other hand, some agents are enthusiastic about using newest technologies, or about implementing rigorous protocols that are perceived as robust and informative. Similar feelings of meaning loss are found in the sphere of work in general (Dejours, 2009). However, it is interesting to note that this tendency can even worry MPA agents who exhibit strong passionate vocations towards their profession.

At the national scale, biodiversity conservation policies experience the same funding conditions as MPAs. Agents of the "public" MPAs (e.g. Marine Natural Park, National Parks) belong to the same corps of civil servants and navigate between the different structures as they want to transfer. Financial conditions are decided

by the Ministry of Ecology and reflected uniformly to all biodiversity institutions in France. Underfunding biodiversity policies leads to a double risk in protected areas when the stated objectives in terms of ecological expertise become difficult to achieve. The lack of human resources raises risks, on the one hand, to the quality and quantity of ecological expertise, and on the other hand, to the quality of the working conditions of the agents.
In 2013, Céline Granjou pointed out that the trends of decreasing budgets are not specific to MPAs but weigh on all biodiversity institutions. At the national scale, disinvestment affects a large part of public institutions (Frajerman, 2019; Simonet, 2021). Decrease or even the end of the recruitment of permanent civil servants positions in favor of the hiring of fixed-terms agents, growing importance of governance through calls for proposals, and the rationing of financial choices illustrate the inclusion of *new public management* strategies into public policies, including those for the protection of biodiversity (Merrien, 2002; Pesqueux, 2020).

4.2 Insufficiency of ecological expertise regarding the governance of conservation policies

Holding ecological expertise should be an indispensable prerequisite for environmental decision-making (Alphandéry & Fortier, 2015; Mathevet & Mauchamp, 2005). However, MPA agents recognize the insufficiency of ecological evidence when trying to implement environmental policies. Measures to protect the marine environment are not unquestionably based on ecological results. Evidence-based conservation (Sutherland et al., 2004) faces the round reality and the local sociological context (Mathevet & Mauchamp, 2005). MPA agents considered sociological mechanisms at work and socioeconomic staked to be determinant in the decision-making process, as highlighted by Vimal & Mathevet (2011). To play a role in political decision-making, protected areas promote their fine ecological expertise of the territory and claim skills in conducting deliberative processes (Granjou et al., 2010; Mazurek et al., 2019). Thus, MPAs positioned themselves in the political arena with multiple types of expertise. Following Carolan (2006) classification of expertise, MPAs do not only hold *contributory expertise* via scientific expertise and technical knowledge, but they also know how to bring scientific and technical knowledge into dialogue with other actors, which is called *interactional expertise* (Carolan (2006); Stem et al. (2005)). Ecological expertise is no longer just unquestionable information. Ecological knowledge is rooted in a social, political and cultural context that must be understood and mobilized appropriately in the arena of biodiversity management policies (Alphandéry & Fortier, 2015).

One might see a paradox between oversized ambitious ecological expertise and environmental policies that are ultimately little affected by ecological evidence. In the context of limited funding, overemphasis on ecological monitoring could be detrimental to other MPA actions such as police surveillance or conservation education, as illustrated in other protected areas (Gardner et al., 2008; Mueller-Hirth, 2012). Beyond the poor contribution of ecological expertise to decision making, MPA agents pointed out to the slow implementation of biodiversity protection measures, echoing the literature on paper parks (Costello & Ballantine, 2015, 2015). Magris & Pressey (2018). However, MPA remains ubiquitous despite the criticisms made against the MPA label. The area covered by MPAs is the metric used and valued in policy agenda (Costello & Ballantine, 2015; Maxwell et al., 2020), and the international goals of the Convention on Biological Diversity set a target of 10% of the oceans under MPA by 2020. Then, to respect these commitments, many MPAs have been created but many are not accompanied by sufficient resources (Amengual & Alvarez-Berastegui, 2018). This is the case of some MPAs in the French Mediterranean that are very large and allow to meet communication and surface targets without having to implement concrete protection measures, as testified by an agent about marine Natura 2000 areas.

Beyond our research, trends of underfunding biodiversity protection are international (Coad et al., 2019). Western governments, including the European Union, mobilize a series of strategies to align conservation policies within a typically neoliberal framework of cost reduction and public disinvestment (Apostolopoulou et al., 2014). Among other things, we observe the public disinvestment from biodiversity management and protection operations (sometimes to the benefit of non-governmental organizations), the rescaling of conservation policies towards local authorities and communities, the increase of public-private partnerships for biodiversity management, along with a rhetoric of deliberative and consensual approaches (Apostolopoulou et al., 2014; Igoe & Brockington, 2007). Within marine conservation policies in France, we identified several of these dynamics. Marine Natural Parks, the most recent management tools, illustrate the decentralization of biodiversity protection policies giving decision-making power to a deliberative management board, with the associated limits in terms of protection efficiency (Mazurek et al., 2019). Investigating the practices of protected area managers sheds light on how biodiversity conservation takes place within the socio-economic context of today's dominant neoliberal model and helps to expose its contradictions (Apostolopoulou et al., 2014).

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Appendix 1 – Interview guide

Valentin Lauret, Olivier Gimenez, Hélène Labach, Nicolas Lescureux

Objectif : Étudier la perception des suivis écologiques par les gestionnaires d'Aires Marines Protégées (AMP) de Méditerranée française.

Talon sociologique et questions de départ

- Données administratives sur le statut et rôle de l'AMP
- Poste de l'interviewé dans l'AMP, missions précises
- Lieux de travail et postes précédents dans les aires protégées.
- Quels sont les grands types de suivis engagés par l'AMP ?
- A quels suivis participez-vous personnellement ?
- Niveau d'étude

Légende : Tous les « seconds points » (a.) et les (i., ii., etc) sont des options. Pas forcément des éléments qui <u>doivent</u> être abordés mais plutôt des éléments de relance sur ce qui sortira.

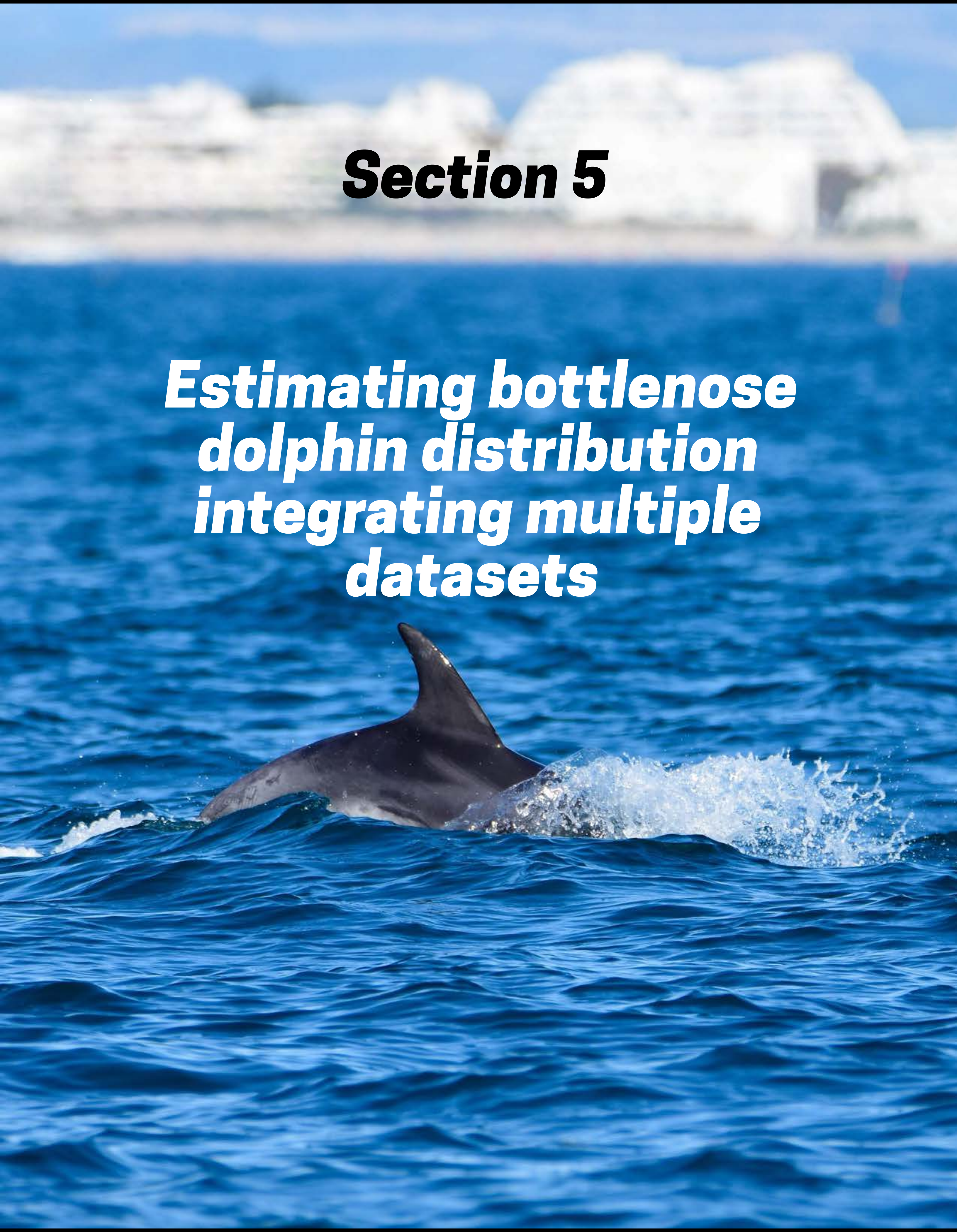
Thèmes	Sous-thèmes
I. Sur le métier de l'enquêté dans l'AMP	- Quelles sont vos missions dans l'AMP ? - Depuis quand travaillez-vous dans le domaine de la conservation ? *Éléments d'histoire de vie : études, motivations, mutations, etc* Idée : Commencer par une question très large : Pourquoi vous faites des suivis et comment ?

II. Le déroulement des suivis écologiques	**1. La mise en place d'un suivi écologique** a. Les objectifs sont-ils clairs ? b. Qui décide du protocole ? des indicateurs ? ▪ Marge de manœuvre c. D'où vient la « commande » de ces suivis ? **2. La récolte des données** *Quelles difficultés rencontrez-vous lors de la mise en place des protocoles de suivi ?* a. Faisabilité des protocoles i. Possibilités techniques (adéquates avec les objectifs) ii. Imprécision dans les mesures / Du gâchis lors de la récolte b. Appropriation des méthodes de suivi i. Capacité, formation pour une récolte adéquate ii. Compréhension des objectifs de suivi et des méthodes c. Saisie des données sur le terrain i. Multiplication des plateformes de saisie **3. Le post-collecte : saisie et traitement** *Une fois la donnée collectée, où va-t-elle ? quel est son traitement ?* a. Bases de données / stockage des données. Entrer les données manuellement ? *time consuming ?* b. Analyse des données : par l'AMP ? sous-traitance ? c. Qui utilise les données ? **4. La restitution** *Quelle utilisation est faite des données collectées ?* a. La valorisation en termes de publications scientifiques ? *Les résultats des analyses sont-ils communiqués ?* b. Les résultats sont-ils communiqués i. Au sein de l'AMP ? ii. Au grand public ? iii. Autres

III. Rôle des suivis dans la gestion des AMP	**1. La place des suivis scientifiques dans le plan de gestion** *Comment sont utilisées les informations collectées pour la mise en place des mesures, des politiques de gestion ?* i. Au niveau de l'AMP / Au niveau façade. ii. Les suivis suffisent ils à prendre les décisions ? iii. D'autres informations complètent la prise de décision ? *Quelles sont pour vous les informations écologiques nécessaires pour une AMP ?* **2. La place des suivis dans les actions de l'AMP** *Parmi les actions de l'AMP (sensibilisation, police, etc), comment définissez-vous la place des suivis écologiques ?* i. Une activité primordiale ? optionnelle ? ii. Une activité à coordonner avec les autres missions (contrôle / police / sensi) iii. Quelle place ont les suivis en termes de temps de travail ? *Quel est selon vous l'autonomie d'une AMP pour la collecte de données ?* i. Qui sont les pièces centrales des suivis écologiques ? AMP ? scientifiques ? ONG ? ii. Quel lien avec les suivis institutionnels (SAMM) ? **3. Organisation des suivis à l'échelle du réseau d'AMP** *Que pensez-vous de la coordination des AMP de la façade pour les protocoles de suivis ?* a. Centralisation des thématiques b. Prise en compte des particularités de chaque AMP
IV. Évolution et perspectives	**1. Quelles évolutions pour les suivis écologiques dans les AMP ?** **2. Quel avenir pour votre profession ?** *Comment voyez-vous l'avenir de votre profession ? et l'avenir des suivis écologiques dans les AMP ?* **3. Des attentes particulières sur l'évolution des suivis ?**

Section 5

Estimating bottlenose dolphin distribution integrating multiple datasets



Section 5

Article 2: Using single visits into integrated occupancy models to make the most of existing monitoring programs

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French abstract and keywords

Résumé : Un défi majeur en écologie statistique consiste à produire des indicateurs écologiques fiables tout en intégrant différents jeux de données. Pour estimer la distribution des espèces, les modèles d'occupancy constituent un outil flexible qui peut s'étendre à l'analyse de plusieurs jeux de données obtenus à partir de différents protocoles de suivis. Cependant, la répétition des visites sur les sites d'échantillonnage est une condition préalable à l'utilisation des modèles d'occupancy classiques. Récemment, des modèles d'occupancy ont été développés pour analyser les données de détection/non-détection recueillies lors d'une seule visite, on parle de modèles d'occupancy de type single-visit. À ce jour, les modèles d'occupancy single-visit n'ont jamais été adaptés pour intégrer plusieurs jeux de données.
Ici, nous présentons une approche qui combine deux jeux de données single-visit dans un modèle d'occupancy intégré. Comme cas d'étude, nous estimons la distribution du grand dauphin (*Tursiops truncatus*) en Méditerranée française en combinant les données issues de 24 624 km de survols aérien avec les données provenant de 21 464 km de suivi en bateau. Nous avons comparé les résultats des modèles d'occupancy single-visit aux modèles d'occupancy classiques à visites répétées, y compris pour des modèles d'occupancy intégrés. Les modèles intégrés permettent une meilleure couverture d'échantillonnage de la population de grand dauphin, ce qui se traduit par une précision accrue des estimations d'occupancy par rapport aux modèles utilisant les jeux de données séparément. Dans l'ensemble, les modèles d'occupancy single-visit et à visites répétées produisent des inférences similaires sur la distribution des grands dauphins. Les modèles intégrés d'occupancy single-visit ouvrent des perspectives prometteuses pour l'utilisation des jeux de données écologiques dans les contextes de conservation où plusieurs protocoles de suivis écologiques coexistent.

Mots-clés : grand dauphin, modèles intégrés de distribution d'espèces, modèles d'occupancy, single-visit, suivis écologiques

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Contribution: I developed occupancy models, and performed the simulations presented in the appendices of the article I extracted environmental variables and formatted the bottlenose dolphin detections and sampling effort data that I obtained from Hélène Labach and Matthieu Authier. Once the results were obtained, I led the writing and publication of the following article. Olivier Gimenez supervised all steps.

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Using single visits into integrated occupancy models to make the most of existing monitoring programs

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Abstract: A major challenge in statistical ecology consists of integrating knowledge from different datasets to produce robust ecological indicators. To estimate species distribution, occupancy models are a flexible framework that can accommodate several datasets obtained from different sampling methods. However, repeating visits at sampling sites is a prerequisite for using standard occupancy models. Occupancy models were recently developed to analyze detection/non-detection data collected during a single visit. To date, single-visit occupancy models have never been used to integrate several different datasets. Here, we showcase an approach that combines two datasets into an integrated single-visit occupancy model. As a case study, we estimated the distribution of common bottlenose dolphin (*Tursiops truncatus*) over the North-western Mediterranean Sea by combining 24,624 km of aerial surveys and 21,464 km of at-sea monitoring. We compared the outputs of single- vs. repeated-visit occupancy models into integrated occupancy models. Integrated models allowed a better sampling coverage of the targeted population, which provided a better precision for occupancy estimates than occupancy models using datasets in isolation. Overall, single- and repeated-visit integrated occupancy models produced similar inference about the distribution of bottlenose dolphins. We suggest that single-visit occupancy models open promising perspectives for the use of existing ecological datasets.

Keywords: *Bottlenose dolphins, Ecological monitoring, Integrated species distribution models, Multi-method, Occupancy models, Single-visit*

1 Introduction

In large-scale ecological analysis, several parallel monitoring programs are often carried out to collect ecological data (Zipkin & Saunders, 2018). Ecological monitoring programs are conducted by organizations operating across different time scales, geographic scales and funding initiatives (Lindenmayer & Likens, 2010). A major challenge is integrating knowledge from different monitoring programs to produce robust ecological indicators that may be used to inform decision-making (Fletcher et al., 2019; Zipkin et al., 2021). Recently, modeling tools have emerged to combine multiple data sources to estimate species distributions and Integrated models refer to the approaches that combine different data sources (Isaac et al., 2019; Miller et al., 2019). The main purpose of integrated models is to improve the accuracy of ecological indicators (Fletcher et al., 2019; Zipkin et al., 2019). Species distributed over large areas could particularly benefit from integrated models because they allow for a global coverage of species occurrence by combining different data sources collected at different spatial scales (Miller et al., 2019). To estimate species distribution in the face of uncertainties inherent to data collection, occupancy models are commonly used statistical tools (Mackenzie et al., 2002). Occupancy models have been developed to estimate species distribution while accounting for false negatives in the observation process (Mackenzie et al., 2002). Estimating occupancy when species detection is not perfect requires performing repeated visits to a set of sites to assess the detection probability (MacKenzie, 2006). However, repeating visits is sometimes unfeasible due to associated costs and logistical issues. In this context, two relevant developments of occupancy models have been recently proposed. First, integrated occupancy models combine data from different monitoring programs to improve the estimation of species distribution (Fletcher et al., 2019; Miller et al., 2019; Nichols et al., 2008). Second, Lele et al. (2012) used occupancy models to estimate species distribution and detectability while having only one visit at the sampling site, i.e. hereafter single-visit occupancy models. An increasing number of studies suggest that under certain conditions, single-visit models produce robust estimates of occupancy without repeating visits at the sampling sites (Lele et al., 2012; Peach et al., 2017; Sólymos & Lele, 2016). Besides, single-visit occupancy offers the possibility to work with existing datasets that did not carry out repeated visits, which is relevant to population biology and management. In this paper, we develop an integrated approach that combines two single-visit occupancy models and demonstrate that combining several datasets into integrated single-visit occupancy models leads to accurate ecological parameter estimation. We also investigate the performance of single-visit vs. repeated-visit occupancy models. As a case study, we focused on the distribution of Bottlenose dolphins (*Tursiops truncatus*) in the North-

Western Mediterranean Sea. We combined aerial surveys and at-sea monitoring into integrated occupancy models and we compared the outputs of integrated occupancy models to occupancy models using each dataset in isolation. Last, we discuss the advantages of integrated single-visit occupancy models to deal with existing ecological monitoring programs.

2 Methods

2.1 Model description

2.1.1 Latent ecological process

Occupancy models estimate spatial distribution while accounting for imperfect species detection (Mackenzie et al., 2002). The formulation of occupancy models as state-space models allows distinguishing the latent ecological state process (i.e. species present or absent at a grid-cell) from the detection process (Royle & Kéry, 2007). We denote z_i the latent occupancy of grid-cell i ($z = 1$, presence; $z = 0$, absence). We assume zi is drawn from a Bernoulli distribution with ψ_i the probability that the species is present at grid-cell i:

$$z_i \sim Bernoulli(\psi_i)$$

We modelled ψ as a function of some environmental covariate on a logit scale, say habitat.

$$logit(\psi_i) = \beta_0 + \beta_1 habitat_i$$

where parameters $beta_0$, and β_1 are to be estimated.

2.1.2 Repeated-visit observation process

In standard occupancy designs, each grid-cell is visited J times to estimate the detection probability. We denote $y_{i,j}$ ($y_{i,j} = 0$, no detection ; $y_{i,j} = 1$, detection) the observations corresponding to the data collected at grid-cell i during visit j ($j = 1, .., J$). Repeating visits at a grid-cell allows estimating species detectability, with $p_{i,j}$ being the probability of detecting the species at visit j given it is present at grid-cell i:

$$y_{i,j} | z_i \sim Bernoulli(z_i p_{i,j})$$

2.1.3 Single-visit observation process

The difference with repeated-visit occupancy models lies in the number of sampling occasions which is $J = 1$ in single-visit occupancy models. The j subscript is dropped and we denoted y_i the observation corresponding to the data collected at site i. Subsequently, p_i is the probability of detecting the species during the single visit given it is present at site i:

$$y_i | z_i \sim Bernoulli(z_i p_i)$$

. Single-visit occupancy models require certain conditions to be fulfilled for estimating detection probabilities reliably. First, different continuous covariates should be used to estimate detection and occupancy probabilities (Lele et al., 2012; Peach et al., 2017). Second, the number of detections may affect the estimation of occupancy in the case of rare or ubiquitous species (Peach et al., 2017). Third, the use of inappropriate link functions to model the detection process may lead to model misspecification and biased interpretation (e.g. log-link and scaled logit link function on detection, Knape & Korner-Nievergelt (2015)). However, most often, the logit link function is used for detection, which makes the single-visit approach valid (Sólymos & Lele, 2016). Despite these concerns, simulation studies have showed that situations where single-visit occupancy models fail are rare (Peach et al., 2017; Sólymos & Lele, 2016) and, in practice, the conditions for a valid application of single-visit occupancy models are often fulfilled (Sólymos & Lele, 2016). We detailed the modeling assumptions of single-visit occupancy models in Appendix S4. Because the number of detections is an important condition to accurately estimate single-visit occupancy parameters (Peach et al., 2017), we expect that integrated approaches will be beneficial to single-visit occupancy modeling by increasing the number of detections (true occupancy) available.

2.1.4 Integrated occupancy models

We developed an integrated occupancy model using data from two independent monitoring programs, say A and B. The state process driving the latent occupancy state of site i, z_i, remains unchanged and is drawn from a Bernoulli distribution with probability ψ, which is modeled as a function of environmental covariates. The observation of the targeted species at site i during occasion j may take four values with $y_{i,j} = 0$ for no detection, $y_{i,j} = 1$ for detection in dataset A, $y_{i,j} = 2$ for detection in dataset B, and $y_{i,j} = 3$ for detection in both datasets A and B. For convenience, we drop the subscripts in the notation as the formulation of the integrated observation process is identical whether we consider single-visit occupancy (i.e. $J = 1$) or repeated-visit occupancy ($J > 1$). Assuming that detection methods are independent, the observation process can be written using detection probability by the monitoring program A (p_A) and detection probability by the monitoring program B (p_B):

$$y | z \sim Multinomial(1, z\pi)$$

with

$$\pi = [p_0, p_1, p_2, p_3] = [pr(y = 0), pr(y = 1), pr(y = 2), pr(y = 3)]$$

$$\pi = [1 - p_A - p_B + p_A p_B, p_A(1 - p_B), p_B(1 - p_A), p_A p_B]$$

We modeled monitoring-specific detection probabilities as functions of the sampling effort of each monitoring program:

$$logit(p_A) = \alpha_{0A} + \alpha_{1A} log(SeffA)$$

$$logit(p_B) = \alpha_{0B} + \alpha_{1B} log(SeffB)$$

where the parameters α_{0A}, α_{1A}, α_{0B}, and α_{1B} are to be estimated. For example, if we assume that the detection history at site i is $y_i = 2, 0, 1, 2$ over $J = 4$ sampling occasions, i.e. the species was detected by monitoring program B only at sampling occasions $j = 1$ and $j = 4$, then went undetected at $j = 2$, and was detected by monitoring program A only at $j = 3$, then for single-visit integrated occupancy we consider $y_i = 3$ because both monitoring programs detected the species at site i. We ran a simulation study comparing the performance of single- vs. repeated-visit occupancy over different scenarios affecting occupancy, and detection probabilities (Appendix S1).

2.2 Bottlenose dolphins case study

We aimed at estimating bottlenose dolphin (*Tursiops truncatus*) distribution in an area of 255,000 km2 covering the North-Western Mediterranean. The protected status of this species within the French seas led to the development of specific programs to monitor Mediterranean bottlenose dolphins within the implementation of the European Marine Strategy Framework Directive (2008/56/EC; MSFD), which involve estimating common bottlenose dolphin distribution. We considered two large-scale monitoring programs about bottlenose dolphins. We divided the study area in 4,356 contiguous pixel/grid-cells creating a 5'x5' Mardsen grid (WGS 84) that we used for all the occupancy models we considered. We used data from at-sea surveys over 21,464 km of the French continental shelf (456 grid-cells sampled, 10.46% of the total number of grid-cells). Observers performed monitoring aboard small sailing and motor boats to locate and photo-identify bottlenose dolphins all year long between 2013 and 2015 (Labach et al., 2021). At-sea surveys detected 129 distinct bottlenose dolphin groups located in 89 different grid-cells. At-sea surveys did not include planned repeated visits, some grid-cells have been visited once, and others have been visited 50 times. Then, using repeated-visits occupancy models to analyze the at-sea monitoring data requires considering only the grid-cells sampled multiple times and hence to drop the data collected in grid-cells sampled only once. Single-visit models enable us to include all data, even data collected in grid-cells that were surveyed only once, which make at-sea a relevant candidate for single-visit model implementation. Besides, we considered data collected during aerial line-transects covering 24,624 km of the French Exclusive Economic Zone (EEZ), targeting marine megafauna, and following a distance sampling protocol. The survey sampled 1336 grid-cells (i.e. 30.67% of the total number of grid-cells). Aerial surveys produced 130 distinct bottlenose dolphin detections located in 87 grid-cells. Sampling effort for aerial surveys was homogeneous over the study area with three or four replicates per line-transect between November 2011 and August 2012 (Laran et al., 2017). Because we used occupancy models, we only considered detection/no-detection data, which lead to a binary 0/1 dataset. Hence, multiple sightings detected in the same groups were coded as 1. Thus, we obtain the two aerial and at-sea detection/no-detection datasets that we analyzed with occupancy models. An important assumption of single-season occupancy models is that the latent ecological state of a grid-cell (the z_i's) remains unchanged between the repeated visits (MacKenzie, 2006). When monitoring highly mobile species, such as cetaceans, the closure assumption is likely to be violated because individuals can move into and out of the sampling grid-cell. The size of the grid-cells is much lower than dolphins' range of activity. If individuals' movement in and out of the sampling units is random, then the occupancy estimator is unbiased (Kendall et al., 2013). However, it is unlikely the case for bottlenose dolphins because their use of space is driven by ecological and environmental factors, and occupied locations are used only temporarily by individuals (MacKenzie, 2006; Neilson et al., 2018). Closure assumption is crucial to the interpretation of occupancy model's parameters. In cases where this assumption is known to be violated, the parameter is usually interpreted as the probability that a location is used by the species as opposed to probability of species presence. In this situation, the occupancy estimator ψ_i represents the probability that grid-cell i is used by the target species (Kendall et al., 2013), being interpreted as space-use by bottlenose dolphins. Occupancy and space-use refer to distinct ecological concepts. Occupancy describes the species home range that can be defined as the geographic range of occurrence, while space-use refers to the usage made by individuals of the different components of the home range (e.g. feeding locations, migratory routes, Johnson (1980)). Then, both single-visit and repeated-visits occupancy models infer the probability that a particular grid-cell is used by the species. The detection probability now accounts for both the probability of detecting the species given that the species is available for sampling, and the probability that the species is using the grid-cell during the sampling, reflecting that the species might occupy the grid-cell but not during the sampling occasion (MacKenzie, 2006). As stated above, single-visit occupancy relaxed the closure assumption because the inference of the detection probability does not require site closure between the repeated visits. However, the interpretation of the occupancy parameter is always space-use in the case of our bottlenose dolphin case study because our data is collected during multiple years and dolphins are expected to move in and out the sampling unit area during the sampling period. Because at-sea and aerial surveys were performed during different years, we considered them as independent. In 2018, recent Mediterranean scale aerial monitoring program sampled French Mediterranean following the same line-transect protocol as the aerial dataset we analyzed (ACCOBAMS Survey Initative, Initiative (2018)). Preliminary and unpublished results from the 2018 program estimated similar common bottlenose dolphin distribution to that of 2011-2012. Then, we assumed that space-use remained unchanged during the monitoring period (i.e. 2011 to 2015). Besides, we neglected the seasonal variation in the bottlenose dolphin space-use in this case study. Concerning the ecological process, we used two environmental covariates to estimate the space-use of bottlenose dolphins: i) bathymetry, which is expected to have a positive effect on bottlenose dolphins' occurrence (Bearzi et al., 2009; Labach et al., 2021), and ii) sea surface temperature (SST, AQUA MODIS | NASA 2019, https://neo.sci.gsfc.nasa.gov/), which is locally related to dolphins' prey abundance and hence expected to affect local distribution of bottlenose dolphins (Bearzi et al., 2009). We extracted average SST between 2011 and 2015 value in each grid-cell, making SST a cell-specific covariate. Similarly, bathymetry had a single value per grid-cell. We checked for correlation between the two covariates and the Pearson coefficient was < 0.3. Then, we modelled ψ as a function of bathymetry, SST, and the interaction between bathymetry and SST on a logit scale:

$$logit(\psi_i) = \beta_0 + \beta_1 bathymetry_i + \beta_2 SST_i + \beta_3 bathymetry_i SST_i$$

Regarding the observation process, we calculated the transect length (in km) prospected by each monitoring protocol within each grid-cell during a time period. Sampling effort was therefore a grid-cell-specific and time-specific covariate; $SeffA$ refers to the sampling effort of the aerial monitoring program while $SeffS$ refers to the sampling effort of the at-sea monitoring program. We modeled monitoring-specific detection probabilities as functions of the relevant sampling effort:

$$logit(p_a) = \alpha_0 + \alpha_1 log(SeffA)$$

$$logit(p_s) = \alpha'_0 + \alpha'_1 log(SeffS)$$

Regarding the repeated-visit occupancy models, we divided the detection/non-detection datasets into four sampling occasions ($J = 4$): winter (January, February, March), spring (April, May, June), summer (July, August, September), autumn (October, November, December). For the single-visit occupancy models, we considered the entire monitoring program in a single occasion. For example, let us assume that the detection history at site i is $y_i = 0, 1, 1, 0$ in repeated-visit occupancy, i.e. the species was detected at sampling occasions $j = 2$ and $j = 3$, and went undetected at $j = 1$, and $j = 4$, then for single-visit occupancy we have $y_i = 1$. In addition, the single-visit sampling effort in a grid-cell was equal to the sum of the sampling effort over the 4 sampling occasions of the repeated-visit occupancy model.

2.2.1 Performances of integrated models

To assess the added value of combining aerial and at-sea datasets into integrated single-visit occupancy models, we analyzed 3 datasets: i) the aerial dataset, ii) the at-sea dataset, and iii) the two datasets together into an integrated occupancy model. For each of these datasets, we applied repeated-visit and single-visit occupancy models. Besides the case study, we also carried out a simulation study to test for the performances of integrated occupancy models (Appendix S2). In Appendix S5, we go through a worked example of the likelihood functions for single-visit, repeated-visit, integrated repeated-visit, and integrated single-visit occupancy models. In Appendix S4, we listed the modeling assumptions required to run the different occupancy models.

2.2.2 Bayesian implementation

We ran all models with three Markov Chain Monte Carlo chains with 100,000 iterations each in JAGS called from R (R Development Core Team, 2021) using the r2jags package (Su & Yajima, 2015). We checked for convergence calculating the R-hat parameter (Gelman et al., 2013) and reported posterior means and 95% credible intervals (CI) for each regression coefficient of covariates affecting space-use probability (Fig. 1). Hereafter, we considered effect size of a covariate as the estimate of its regression coefficient. We discussed the effect of a covariate whenever the 95% CI of its associated parameter did not include 0. From covariates' effect size, we calculated the predicted space-use by bottlenose dolphins (i.e. ψ, Fig. 2). We reported maps of standard deviation of ψ (Fig. 2B). On the maps, we displayed mean and standard deviation of ψ for coastal and pelagic seas according to a 500m deep boundary that corresponds to the separation of continental shelf from the abysses. Data and codes are available on Data S1, and on GitHub at https://github.com/valentinlauret/IntegratedSingleVisitOccupancy.

3 Results

All models produced similar predictions of space used by bottlenose dolphins (Fig. 2). The 95% CI of SST, and of the interaction between SST and bathymetry included 0 in all models (Fig. 1). The probability of space-use increased with decreasing bathymetry for all models (Fig. 1). Bathymetry ranges from altitude of 0 m to -3,488 m deep, hence a positive influence of bathymetry referred to a preference for a high seafloor (e.g. 0-200m depth). Overall, maps showed greater probabilities of space-use on the continental shelf (mean $\psi = 0.76\ SD \pm 0.17$) than on the high seas (mean $\psi = 0.40\ SD \pm 0.15$), although magnitudes of ψ were different between models (Fig. 2). Bathymetry posterior means were highest for at-sea occupancy (although the 95% CI of effect

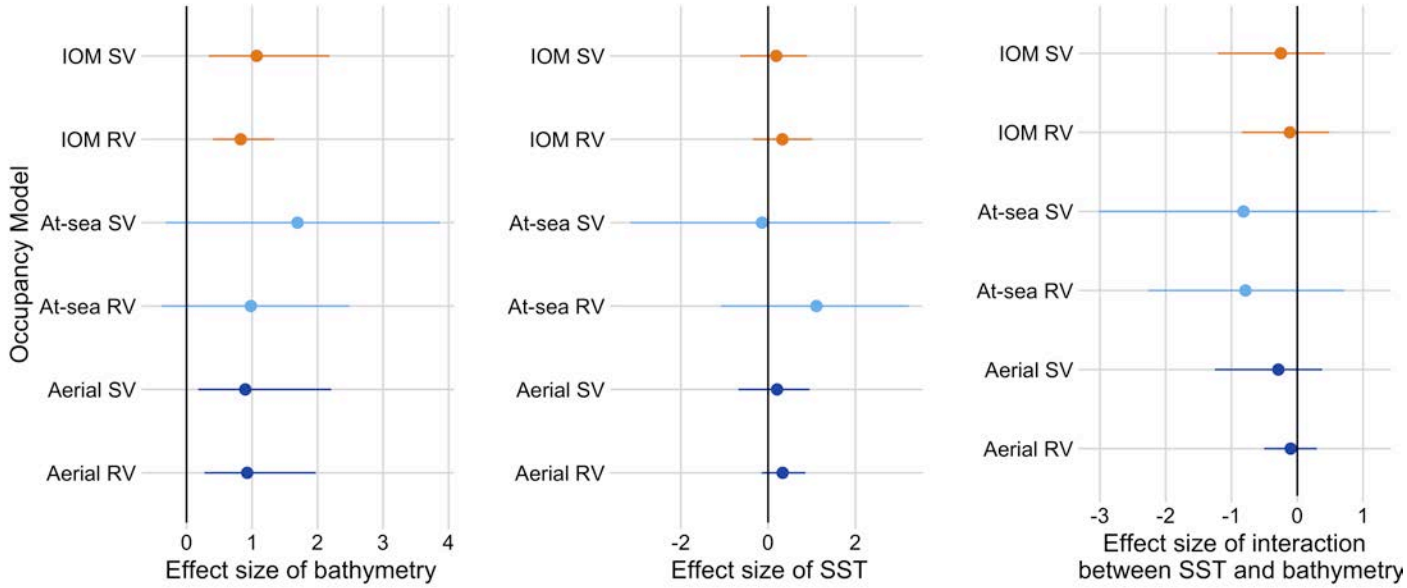

Figure 1: Effect size of bathymetry, sea surface temperature (SST), and interaction between SST and bathymetry on the probability ψ that a site is used by Bottlenose dolphins (Tursiops truncatus). The posterior mean is provided with the associated credible interval. "SV" refers to single-visit occupancy models, "RV" to repeated visit occupancy models, and "IOM" stands for integrated occupancy models, in which aerial surveys and at-sea surveys are combined. Estimates are given on the logit scale.

size included 0), which resulted in models using only at-sea survey data predicting the highest contrast between the continental shelf and the high-seas. Bathymetry effect size was the lowest for aerial occupancy while maps from integrated occupancy models displayed moderate contrast of space-use between shelf and pelagic waters (Fig. 2). Single-visit occupancy models exhibited similar covariates estimates to those of repeated-visit occupancy models (Fig. 1). For aerial occupancy, we noticed similar space-use prediction between single- and repeated-visit (Fig. 2A). For at-sea, predicted space-use probabilities were different between single-visit and repeated-visit occupancy models (Fig. 2). When considering the covariates' effect size (Fig. 1), the widths of the 95% CI were not smaller for integrated occupancy than for occupancy models using datasets in isolation. However, when looking at the standard deviation of the predicted probability of space-use, integrated occupancy models had a better precision than aerial or at-sea occupancy models separately, (Fig. 2B). The use of integrated single-visit occupancy models also improved precision in predicted space-use compared to single-visit occupancy built from aerial and at-sea datasets separately (Fig.2B). Inspecting the simulation results, we found that 1) integrated occupancy models produced more precise estimates of covariates effect size than occupancy models fitted to a single dataset (Appendix S2), and 2) single-visit occupancy models produced similar results to repeated-visit occupancy models (Appendix S1).

4 Discussion

4.1 Integrated single-visit occupancy models provide reliable ecological inference

Ecological inference from integrated occupancy models lied within the range of the estimates obtained with each dataset separately (Fig. 1). Across all occupancy models, the effects of environmental covariates were similar and consistent with previous studies. Bottlenose dolphins were more likely to use shallower seas (Bearzi et al., 2009; Labach et al., 2021), and depth had a stronger effect than SST on the use of space by bottlenose dolphins (Torres et al., 2008). However, we found variations among models in the estimation of the probability of space-use by dolphins (Fig. 1). In particular, at-sea occupancy models predicted that dolphins make little use of the pelagic seas compared to the continental shelf, while aerial occupancy models predict more homogeneous space-use between coasts and pelagic seas. Aerial surveys detected several dolphin groups in the high depths while at-sea surveys detected none. Detecting offshores groups tempered the preference for low-depth seafloors in aerial occupancy models (Appendix S6). Besides, we recommend caution in interpreting predicted maps of space-use as predicted space-use was sensitive to the mean value of covariate effect size. Therefore, depth being the only covariate that affect space-use probability, maps of predicted space-use were mostly driven by bathymetry effect size, and

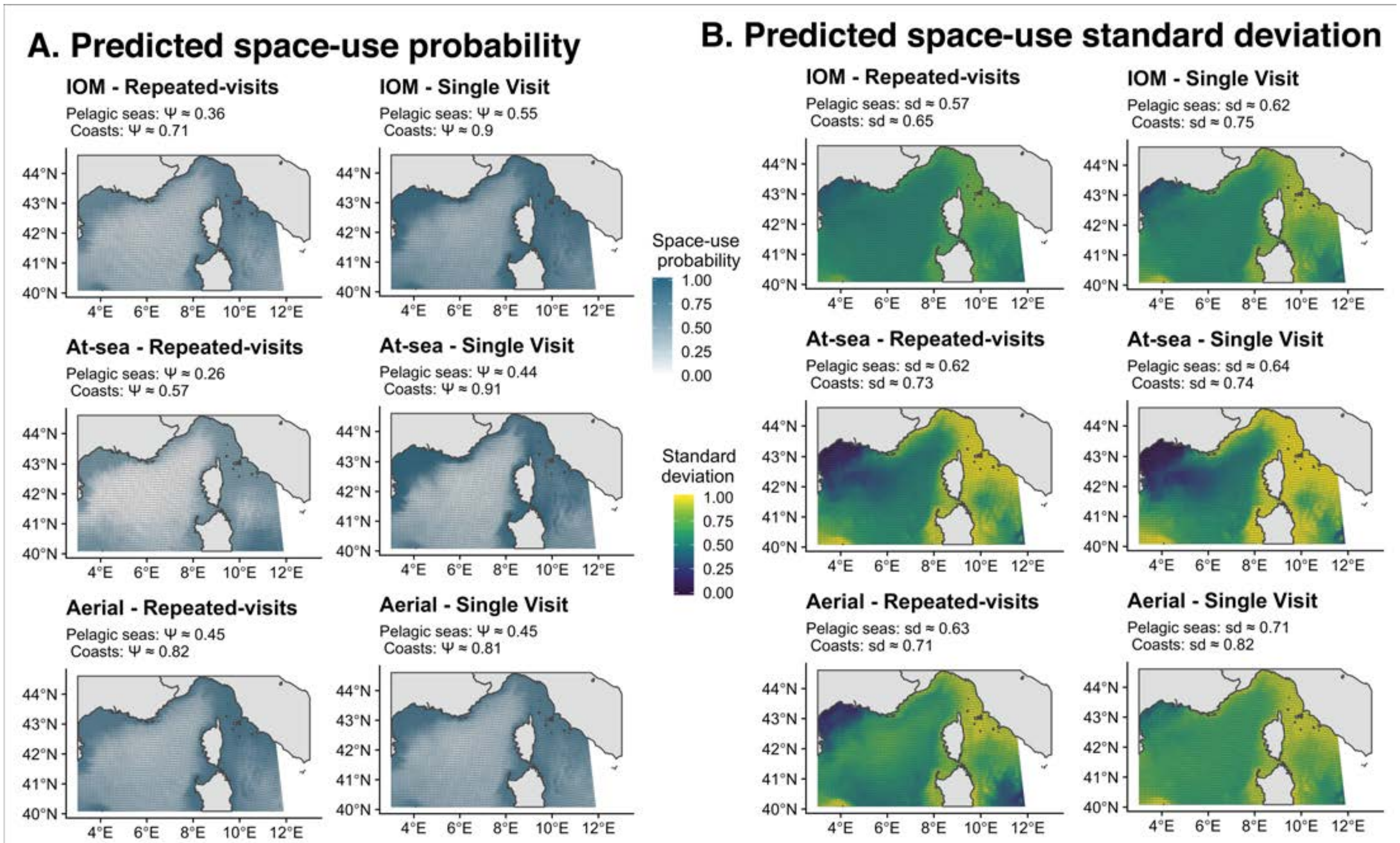

Figure 2: **A. Probability of predicted space-use by Bottlenose dolphins (Tursiops truncatus) over the NW Mediterranean Sea.** Using the posterior mean of covariates effect size, we estimated the probability that a grid-cell was used by bottlenose dolphins. For each occupancy model, we added the mean space-use probability (ψ) for coasts (bathymetry < 500 m) and pelagic seas (bathymetry > 500 m). **B. Standard deviation of predicted space-use.** Using the posterior standard deviation of covariates effect size, we estimated the standard deviation associated with the space-use probability. For each occupancy model, we added the mean standard-deviation (sd) associated with (ψ) for coasts (bathymetry < 500 m) and pelagic seas (bathymetry > 500 m). "IOM" stands for integrated occupancy models, in which aerial surveys and at-sea surveys are combined. Repeated-visit occupancy maps refer to occupancy models with 4 sampling occasions. Single-visit maps refer to occupancy models considering 1 sampling occasion.

did not account for precision associated with space-use prediction. Because depth posterior mean was similar between occupancy models, differences between predicted space-use maps do not provide a relevant illustration to compare occupancy models performances, nor they reflect the uncertainty associated with the occupancy models' estimates. To study the benefits of single-visit and integrated occupancy models to accommodate existing ecological datasets, we emphasize standard deviation maps and the credible intervals of covariates effect size (Fig. 1-2B). Integrated occupancy models had a better precision in space-use than models using aerial or at-sea surveys separately (Fig. 2). This result was supported by our simulation study which demonstrates the better performance of integrated occupancy models at estimating covariate effect size compared to occupancy models from a single dataset (Appendix S2). Single-visit occupancy models gave similar estimates to those obtained with repeated-visit occupancy models, although repeated-visit occupancy models exhibited better precision (Fig. 1-2B), as well as in our simulations (Appendix S1). In the bottlenose dolphins case study, we considered two existing monitoring programs that were not initially designed for occupancy modeling. In the at-sea monitoring, repeated line-transects were not implemented, nor the high depths were sampled, which made at-sea occupancy unlikely to exhibit precise estimates at our spatial extent. The two datasets exhibit complementary features. While aerial surveys covered a larger spatial scale than at-sea surveys, at-sea surveys exhibited a better detection rate. Detection probability was greater for at-sea surveys ($p = 0.18\ SD \pm 0.04$) than for aerial surveys ($p = 0.10\ SD \pm 0.03$). Regarding the aerial dataset, the number of occurrences was low despite the important coverage of the monitoring design (i.e. bottlenose dolphins were detected in 6.5% of sampled grid-cells), which might hinder the implementation of single-visit occupancy when the number of occurrences is less than 10% of the sampling units (Peach et al., 2017). However, the at-sea dataset had occurrences in 19.5% of sampled units. Using integrated occupancy models enables to combine low-frequency occurrence data like the aerial dataset with another dataset to increase the amount of information about the ecological state process and helps mitigating the issue of low number of occurrences.

4.2 Ecological implications and perspectives

Overall, we illustrate that: i) Integrating datasets into occupancy models improves the precision of space-use estimates, and ii) Single-visit occupancy models can reliably accommodate the lack of repeated visits that occurs frequently. Integrated occupancy models produced more reliable estimates than occupancy models using datasets in isolation in both the bottlenose dolphin data analyzes and the simulations. Our finding on the bottlenose dolphins case study is a good illustration of the well-known benefit of combining datasets into integrated species distribution models to increase precision in ecological inference (Fletcher et al., 2019). Although we adapted a standard multinomial detection process of integrated (or multi-methods) occupancy models, some advanced developments allow combining datasets to estimate occupancy parameters at multiple spatial scales (Nichols et al., 2008; Pavlacky et al., 2012). Besides, integrated occupancy modeling has also been used to evaluate ecological monitoring programs prior to their implementation (e.g., comparing capabilities of different detection devices, Otto & Roloff (2011); Haynes et al. (2013)). Here, we emphasize the benefit of considering integrated methods combined with single-visit occupancy modeling after data collection. When the species of interest either occurs over a large spatial scale or is a highly mobile species (such as bottlenose dolphins), considering multiple sampling methods is effective to monitor the entire population making the most of each device (Zipkin & Saunders, 2018). In particular, integrating a large volume of data, such as those that can be leveraged through citizen-science programs or with dedicated NGOs over the years can make the most of ecological monitoring programs for the furthering of many applied situations (Zipkin et al., 2019). One could also extend integrated occupancy models to more than two datasets. However, caution should be taken as integrating data is not always beneficial and requires additional modeling assumptions according to the particularity of each dataset to include (Dupont et al., 2019; Farr et al., 2020; Fletcher et al., 2019; Lele & Allen, 2006; Simmonds et al., 2020). Although repeated-visit occupancy models remain statistically more precise, there are benefits in using single-visit occupancy models. The ability of single-visit occupancy to relax the closure assumption is appealing, because this assumption is often incompatible with the behavior of mobile species and for numerous monitoring programs of animal populations (Issaris et al., 2012; Kendall et al., 2013; Lele et al., 2012; Rota et al., 2009; Sólymos & Lele, 2016). However, in a single-visit occupancy model that integrate multiple datasets, one need to account for site closure during the time span of the monitoring programs. In this study, the closure assumption is unlikely to be valid for bottlenose dolphins over the time span of the two monitoring programs, because dolphins obviously would not remain into the same grid-cell, hence we interpreted the occupancy parameter as space-use. Besides, when financial or logistical costs are limited, implementing a single-visit monitoring design could provide robust ecological inference while explicitly accounting for imperfect species detection (Dénes et al., 2017; Lele et al., 2012). Overall, increasing quantity and types of biodiversity data are becoming available (Isaac et al., 2019). Numerous monitoring programs do not rely on protocols implementing repeated visits like, e.g., historical monitoring programs, or citizen science programs (Tingley & Beissinger, 2009; Zipkin & Saunders, 2018). Then, using single-visit occupancy models helps making efficient use of available data, which is of great interest in many ecological applications (Nichols & Williams, 2006; Sólymos & Lele, 2016). In this context, Miller et al. (2019) encouraged further developments of methods mixing standardized and non-standardized datasets. To illustrate, we built an integrated occupancy model mixing repeated-visit occupancy models for aerial surveys and single-visit occupancy models for at-sea surveys (Appendix S3). The flexibility of occupancy models provided a relevant framework to combine monitoring programs and to accommodate different types of data collection. Integrated and single-visit occupancy models contribute to widen the scope of possibilities. We emphasize the usefulness of both integrated and single-visit approaches to deal with existing datasets. We anticipate that their combination into integrated single-visit approaches will be of most interest for many parties in ecological research.

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Appendix S1: Simulation study of repeated-visits and single-visit occupancy models

Valentin Lauret, Hélène Labach, Matthieu Authier, Olivier Gimenez, Using single visits into integrated occupancy models to make the most of existing monitoring programs, Ecology

Contents

Supporting information of the article *Using single visits into integrated occupancy models to make the most of existing monitoring programs.*

You can *download codes and results on Github*

The objective of this document is to perform a simulation study of the single-visit (SV) occupancy models and to compare their estimation to those of repeated-visits (RV) occupancy models.

SV occupancy has been developed by Lele, Moreno, and Bayne (2012). Unlike classical RV occupancy models, they support that robust occupancy estimations can be obtained from a single-visit per sampling unit. However, SV occupancy models require certain conditions to be fulfilled for estimating detection probabilities reliably. First, different continuous covariates should be used to estimate detection and occupancy probabilities (Lele, Moreno, and Bayne (2012)). Second, the number of detections is an important parameter that may affect the results in the case of rare or ubiquitous species (Peach, Cohen, and Frair (2017)). Third, the use of inappropriate link functions to model the detection process may lead to model misspecification and biased interpretation (Knape and Korner-Nievergelt (2015)). We simulated presence-absence datasets and we aimed to compare the outputs of SV and RV occupancy models at estimating occupancy parameters. We compared SV and RV occupancy models over a large range of occupancy and detection probabilities.

Methods

We simulated occupancy data based on a fictive covariate affecting the latent occupancy process, and 4 sampling occasions. Then, we considered two different datasets to fit occupancy models: i) a dataset with the 4 sampling occasions to fit repeated-visits occupancy model, ii) a dataset in which we considered only one sampling occasion to fit a single-visit occupancy model.

We simulated occupancy datasets with four sets of occupancy probability ($\Psi \approx 0.1$, $\Psi \approx 0.3$, $\Psi \approx 0.5$, $\Psi \approx 0.9$), and four sets of detection probabilities ($p \approx 0.1$, $p \approx 0.3$, $p \approx 0.5$, $p \approx 0.8$).

To compare model precision and bias, we calculated the relative bias (RB) and root mean square error (RMSE) of occupancy estimates over `S = 500` simulations:

- Relative bias: $RB = \frac{1}{S}\sum_1^S \frac{(\hat{\theta}_s - \theta)}{\theta}$
- Root Mean Square Error: $RMSE = \sqrt{\frac{1}{S}\sum_1^S (\hat{\theta}_s - \theta)^2}$

where θ_i is the estimate of parameter θ in the i-th simulation. We reported RB and RMSE for the regression coefficient of covariate affecting occupancy probability, and for occupancy probability itself.

Data simulation

State process

The occupancy state z was drawn from a Bernoulli distribution with parameter ψ, $z \sim dbern(psi)$. We wrote ψ as a logistic function of an environmental covariate `cov`:

$$\text{logit}(\psi) = \alpha_0 + \alpha_1 \text{ cov}$$

where α_0 and α_1 are unknown parameters that need to be estimated.

We considered 4 sets of values for the alpha's:

- $\alpha_0 = -1.9$ and $\alpha_1 = 0.2$ that led to ψ approx. equal to 0.1
- $\alpha_0 = -0.5$ and $\alpha_1 = 0.2$ that led to ψ approx. equal to 0.3
- $\alpha_0 = 0.5$ and $\alpha_1 = 0.2$ that led to ψ approx. equal to 0.5
- $\alpha_0 = 2.5$ and $\alpha_1 = 0.15$ that led to ψ approx. equal to 0.9

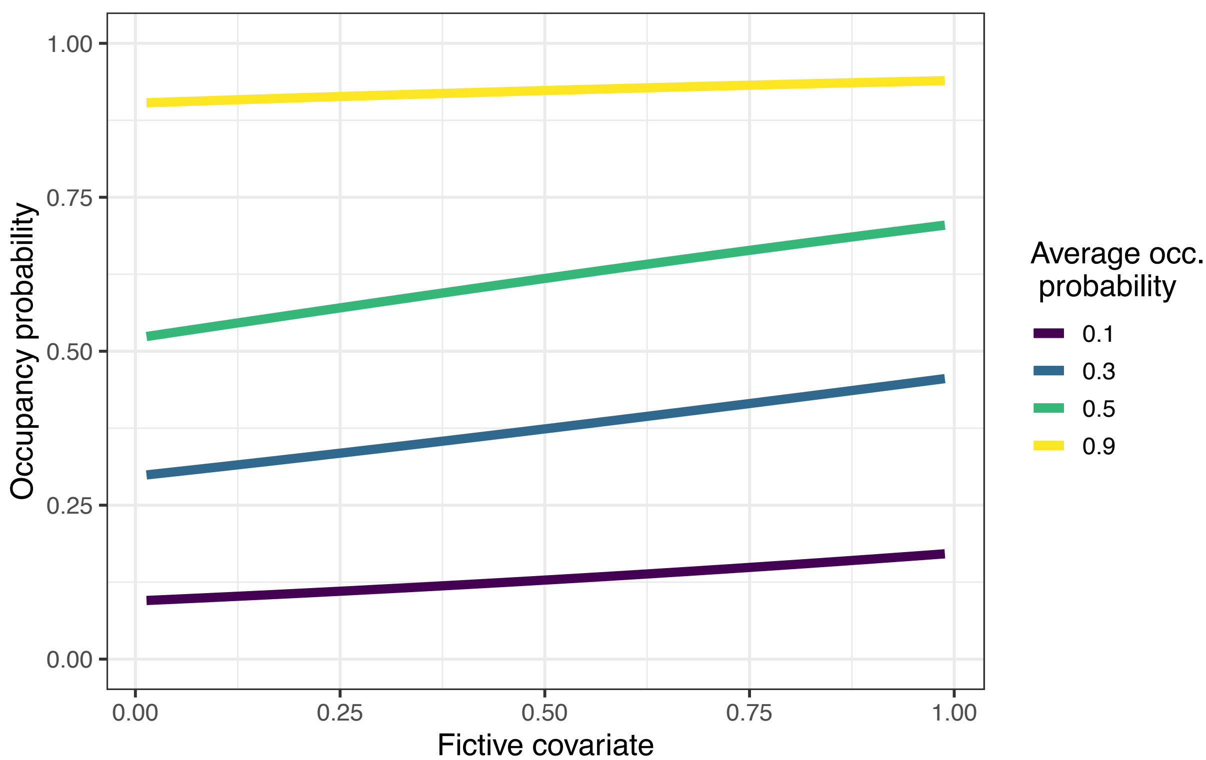

Figure 1: Occupancy probability as a function of a fictive covariate

Observation process

Observations are drawn from a Bernoulli distribution with parameter p. We wrote p as a logistic function of a sampling effort covariate seff:

$$\text{logit}(p) = \beta_0 + \beta_1 \text{ seff}$$

where β_0 and β_1 are unknown parameters that need to be estimated.

We considered 4 sets of values for the beta's:

- $\beta_0 = -1.5$ and $\beta_1 = 0.26$ that led to p approx. equal to 0.15
- $\beta_0 = -0.6$ and $\beta_1 = 0.25$ that led to p approx. equal to 0.35
- $\beta_0 = 0.3$ and $\beta_1 = 0.26$ that led to p approx. equal to 0.5
- $\beta_0 = 1.8$ and $\beta_1 = 0.3$ that led to p approx. equal to 0.8

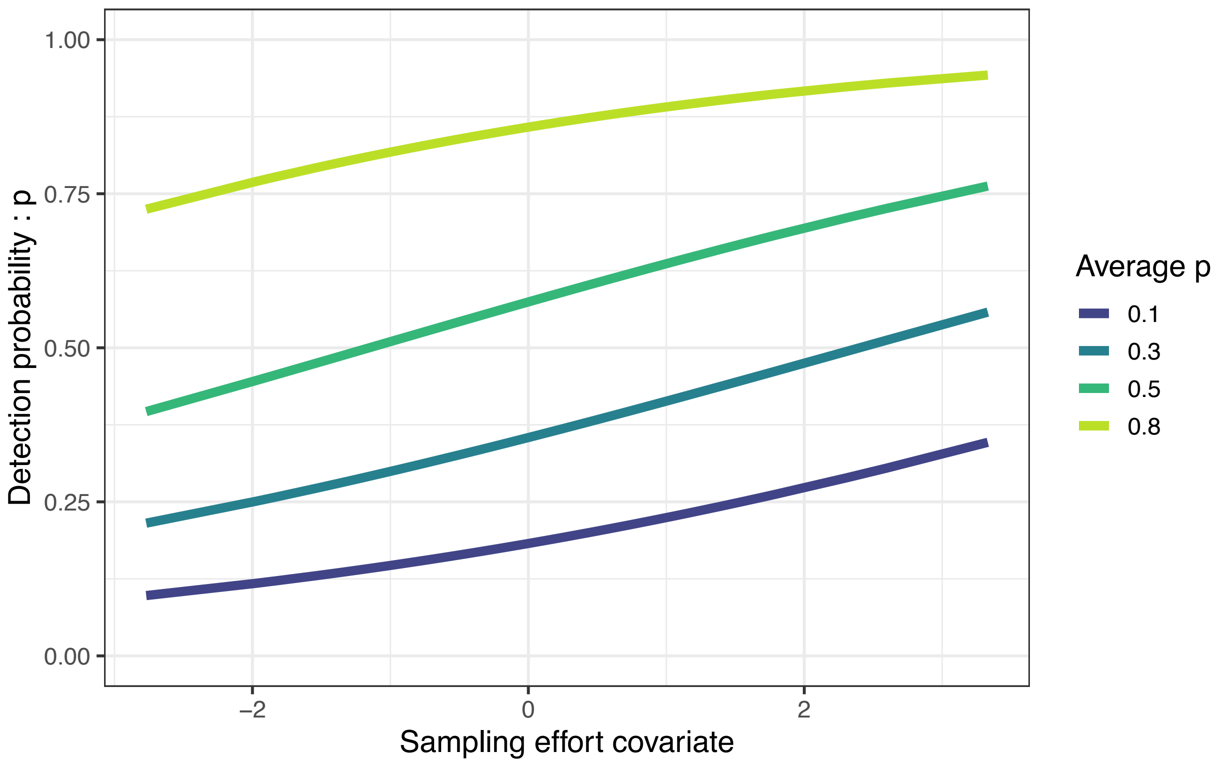

Figure 2: Detection probability as a function of a fictive sampling effort

Study area

We simulated z and y for study areas of 100 sites.

Models

For each combination of ψ and p we fitted 2 occupancy models:

- Repeated-visit occupancy model (RV)
- Single-visit occupancy model (SV)

We have 32 ecological situations depending on ψ and p.

For each scenario, we ran 500 simulations and fitted the 2 occupancy models.

Results

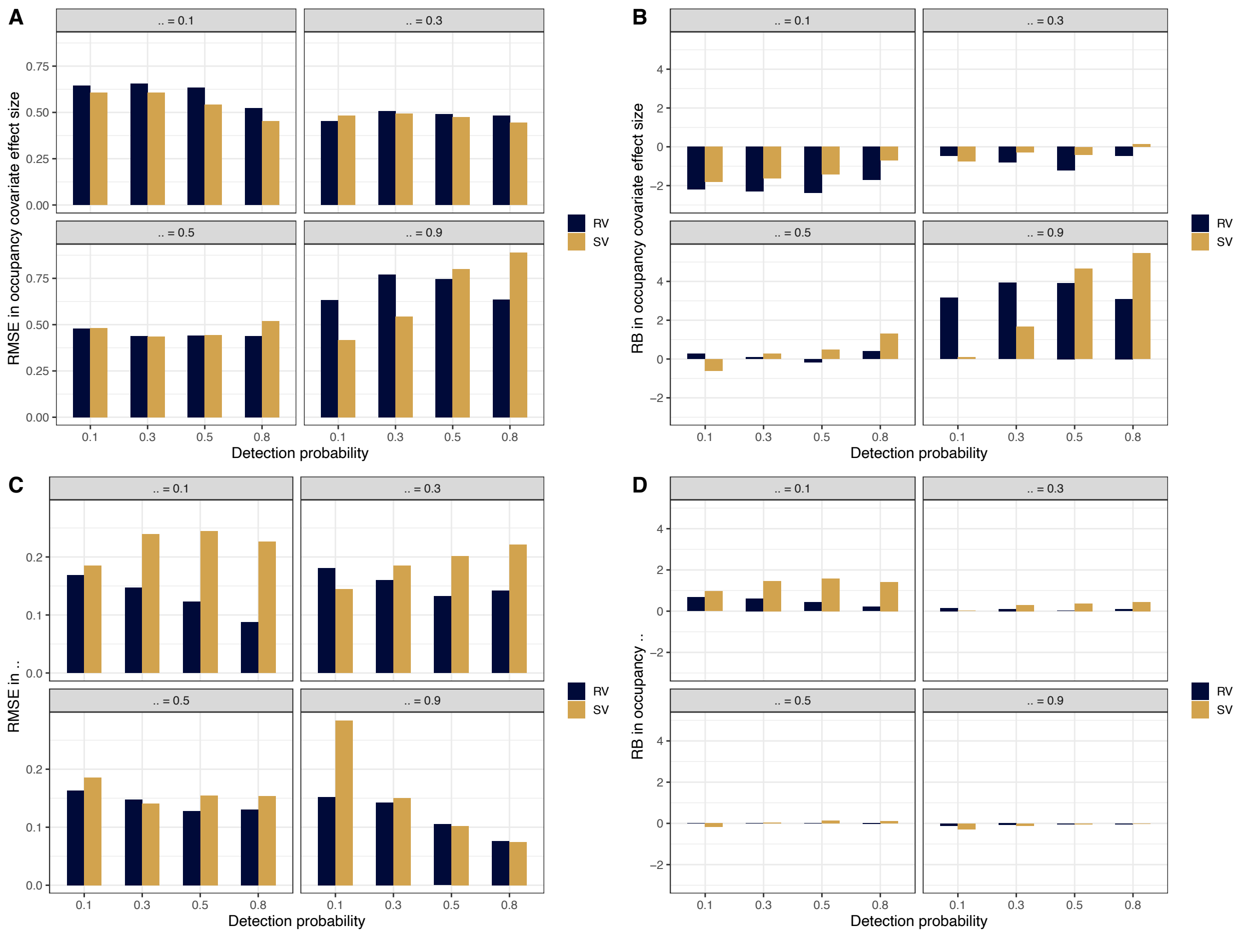

Figure 3: Root-mean square error (RMSE) and Relative Bias (RB) of repeated- and single-visit occupancy models based on simulated data

Covariate effect size

Regarding the covariate effect size on ψ (Fig.3A-B), we found close RMSE and RB between repeated- and single-visit occupancy. In the case, of high occupancy ($\psi = 0.9$), differences in RB are greater although they are close in precision. Overall, the results were similar whatever the occupancy models we considered.

Occupancy prediction

Predicted occupancy probability between single- and repeated-visits models are closed to each other in Fig. 3C-D. However, precision and bias are greater for low occupancy $\psi = 0.1$, which is consistent with Peach, Cohen, and Frair (2017) findings. Same results when detection probability is low and when ψ is high. Although, note that RMSE plotting scale is smaller in Fig. 3C than in Fig. 3A.

Discussion

Our simulations study showed that single-visit and repeated-visit occupancy models had similar results in the estimation of covariate effect size for ocucpancy. We explored simple logistic regressions to describe models paramters. To be consistent with our manuscript, we reported performances of covariates effect size and predicted occupancy. To have a complete understanding of models performances, one might want to look at wider range of relationships, and observe all models parameters (e.g. intercept, sampling effort effect size on detection probability).

Overall, our simulation results support that single-visit occupancy models can be used to obtain reliable estimates of occupancy.

References

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Lele, S. R., M. Moreno, and E. Bayne. 2012. "Dealing with Detection Error in Site Occupancy Surveys: What Can We Do with a Single Survey?" *Journal of Plant Ecology* 5 (1): 22–31. https://doi.org/10.1093/jpe/rtr042.

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Appendix S2: Integrated single-visit occupancy models, a simulation study

Valentin Lauret, Hélène Labach, Matthieu Authier, Olivier Gimenez, Using single visits into integrated occupancy models to make the most of existing monitoring programs, Ecology

Contents

Supporting information of the article *Using single visits into integrated occupancy models to make the most of existing monitoring programs.*

You can *download codes and results on Github*

The objective of this document is to perform a simulation study to assess the performance of integrated occupancy models. We explored whether single-visit (SV) or repeated-visits (RV) occupancy models benefit from data integration, and we explored the effect of number of detections to estimate the SV occupancy model parameters.

Methods

We simulated occupancy data based on a fictive covariate affecting the latent occupancy process, and 4 sampling occasions. Then, we considered two different datasets to fit occupancy models: i) a dataset with the 4 sampling occasions to fit RV occupancy model, and ii) a dataset in which we pooled the 4 occasions to fit a SV occupancy model considering with the entire dataset simulated as a single sampling occasion.

We simulated occupancy datasets with two sets of value for occupancy probability ($\psi \approx 0.1$, and $\psi \approx 0.3$), and two sets of detection probabilities: $p \approx 0.1$, $p \approx 0.5$. Finally, we analysed the datasets of detection probability $p \approx 0.1$, and $p \approx 0.5$ jointly into integrated occupancy models.

To compare model precision and bias, we calculated the relative bias (RB) and root mean square error (RMSE) of occupancy estimates over `S = 500` simulations:

- Relative bias: $RB = \frac{1}{S}\sum_1^S \frac{(\hat{\theta}_s - \theta)}{\theta}$
- Root Mean Square Error: $RMSE = \sqrt{\frac{1}{S}\sum_1^S (\hat{\theta}_s - \theta)^2}$

where θ_i is the estimate of parameter θ in the i-th simulation. We reported RB and RMSE for the regression coefficient of covariate affecting occupancy probability, and for occupancy probability itself.

Data simulation

State process

The occupancy state z was drawn from a Bernoulli distribution with parameter ψ, $z \sim dbern(psi)$. We wrote ψ as a logistic function of an environmental covariate `cov`:

$$\text{logit}(\psi) = \alpha_0 + \alpha_1 \text{ cov}$$

where α_0 and α_1 are unknown parameters that need to be estimated.

We considered 2 sets of values for the alpha's:

- $\alpha_0 = -1.9$ and $\alpha_1 = 0.2$ that led to ψ approx. equal to 0.1
- $\alpha_0 = -0.5$ and $\alpha_1 = 0.2$ that led to ψ approx. equal to 0.3

Observation processes

Observations are drawn from a Bernoulli distribution with parameter p. We wrote p as a logistic function of a sampling effort covariate seff:

$$\text{logit}(p) = \beta_0 + \beta_1 \text{ seff}$$

where β_0 and β_1 are unknown parameters that need to be estimated.

We considered 2 sets of values for the beta's:

- $\beta_0 = -1.5$ and $\beta_1 = 0.26$ that led to p approx. equal to 0.1
- $\beta_0 = 0.3$ and $\beta_1 = 0.26$ that led to p approx. equal to 0.5

We simulated 3 different datasets to fit occupancy models:

- RV occupancy dataset considering four sampling occasions (`J=4`), hereafter 'RV'
- SV occupancy dataset considering the one single sampling occasion (`J=1`), hereafter 'SV'

Models

For each value of ψ ($\Psi \approx 0.1$, and $\Psi \approx 0.3$), we built RV, and SV datasets with:

- low detection probability simulations, $p \approx 0.1$
- high detection probability simumations, $p \approx 0.5$
- both datasets combined in an integrated dataset.

Overall, we obtained occupancy models to 18 datasets.

Note that for the integrated occupancy, we combined datasets generated from the same z ecological states with two different detection probabilities, i.e. we combined one monitoring with 0.5 detection probability (i.e. 'low p'), and one monitoring with 0.8 detection probability (i.e. 'high p').

Results

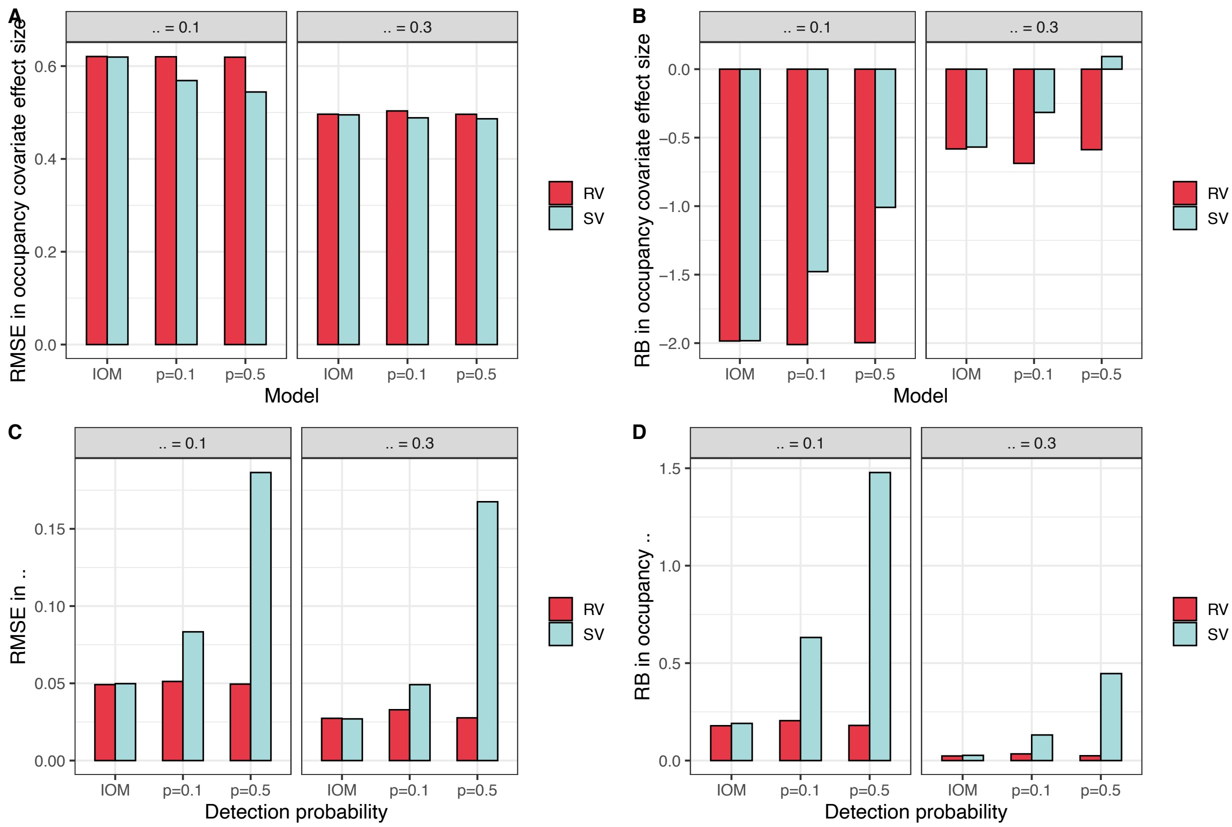

Figure 1: Root-mean square error (RMSE) and Relative Bias (RB) of occupancy models based on simulated data. IOM stands for "Integrated Occupancy Models"

Regarding the covariate effect size on occupancy probability (Fig. 1A-B), the RMSE values were similar whatever the occupancy model we considered. Overall, we found a better precision and bias for higher occupancy (= 0.3). When reconstructing the occupancy probability (Fig. 1C-D), the results between single-visit and repeated-visits were similar to each other, although single-visit occupancy models exhibited a slightly greater RMSE and RB. For single-visit occupancy models, integrated occupancy models exhibited better precision and bias than occupancy models using the dataset in isolation.

Discussion

Our simulations showed that integrated occupancy models particularly benefit to single-visit occupancy models to improve the precision and bias when estimating occupancy probability. We suggest that care should be taken when considering SV occupancy for datasets that arise from reduced sampling effort coupled with low detection probability, which can produce small numbers of detections which, in turn, leads to degraded performance of single-visit occupancy models. To overcome this issue, reducing the amount of sampling effort per grid-cell could be balanced by an increase in the number of sampled sites not to decrease precision in occupancy estimates. Results from both Peach et al. (2017) and our simulation study comparing single- and repeated-visit pointed out the limited performances of single-visit occupancy models in the case of low occupancy (Supporting information 1), and when the number of detections is limited.

Overall, our simulations underline that integrated single-visit occupancy models can be used to obtain reliable estimates of occupancy.

References

Peach, M. A., Cohen, J. B., & Frair, J. L. (2017). Single-visit dynamic occupancy models: An approach to account for imperfect detection with Atlas data. *Journal of Applied Ecology*, *54*(6), 2033–2042. https://doi.org/10.1111/1365-2664.12925

Appendix S3: Integrated "mixed" single-visit occupancy models

Valentin Lauret, Hélène Labach, Matthieu Authier, Olivier Gimenez, Using single visits into integrated occupancy models to make the most of existing monitoring programs, Ecology

Contents

Supporting information of the article *Using single visits into integrated occupancy models to make the most of existing monitoring programs.*

You can *download codes and results on Github*

The objective of this document is to explore how to build a "mixed" integrated occupancy model analyzing a repeated-visit dataset along with a single-visit dataset.

Methods

Based on the bottlenose dolphin (*Tursiops truncatus*) case study of the paper *Using single visits into integrated occupancy models to make the most of existing monitoring programs*, we built a 'mixed' integrated occupancy models considering a repeated-vists (RV) observation process for the aerial-dataset, and a single-visit (SV) observation process for the at-sea dataset.

State process

The occupancy state z was drawn from a Bernoulli distribution with parameter ψ, $z \sim \text{Bernoulli}(\psi)$. We wrote ψ as a logistic function of two environmental covariates bathy (bathymetry), and SST (Sea Surface Temperature):

$$\text{logit}(\psi) = \alpha_0 + \alpha_1 \text{ bathy} + +\alpha_2 \text{ SST}$$

where α_0, α_1, and α_2 are unknown parameters that need to be estimated.

Observation process

The observations are drawn from a Bernoulli distribution with parameter p. We wrote p as a logistic function of a sampling effort covariate seff:

$$\text{logit}(p) = \beta_0 + \beta_1 \text{ seff}$$

where β_0 and β_1 are unknown parameters that need to be estimated.

Mixed observation process

In this 'mixed' integrated occupancy model, the state process remains enchanged. However, there are 2 separated observation processes, while we analyzed jointly the detections into the same observation process in the 'classical' integrated model that considered the same number of sampling occasions (`J`). The two observation processes informed the latent ecological layer.

We separated the RV aerial detections ya (with 4 sampling occasions, `J=4`), from the SV at-sea detections ys (i.e. 1 sampling occasion, `J=1`).

Both ya and ys are binary datasets (O/1) modeled as draws in Bernoulli distributions, with associated detection probabilities pa, and ps. For grid-cell i, during sampling occasion j:

- $ya_{i,j} \sim \text{Bernoulli}(z_i \; pa_{i,j})$
- $ys_i \sim \text{Bernoulli}(z_i \; ps_i)$

BUGS model

Hereafter, you would find the JAGS formulation of this occupancy model.

```
# Specify model in BUGS language
sink("mixed_iom.jags")
cat("
    model {

   # priors

    alpha.psi ~ dnorm(0,0.444) # occupancy intercept
    alpha.pa  ~ dnorm(0,0.444) # detection aerial intercept
    alpha.ps  ~ dnorm(0,0.444) # detection at-sea intercept

    beta.sst  ~ dnorm(0,0.444) # slope sst effect
    beta.bathy~ dnorm(0,0.444)  # slope bathy effect
    beta.eff.a~ dnorm(0,0.444)  # slope aerial survey effort effect
    beta.eff.s~ dnorm(0,0.444)  # slope at-sea survey effort effect
    beta.occ2 ~ dnorm(0,0.444) # occasion effect
    beta.occ3 ~ dnorm(0,0.444) # occasion effect
    beta.occ4 ~ dnorm(0,0.444) # occasion effect

    # State process

   for (i in 1:nsite){
      z[i] ~ dbern(psi[i])

     logit(psi[i]) <- lpsi[i]

     lpsi[i] <- alpha.psi + beta.sst * SST[i] + beta.bathy * BATHY[i]

  }  # i
```

```
     # Detection process

    # At-sea monitoring
    for(i in 1:nsite){

     mu.p_s[i] <- z[i] * p_s[i]

    logit(p_s[i]) <- alpha.ps + beta.eff.s*eff.s[i]

   y_s[i] ~ dbern(mu.p_s[i])

    } #i

    # Aerial monitoring
    for(i in 1:nsite){
      for (j in 1:nrep){

            mu.p_a[i,j] <- z[i] * p_a[i,j]

            logit(p_a[i,j]) <- lp_a[i,j]

            lp_a[i,j] <- alpha.p_a + beta.eff.a * eff.a[i,j] + beta.occ2 * equals(j,2) + beta.occ3 * equ

            y_a[i,j] ~ dbern(mu.p_a[i,j])

    } #j

  } #i

    }#fin du modele
    ", fill = TRUE)

sink()
```

Results

Hereafter, we displayed the effect size of the environmental covariate on the estimated occupancy probability (ψ).

The Mixed IOM model displayed similar estimates of effect size to estimates obtained from other occupancy models presented in the manuscript. We considered that the Mixed - IOM model had a better performance than the IOM SV model. Mixed model exhibited a better precision of the covariate effect size on ψ than SV integrated model on (Fig. 1), but precision was equivalent to RV integrated model.

Discussion

This extension of SV and RV integrated occupancy modles highlights the flexibility of occupancy model to fit with the sampling designs of existing datasets. However, the separated formulation of the detection process into 2 Bernoulli draws is relevant only if the monitoring programs are independant. Dependance between monitoring devies requires to model explicitly the covariation between detection probabilities Clare et al. (2017).

Miller et al. (2019) encouraged further developments of methods mixing standardized and non-standardized datasets. We support that occupancy models provide a relevant framework to integrate monitoring pro-

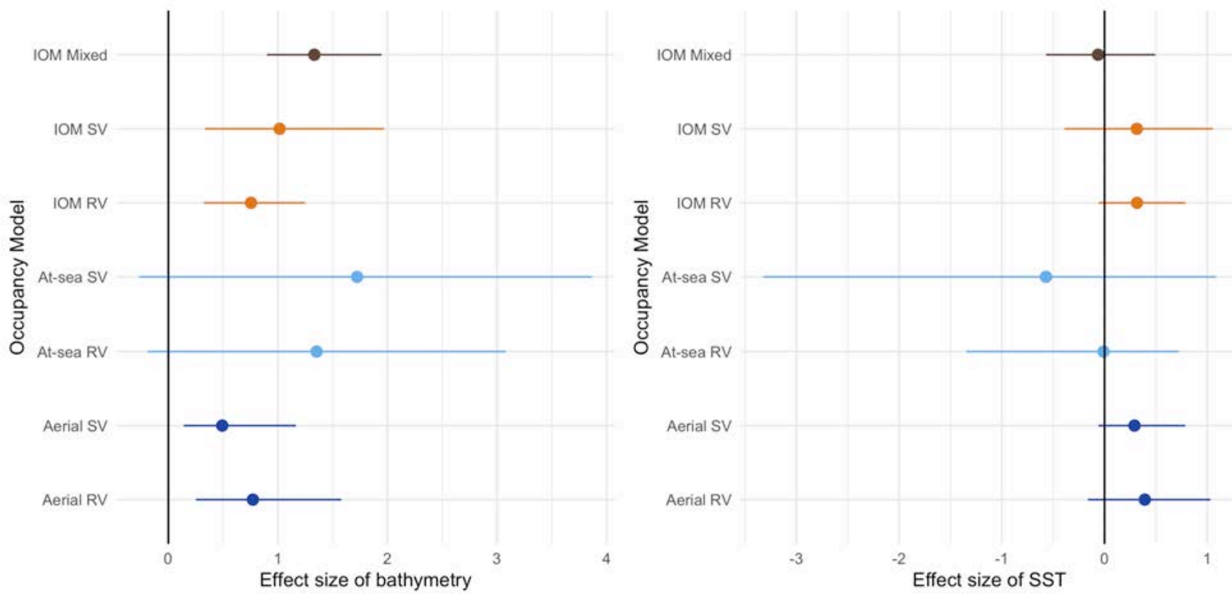

Figure 1: Figure 1 :Effect size of sea surface temperature (SST) and bathymetry on the space-use probability. Posterior mean is given with the associated 95% credible interval. Estimates are given on the logit scale. "SV" refers to single-visit occupancy models. "RV" refers to repeated-visit occupancy models. "IOM" stands for integrated occupancy models, in which aerial surveys and at-sea surveys are combined. "IOM - Mixed" refers to the 'mixed' model described above in this document.

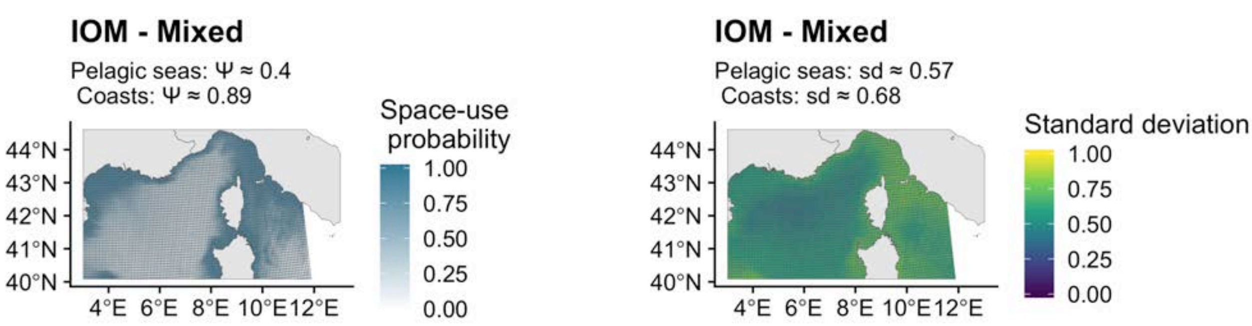

Figure 2: Figure 2: Map of predicted space use and associated standard deviation for the mixed model

grams and to accommodate different types of data collection. Integrated and single-visit occupancy models contribute to widen the scope of possibilities.

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Appendix S4: Modeling assumptions of repeated-visit, single-visit, and integrated occupancy models

Valentin Lauret, Hélène Labach, Matthieu Authier, Olivier Gimenez, Using single visits into integrated occupancy models to make the most of existing monitoring programs, Ecology

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Supporting information of the article *Using single visits into integrated occupancy models to make the most of existing monitoring programs,* in *Ecology.*

Modeling assumptions

In this section we aimed to list the modeling assumptions of the Repeated-Visit (RV), Single-Visit (SV), and Integrated occupancy models that we used.

Repeated-visits occupancy models

There are several critical assumptions for the standard occupancy model, i.e. RV occupancy (MacKenzie 2006).

1. Occupancy status at each site does not change over the survey season; that is, sites are “closed” to changes in occupancy.
2. The probability of occupancy is constant across sites, or differences in occupancy probability are modeled using covariates.
3. The probability of detection is constant across all sites and surveys or is a function of site-survey covariates.
4. There is no unmodeled heterogeneity in detection probabilities.
5. Detection of species and detection histories at each location are independent.

Single-visit occupancy

(Lele, Moreno, and Bayne 2012) underlined that SV occupancy models relax the closure assumption of sampled sites between visits. Besides, the literature about SV provide some requirements and guidance to a valid application of SV occupancy models. We listed the elements below:

1. Occupancy probability and detection probability depend on covariates

2. At least two independent continuous covariates are used to estimate occupancy probability and detection probability. Shared covariates can result in biased estimates for regression coefficients.

3. There should be an adequate numbers of occurrence. (Peach, Cohen, and Frair 2017), suggested that "estimates of occupancy probability remained unbiased across our scenarios, whereas colonization and extinction estimates became biased as occupancy probability approached extremes (i.e. 0.1 or 0.9)."

4. Nonlinear detection model should be preferred to provide accurate parameter estimates and to assume a more realistic relationship between detection and effort (Knape and Korner-Nievergelt 2015).

Integrated occupancy models

Combining multiple datasets into occupancy models have been developed previously by (Nichols et al. 2008) in details for estimating occupancy at two the spatial scales. In our approach, we extended the parametrization of a standard occupancy model detection process to include two different datasets with different detection probabilities. Doing it, our model relies on the following assumption:

- The two monitoring programs are independent, i.e. detection by program 1 does not affect detection probability of program 2, and vice-versa.

Subsequently, integrated repeated-visis occupancy models have the same modeling assumption of both RV occupancy and of integrated occupancy. Similarly, using integrated single-visit occupancy models combine the assumptions of SV occupancy and integrated occupancy.

Table summarizing assumptions for all models

Modeling assumptions	RV occupancy	SV occupancy
Closure assumption, i.e. site does not change over the survey season	Yes	No
Latent occupancy process	Occupancy prob. constant across sites, or modeled with covariates	Continuous covariate needed, **independent from the covariate used for the detection prob.**
Detection process	Detection prob. constant across sites, or modeled with covariates	Continuous covariate needed, **independent from the covariate used for the occupancy prob.**
No unmodeled heterogeneity in detection prob.	Yes	Yes
Detection of species and detection histories at each site are independent	Yes	Yes
Proportion of occurence over the total number of sites is > 10%	No	Yes
Data integration Detection process	**Integrated RV occupancy** Monitoring programs must be independent, or dependency must be accounted for.	**Integrated SV occupancy** Monitoring programs must be independent, or dependency must be accounted for.

Literature cited

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Appendix S5: Worked example of the likelihood functions for repeated-visit, single-visit, and integrated occupancy models

Valentin Lauret, Hélène Labach, Matthieu Authier, Olivier Gimenez, Using single visits into integrated occupancy models to make the most of existing monitoring programs, Ecology

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A worked example

In this section, we provide a worked example of the detection histories and the likelihood functions for SV, RV and Integrated occupancy models for the same hypothetical data. We aimed at clarifying the differences in the methods, as to how the information is used.

Notation

Let's consider a fictive site s, and y_s refers to the detection history made for this site s. Two monitoring programs **A** & **B** collect data at site s during one year. Then, y_s^A and y_s^B refer to the detection histories collected at site s by respectively monitoring program **A** and **B**.

Each monitoring program collected binary data during one year at site s, with $y = 1$ if the species is detected, and $y = 0$ otherwise. For the monitoring period, we considered two situations and applied different occupancy models accordingly:

1. We divided the monitoring period into 4 sampling occasions $j = \{1, ..., 4\}$ with $J = 4$ and analyzed the data with a RV occupancy model.
2. We considered the entire monitoring period as a single sampling occasion and analyzed the data with a SV occupancy model.

Detections histories and associated likelihood

We now present the detection histories we obtain from each of the two approaches presented above to deal with the collected data. Then, we name the relevant occupancy model to analyze the detection history and we display the likelihood to link the detection history and latent occupancy state (*i.e.* site s occupied by the species is $z_s = 1$, site s unoccupied by the species $z_s = 0$).

1. RV occupancy

When dividing the monitoring period into 4 sampling occasion, program **A** detected the species during occasion $j = 2$, and $j = 4$. The species remained undetected during sampling occasions $j = 1$, and $j = 3$.

$$y_s^A = \{0,1,0,1\}$$

To analyze data collected by program **A** when having 4 sampling occasions, we used a standard repeated-visit occupancy model. For each sampling occasion j, we calculated the likelihood of collected data $y_{s,j}^A$ as a Bernoulli draw, $y_{s,j}^A \sim Bernoulli(z_s p_{s,j}^A)$, with $p_{s,j}^A$ the probability of detecting the species with program **A** at site s during sampling occasion j.

Similarly, for program **B**, the detection history is $y_s^B = \{1,0,0,1\}$. We used the same RV occupancy model, and for each j, the likelihood is $y_{s,j}^B \sim Bernoulli(z_s p_{s,j}^B)$

2. SV occupancy

When considering the entire monitoring period as a single sampling occasion, both program **A** and **B** detected the species at site s:

$y_s^A = \{1\}$

$y_s^B = \{1\}$

To analyze data collected by program **A** when considering one single sampling occasion, we used a single-visit occupancy model. We calculated the likelihood of collected data y_s^A as a Bernoulli draw, $y_s^A \sim Bernoulli(z_s p_s^A)$, with p_s^A the probability of detecting the species with program **A** at site s.

Similarly, for program **B**, the detection history is $y_s^B = \{1\}$. We used the same SV occupancy model, and the likelihood is $y_s^B \sim Bernoulli(z_s p_s^B)$

3. Integrated RV occupancy models

When analyzing jointly both programs **A** & **B**, the detection/non-detection is coded differently, we coded $y = 0$ if the species is not detected by program **A** nor by program **B**, $y = 1$ if the species is detected only by program **A**, $y = 2$ if the species is detected only by program **B**, and $y = 3$ if the species is detected by both programs **A** & **B**.

When dividing the monitoring period into 4 sampling occasions, we saw above that binary detection histories of both program at site s are $y_s^A = \{0,1,0,1\}$ and $y_s^B = \{1,0,0,1\}$.

Then, when analyzing jointly both programs with a RV detection process, the detection history is:

$$y_s^{AB} = \{2,1,0,3\}$$

To analyze data collected by both programs **A** and **B** when considering 4 sampling occasions, we used an integrated RV occupancy model. We calculated the likelihood of collected data $y_{s,j}^{AB}$ as a multinomial draw, $y_s^A \sim Multinomial(1, z_s \pi_{s,j})$, with

$$\pi_{s,j} = \{P(y_{s,j}^{AB} = 0), P(y_{s,j}^{AB} = 1), P(y_{s,j}^{AB} = 2), P(y_{s,j}^{AB} = 3)\}$$
$$\pi_{s,j} = \{1 - p_{s,j}^A - p_{s,j}^B + p_{s,j}^A p_{s,j}^B, p_{s,j}^A(1 - p_{s,j}^B), p_{s,j}^B(1 - p_{s,j}^A), p_{s,j}^A p_{s,j}^B\}$$

This likelihood formulation requires that the two detection processes are independent.

4. Integrated SV occupancy models

Subsequently, when analyzing jointly both programs **A** and **B** with a SV detection process, the detection history is

$$y_s^{AB} = \{3\}$$

Then, to analyze data collected by both programs **A** and **B** when considering a single sampling occasion, we used an integrated **SV** occupancy model. We calculated the likelihood of collected data y_s^{AB} as a multinomial draw, $y_s^A \sim Multinomial(1, z_s \pi_s)$, with

$$\pi_s = \{P(y_s^{AB} = 0), P(y_s^{AB} = 1), P(y_s^{AB} = 2), P(y_s^{AB} = 3)\}$$
$$\pi_s = \{1 - p_s^A - p_s^B + p_s^A p_s^B, \quad p_s^A(1 - p_s^B), \quad p_s^B(1 - p_s^A), \quad p_s^A p_s^B\}$$

Appendix S6: Data exploration about bottlenose dolphin in the French Mediterranean Sea

Valentin Lauret, Hélène Labach, Matthieu Authier, Olivier Gimenez, Using single visits into integrated occupancy models to make the most of existing monitoring programs, Ecology

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Supporting information of the article *Using single visits into integrated occupancy models to make the most of existing monitoring programs.*

The objective of this document is to provide supplementary information about common bottlenose dolphin data.

About bottlenose dolphins

Figure 1: Bottlenose dolphins in the French Mediterranean Sea

Bottlenose dolphins *(Tursiops truncatus)* in the North-Western Mediterranean Sea. In the marine world, many species of conservation interest are elusive, and ecological data can be costly to obtain. In particular, the high seas are difficult to access and ecological monitoring is often performed through aerial surveys. However, coastal seas allows performing detailed at-sea monitoring. Besides, many species such as marine megafauna are mobile and occur in both coasts and high seas. Combining monitoring programs that are carried out in each realm (i.e. coasts and high seas) has the potential to provide relevant information about these species.

Monitoring programs

We focused on the North-Western Mediterranean, an area of 255,000 km2, which includes the Gulf of Lion and the Ligurian sea, the French coast of Provence, Corsica, and the Northern part of Sardinia (Figure 2). Our study area includes the Pelagos Sanctuary, which is a transboundary marine protected area for Mediterranean marine mammals covering an area of 90,000 km2 between Italy, France and Monaco.
The North-Western Mediterranean Sea is a critical habitat for many cetaceans species. Due to its coastal behaviour, bottlenose dolphins suffer from several anthropogenic pressures (e.g. collisions, fisheries bycatch, pollution, or acoustic perturbations), which raise concerns about their coexistence with human activities. The Mediterranean population of Bottlenose dolphins is considered "vulnerable" by the IUCN Red List and is one of the two cetacean species listed on Annex 2 of the European Habitats Directive (92/43/EEC). The protected status of this species within the French seas led to the development of specific programs to monitor Mediterranean bottlenose dolphins within the implementation of the European Marine Strategy Framework Directive (2008/56/EC; MSFD).

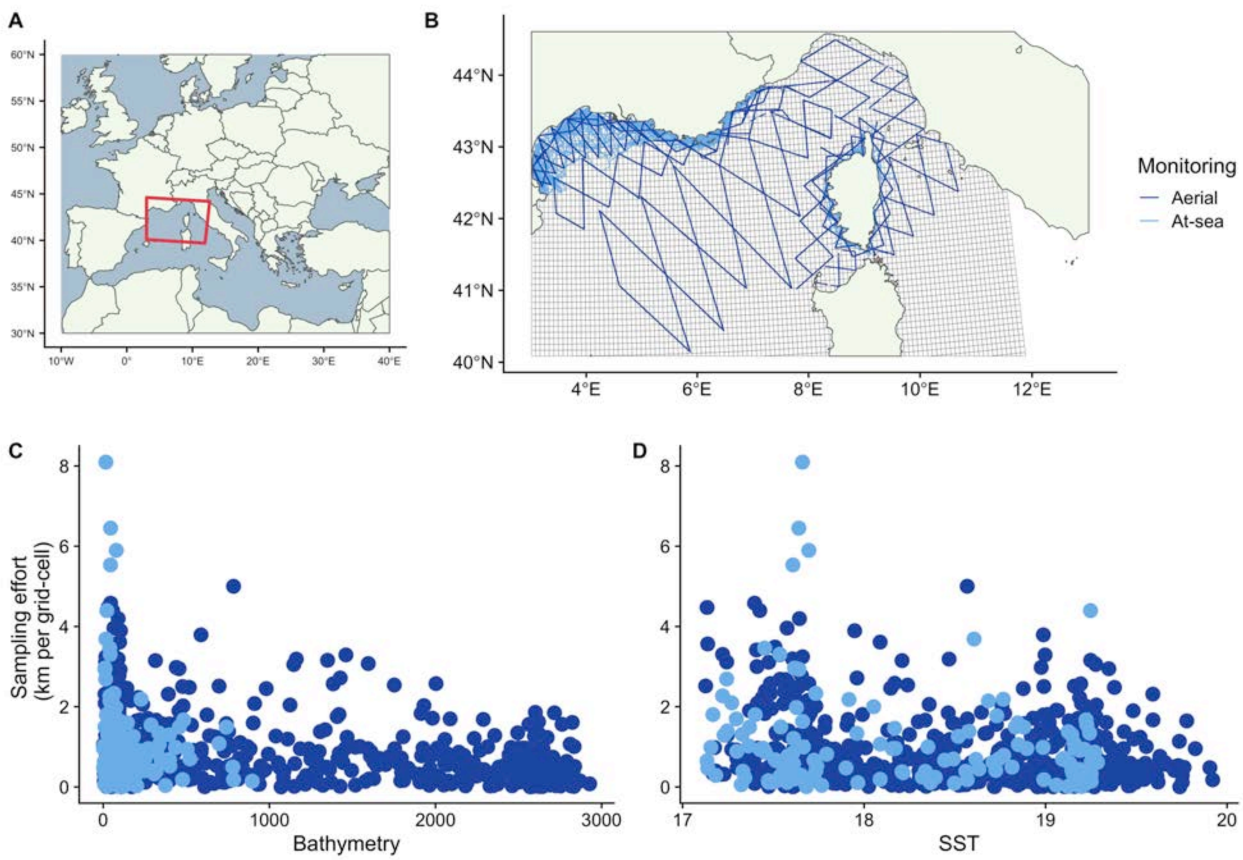


Figure 2: A. Location of study area in the Mediterranean basin. B. Sampling design of the two monitoring programs studied. The aerial surveys (SAMM program; dark blue) prospected 24,624 km of both sea shelf and high seas. At-sea surveys (GDEGeM program; light blue) prospected 21,646 km of the French continental shelf. C. Distribution of sampling effort of each monitoring program over the range of bathymetry. One dot is a grid-cell sampled either by aerial surveys (dark blue dot), or by at-sea surveys (light blue dot). D. Distribution of sampling effort of each monitoring program over the range of Sea Surface Temperature (SST). One dot is a grid-cell sampled either by aerial survey (dark blue dot), or by at-sea survey (light blue dot).

At-sea monitoring

We used data from the first large-scale study of Bottlenose dolphins in the French Mediterranean Sea. Four NGOs and one marine reserve performed at-sea surveys over 21,464 km of the French continental shelf including the Gulf of Lion, the French Riviera, and Corsica (Figure 2). Observers performed monitoring aboard small sailing and motor boats to locate and photo-identify bottlenose dolphins all year long between 2013 and 2015 (observers collected group size, behaviour, and took pictures of the dorsal fin of each individual in the group when possible). Such surveys with small vessels are expected to recorded detailed information while being limited to coastal area. Between summer 2013 and summer 2015, at-sea surveys detected 129 bottlenose dolphin groups located in 89 different grid-cells. The sampling effort of at-sea surveys was heterogeneous in space (i.e. between 1 and more than 500 km prospected per sampled grid-cell), and time (i.e. higher prospection in spring and summer than in autumn and winter). At-sea surveys did not include repeated visits. Some sites have been visited once, and others have been visited 50 times.

Aerial pelagic and coastal monitoring program

Data were collected during aerial surveys targeting the main taxa of marine megafauna within the French Exclusive Economic Zone (EEZ) including the Pelagos Sanctuary. The survey covered 24,624 km of line-transect performed by scientific institutional partners of the French Biodiversity Office and sampled 1336 grid-cells (i.e. 30.67% of the total number of grid-cells, Fig. 1). Two trained observers collected cetacean data following a distance sampling protocol (i.e. recording species identification, group size, declination angle). Aerial surveys were conditional on a good weather forecast and were performed using high-wind aircrafts with bubble windows. Sampling effort for aerial surveys was homogeneous over the studied area with three or four replicates per line-transect between November 2011 and August 2012. While aircrafts surveyed large area quickly, the limited temporal coverage may reduce overall number of detections. In the future, this survey will be conducted every six years to inform the MSFD (for more details).

The two monitoring programs collected either photo-identification or distance sampling data. For both programs, we used the locations of bottlenose dolphins encounters and the survey tracks.We used two environmental covariates to estimate the space-use of bottlenose dolphins: i) bathymetry, and ii) sea surface temperature (SST).

Detection of bottlenose dolphins

In the following maps, we displayed the sampling effort and detections of common bottlenose dolphins made by aerial line-transect, and by the boat at-sea monitoring programs.

Aerial surveys detected several dolphin groups in the high depths while at-sea surveys detected none. Detecting offshores groups tempered the preference for low-depth seafloors in aerial occupancy models.

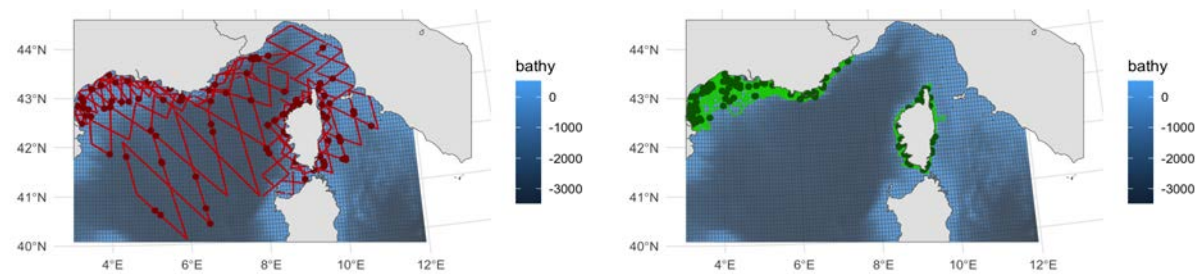
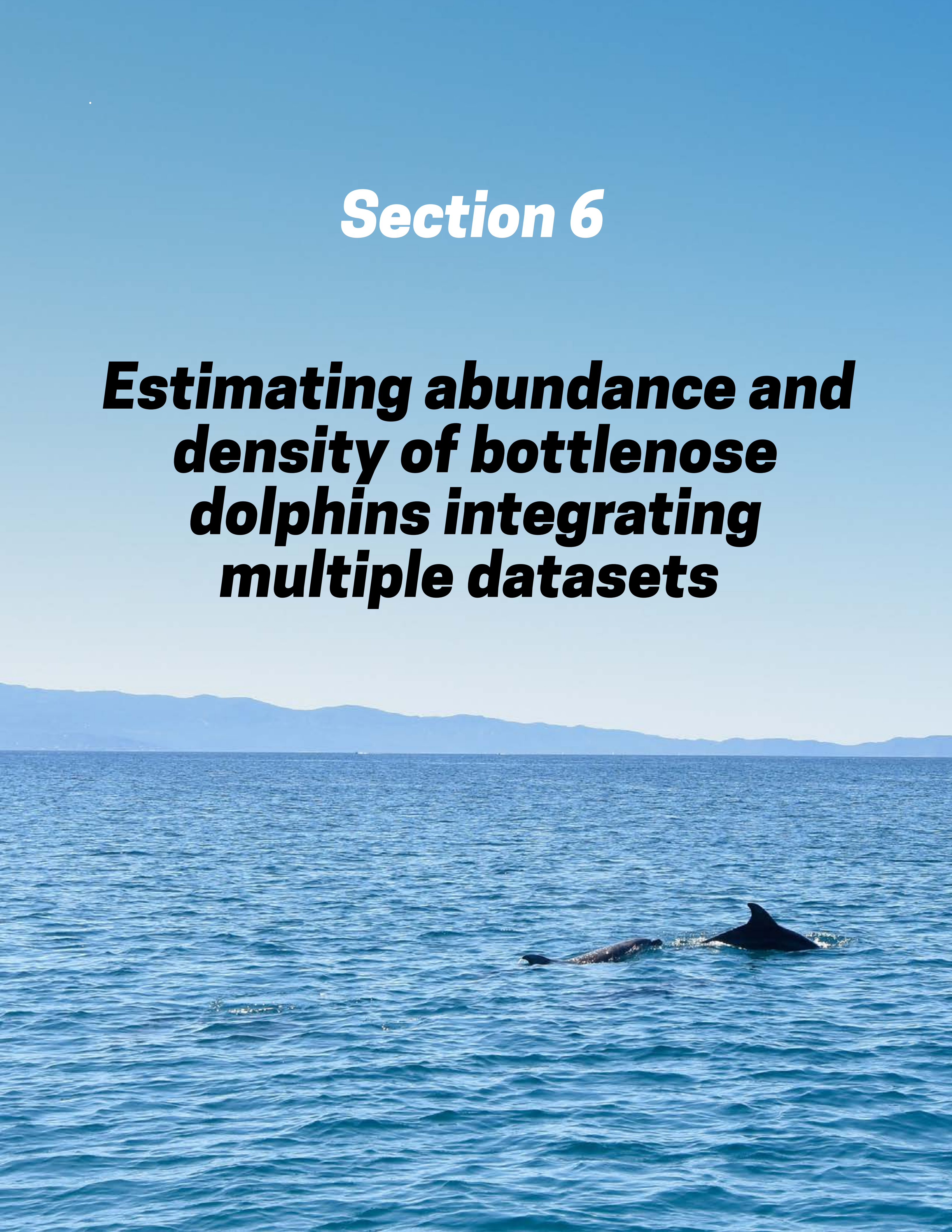


Figure 3: Location of common bottlenose dolphins detection and sampling effort of i) aerial line transect monitoring (left panel)

Section 6

Estimating abundance and density of bottlenose dolphins integrating multiple datasets



Section 6

Article 3: Integrated spatial models foster complementarity between monitoring programs in producing large-scale bottlenose dolphin indicators.

French abstract and keywords

Résumé : Au cours des dernières décennies, l'échelle des études écologiques a sensiblement augmenté, nécessitant la collecte de données écologiques sur une large couverture spatiale et temporelle. Cependant, il est souvent difficile d'obtenir des informations pertinentes à grande échelle à partir d'un seul programme de suivi écologique, et il est alors pertinent d'intégrer plusieurs sources de données éventuellement hétérogènes. Dans ce contexte, les modèles intégrés combinent plusieurs jeux de données en une seule analyse pour quantifier la dynamique de la population étudiée. Travailler à de grandes échelles géographiques nécessite également une spatialisation de l'inférence écologique. En utilisant les informations disponibles à différentes échelles spatiales, les modèles spatiaux intégrés ont le potentiel de produire des estimations écologiques spatialisées difficiles à obtenir si les jeux de données étaient analysés séparément.

Dans cet article, nous illustrons comment la modélisation spatiale intégrée offre un cadre méthodologique pertinent pour réaliser des inférences écologiques à grande échelle sur les effectifs et la densité des populations. En nous concentrant sur les grands dauphins de Méditerranée (*Tursiops truncatus*), nous avons combiné i) 21 464 km de suivis de photo-identification par bateau collectant des données de capture-recapture spatiale, avec ii) 24 624 km de transects linéaires en survol aérien suivant un protocole de distance sampling. Nous avons analysé les données spatiales de capture-recapture avec les données de distance sampling pour estimer l'abondance et la densité des grands dauphins via un modèle spatial intégré. Nous avons comparé les performances du modèle spatial intégré à celles d'un modèle de distance sampling et d'un modèle spatial de capture-recapture séparément.

Les résultats des modèles spatiaux intégrés renseignent sur l'état écologique des grands dauphins en Méditerranée française et fournissent des indicateurs écologiques précis et pertinents pour répondre aux évaluations écologiques à l'échelle régionale, comme par exemple la Directive Cadre Stratégique sur le Milieu Marin (DCSMM). Plus largement, nous discutons de la pertinence d'utiliser les modèles spatiaux intégrés dans les études de conservation de la biodiversité à de grandes échelles spatiales.

Mots-clés : Directive Cadre Stratégique pour le Milieu Marin, distance sampling, grand dauphin, intégration de données, modèles intégrés, NIMBLE, spatial capture-recapture

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Contribution: I developed spatial models of distance sampling, capture-recapture, and integrated spatial model. I formatted the bottlenose dolphin data and environmental variables retrieved from Hélène Labach and Sophie Laran. Daniel Turek helped me to optimize the spatial capture-recapture model with the NIMBLE package. Once the results were obtained, I wrote and started the publication process of the following paper. Olivier Gimenez supervised and participated to all the steps.

Publication: Publication process started, the manuscript is under review in *Animal Conservation*. I presented this work during a talk in EURING conference in June 2021.

Integrated spatial models foster complementarity between monitoring programs in producing large-scale bottlenose dolphin indicators

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Abstract: Over the last decades, large-scale ecological projects have emerged that require collecting ecological data over broad spatial and temporal coverage. Yet, obtaining relevant information about large-scale population dynamics from a single monitoring program is challenging, and often several sources of data, possibly heterogeneous, need to be integrated. In this context, integrated models combine multiple data types into a single analysis to quantify population dynamics of a targeted population. Working at large geographical scales, calls for a spatialization of ecological inference. Using available information at different spatial scales, integrated spatial models have the potential to produce spatial ecological estimates that would be difficult to obtain if data were analyzed separately. In this paper, we illustrate how spatial integrated modeling offers a relevant framework for conducting ecological inference at large scales. Focusing on the Mediterranean bottlenose dolphins (*Tursiops truncatus*), we combined 21,464 km of photo-identification boat surveys collecting spatial capture-recapture data with 24,624 km of aerial line-transect following a distance-sampling protocol. We analyzed spatial capture-recapture data together with distance-sampling data to estimate abundance and density of bottlenose dolphins. We compared the performances of the spatial integrated model, with that of the distance sampling model, and the spatial capture-recapture model separated. The outputs of spatial integrated models inform bottlenose dolphin ecological status in the French Mediterranean Sea and provide ecological indicators that are required for regional scale ecological assessments like the EU Marine Strategy Framework Directive. At a wider extent, integrated spatial models are widely applicable and relevant to conservation research and biodiversity assessment at large spatial scales.

Keywords: *Bottlenose dolphins, data integration, distance sampling, integrated models, Marine Strategy Framework Directive, NIMBLE, spatial capture-recapture*

1 Introduction

Macro-institutions get increasingly involved in large-scale programs for biodiversity conservation over regional and continental areas. Whether these policies aim at assisting governments (e.g., the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services), or at implementing environmental management such as the European Union directives (Habitat Directive, 92/43/EEC, or Marine Strategy Framework Directive, MSFD, 2008/56/EC, *La Directive Cadre Stratégie Pour Le Milieu Marin (DCSMM)* (2008)), conducting large-scale ecological monitoring is required to establish conservation status of targeted species and ecosystems, and to inform decision-making. At large spatial scales, logistical and financial constraints often prevent a detailed coverage of the targeted population using a single collection effort, and different monitoring programs often coexist (Isaac et al., 2019; Lindenmayer & Likens, 2010; Zipkin & Saunders, 2018). The multiplication of monitoring programs over the same conservation context has fostered the development of statistical models that can estimate ecological indicators while accommodating several, possibly heterogeneous, datasets (Besbeas et al., 2002; Farr et al., 2020; Isaac et al., 2019; D. A. W. Miller et al., 2019; Zipkin et al., 2019). Integrating data from several monitoring protocols can give complementary insights on population structure and dynamics (Schaub & Abadi, 2011), increase space and time coverage of the population (Schaub & Abadi, 2011; Zipkin et al., 2019), and produce more precise estimate of ecological indicators (Farr et al., 2020; Isaac et al., 2019; Lauret, Labach, Turek, et al., 2021). A recurrent objective of ecological monitoring programs is to estimate population abundance and density (Williams et al., 2002), for which distance sampling (DS, Buckland et al. (2005)), and capture-recapture (CR, Williams et al. (2002)) methods are widely used. DS and spatial CR methods (SCR) allows accounting for spatial variation in abundance and density (Camp et al., 2020; D. L. Miller et al., 2013; Royle et al., 2014), possibly at large scales (Bischof et al., 2020). Recent modelling tools have emerged to integrate both DS and CR methods into integrated population models (Kéry & Royle, 2020). The extension to integrated spatial models has been proposed to account for spatial variation in abundance and demographic parameters while analyzing jointly DS data and SCR data (Chandler et al., 2018). This integrated modeling approach holds promise for species occurring over large areas that are likely to be the target of multiple monitoring protocols. Besides, working at large geographical scales, require encapsulating spatial dimensions in the estimation of ecological indicators. Integrated spatial models allow to assess spatialized ecological inference, e.g density of individuals. To date, integrated spatial models have been developed and used on open populations to estimate temporal variation in population dynamics and vital rates such as survival and recruitment (Chandler et al., 2018; Chandler & Clark, 2014; Sun et al., 2019). These applications rely on long-term datasets that are not always compatible with conservation objectives. In many cases, ecological information is needed, needed quick, and no temporal depth is available (Lindenmayer & Likens, 2010; Nichols & Williams, 2006). Consequently, ecological inference is often restricted to closed-population indicators (e.g. abundance, density, distribution). When the temporal resolution of monitoring programs does not allow to quantify population dynamics, we argue that an application of integrated spatial models to closed populations can be useful in numerous ecological contexts to deal jointly with existing monitoring programs and assess abundance and density. In this paper, we applied an integrated spatial model demonstrating the relevance of combining DS and SCR to build large scale ecological indicators. We consider the monitoring of common bottlenose dolphins (*Tursiops truncatus*) that are considered as "vulnerable" by the IUCN Red List in the North-Western Mediterranean Sea (IUCN, 2009). The protected status of bottlenose dolphins within the French seas (listed on Annex II of the European Habitats Directive) led to the development of specific programs to monitor Mediterranean bottlenose dolphins within the implementation of the European marine strategy framework directive, which requires assessing the conservation status of this species every 6 years over the large extent of the French Mediterranean Sea (Authier et al., 2017). Increasing efforts are dedicated to develop monitoring programs by the Marine Protected Areas (MPA) network that mainly implement photo-identification protocols locally, while governmental agencies perform large-scale line-transect programs to monitor marine megafauna and fisheries. Hence, multiple data sources coexist about bottlenose dolphins in the French Mediterranean Sea. In this paper, we analyzed jointly the data collected through existing monitoring programs about bottlenose dolphins. We analyzed DS data collected by aerial line-transect surveys over a large area covering coastal and pelagic seas (Laran et al., 2017). We also analyzed SCR data collected by a photo-identification monitoring program restricted to coastal waters (Labach et al., 2021). We compared the abundance and density of bottlenose dolphins estimated from DS model, SCR model, and integrated spatial models to highlight the benefits of the integrated approach in an applied ecological situation. We discussed the promising opportunities of using integrated spatial models in the context of marine monitoring planning in the French Mediterranean. Then, we underlined the conservation implications of using such model at a wider extent to make the best of available datasets.

2 Methods

2.1 Monitoring bottlenose dolphins in the French Mediterranean Sea

Common bottlenose dolphins (*Tursiops truncatus*) occur over large areas throughout the Mediterranean Sea. Because monitoring elusive species in the marine realm is complex, multiple monitoring initiative have emerged to collect data about bottlenose dolphins in the French Mediterranean Sea. In the context of the Marine Strategy Framework Directive, the French government implemented large-scale aerial transects to monitor marine megafauna (Laran et al., 2017). However, the large spatial coverage of the aerial monitoring is impaired by the low resolution of such data (i.e. 1 campaign every 6 years). Then, to collect detailed data, the French agency for biodiversity funded a photo-identification monitoring program to investigate the ecological status of the bottlenose dolphins in the French Mediterranean Sea. This coastal boat photo-identification monitoring has been performed between 2013 and 2015 (Labach et al., 2021). Coastal photo-identification monitoring represents a promising opportunity to produce high resolution information because data can be collected routinely by Marine Protected Areas at high time frequency. Then, large scale aerial line-transect and coastal photo-identification are complementary datasets that coexist about Mediterranean bottlenose dolphins although official ecological assessment for the EU directive only rely on aerial line transects to date.

2.2 Study area and datasets

We focused on an area of 255,000 km2 covering the North-Western Mediterranean Sea within which we considered two monitoring programs about bottlenose dolphins. We used SCR data from at-sea boat surveys over 21,464 km of the French continental shelf. Observers performed monitoring aboard small boats to locate and photo-identify bottlenose dolphins all year long between 2013 and 2015. Taking pictures of the dorsal fin of each individual in the group makes possible the construction of detection history and hence the analysis of the population through capture-recapture methods (Labach et al., 2021). Boat surveys were restricted to the coastal waters of France, and is homogeneous in space and time. We divided the duration of the monitoring programs into 8 equal sampling occasions as in Labach et al. (2021). We also used DS data that were collected during winter and summer aerial line-transect surveys covering 24,624 km of both coastal and pelagic NW Mediterranean Sea between November 2011 to February 2012 and May to August 2012 (Laran et al., 2017). Two trained observers collected cetacean data following a DS protocol (i.e. recording species identification, group size, declination angle). Aerial surveys were conditional on a good weather forecast and aerial sampling effort was homogeneous over the studied area. Although the SCR and DS datasets were collected during separated time frames, we assumed that the bottlenose dolphin abundance did not change much between 2011 and 2015 considering a long-lived species such as bottlenose dolphins (Bearzi et al., 2009). We divided the study area in 4356 contiguous pixel/sites creating a 5'x5' Mardsen grid (WGS 84). To model density of individuals, we used bathymetry as an environmental covariate, which is expected to have a positive effect on bottlenose dolphins' occurrence (Bearzi et al., 2009; Labach et al., 2021). To estimate the sampling effort of aerial and boat surveys, we calculated the transect length (in km) prospected by each monitoring protocol within each site during a time period. Sampling effort was therefore site and occasion-specific in the case of the SCR model, and site specific for the DS model. We used subjective weather condition recorded by plane observers during the line transect protocols. Good weather condition is considered to be positively related to the detection probability.

2.3 Spatial integrated models for closed populations

To integrate DS and SCR data, we used the hierarchical model proposed by Chandler et al. (2018). However, while initially developed for open populations and due to the lack of temporal depth in our datasets, we adapted the model to estimate abundance and density without accounting for demographic parameters (Fig 1). Our integrated spatial model is structured around two layers with i) an ecological model that describes the density of individuals based on an inhomogeneous point process (Spatial abundance section below), and ii) two observation models that describe how the DS and SCR data arise from the latent ecological model (Capture-recapture data and Distance-sampling data sections below).

2.3.1 Spatial abundance

For the ecological model, we use a latent spatial point process modelling the density of individuals and the overall abundance. Over the study area S, an intensity function returns the expected number of individuals at location s in S. To account for spatial variation, we model the latent density surface as an inhomogeneous point process. For every location s in the study area S, the expected abundance λ is written as a log-linear function of an environmental covariate, say habitat:

$$log(\lambda(s)) = \mu_0 + \mu_1 habitat(s) \quad (1)$$

where parameters to be estimated are μ_0 and μ_1 respectively the density intercept and the regression coefficient of the environmental covariate. We used bathymetry as a habitat covariate possibly influencing bottlenose dolphin density. Then, the estimated population size is derived by integrating the intensity function over the study area:

$$E(N) = \int_S \lambda(s)ds \quad (2)$$

The latent ecological process defined by Eq. 1 is an inhomogeneous point process that is common to both the SCR and DS models. SCR and DS data are linked to density λ and informed the parameters of Eq. 1. To account for unseen individuals, we used the data augmentation technique and augmented the observed datasets to reach M = 10,000 individuals (Royle & Dorazio, 2012). Each individual i is considered being ($z_i = 1$) or not ($z_i = 0$) a member of the population according to a draw in a Bernoulli distribution of probability ψ, with

$$z_i \sim Bernoulli(\psi)$$

where ψ is the probability for individual i to be a member of the population, with $\psi = E(N)/M$ and $N = \sum_{i=1}^{M} z_i$.

2.3.2 Capture-recapture data

To link capture-recapture data with the ecological process, we built a SCR model (Royle et al., 2014). Detection history of individuals were collected over $T = 8$ sampling occasions and capture locations were recorded. We stored observations in a three-dimensional array y with y_{ijt} indicating whether individual i was captured at detector j during sampling occasion t. We assume that observation y_{ijt} is an outcome from a Bernoulli distribution with capture probability p_{ijt}, $y_{ijt} \sim Bernoulli(p_{ijt})$. We model capture probability with a half-normal detection function

$$p_{ijt} = p_0 exp(-(d_{ij}^2)/(2\sigma^2))$$

where d_{ij} is the Euclidian distance between the activity center of individual i and the detector location j, σ is the scale parameter of the half-normal function, and p_0 is the baseline encounter rate (Royle et al., 2014). We accounted for spatial and temporal variation in the detection probability through the scale parameter σ which we wrote as a log-linear function of sampling effort E_{jt} at detector j during sampling occasion t: $log(\sigma_{jt}) = \beta_0 + \beta_1 E_{jt}$. We also wrote p_0 as a logit-linear function of E_{jt}: $logit(p0_{jt}) = d_0 + d_1 E_{jt}$. When the sampling effort E_{jt} is null, we fixed p_{ijt} to 0. For each individual i belonging to the sampled population, its activity center is assigned a uniform distribution throughout the study

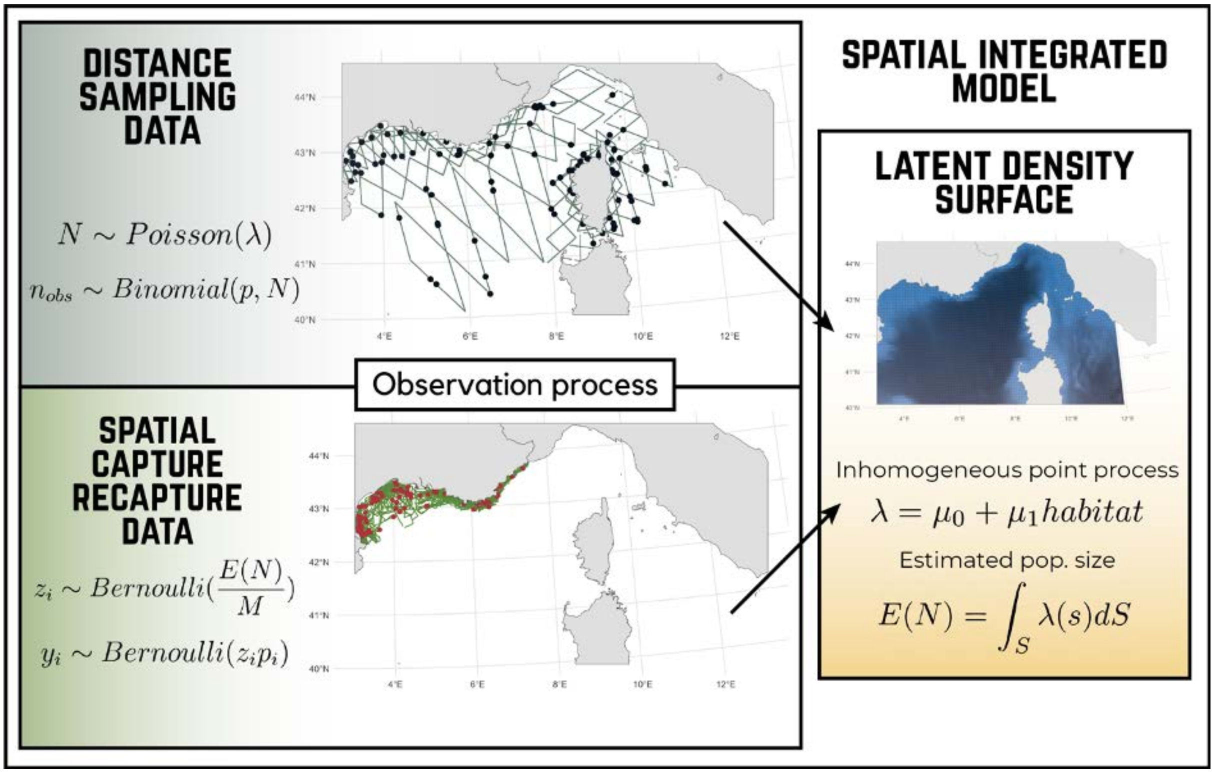

Figure 1: Graphical description of the Spatial Integrated Model (SIM) that combines Spatial Capture Recapture (SCR), and Distance Sampling (DS). The SIM is a hierarchical model with three processes: i) latent population size $E(N)$ and density λ informed by an inhomogeneous point process, ii) DS observation process that link the line-transect dataset to the latent density surface, iii) SCR observation process that links the detection histories to the latent density. The observation process is stochastic according to detection probability. For DS model, the observed group size n_{obs} is a Binomial draw in the latent abundance N at the sampling location. For SCR model, observing an individual i is a Bernoulli draw with a detection probability p_i. Through the data augmentation process with a hypothetical population sizeM, the probability an individual i belong to the study population is the result of a Bernoulli draw of probability

area. The locations of activity centers inform the density of individuals λ. In the SCR model, the abundance at location s is defined as the number of activity centers of bottlenose dolphins. The link between density of individuals λ and capture locations is made via the detection probability that is a decreasing function of distance between activity center of individual i and sample location j. Another option is to model the location of activity center of each individual i as the result of a multinomial draw in the predicted density in each site of the study area.

$$id_i \sim Multinomial(1, \bar{\lambda})$$

where id_i is the activity center of individual i, and $\bar{\lambda}$ represent the vector of the predicted density in each cell of the study area. We did not implement the multinomial distribution because of the computational burden to sample the 4356 grid-cells.

2.3.3 Distance-sampling data

To accommodate distance data, we built a hierarchical DS model (Kéry & Royle, 2016). We model the DS data conditional on the underlying density surface defined by Eqs (1) and (2). We assume that the probability of detecting dolphins in transect l is a decreasing function of d_{il} the perpendicular distance between transect l and dolphins group location i, with

$$r_{il} = r_0 exp(-(d_{il}^2)/(2\eta^2))$$

, where η is the scale parameter of the half-normal function, and r_0 is the probability of detection on the transect, which we will set to 1. Because distance may not be estimated with perfection by observers, we discretized the distance of observation in B distance bins. We assume that density within each transect is uniform and that the number of individuals in each transect is Poisson distributed. Then, $n_{i,b}$ the observed group size detected at location i in distance bin b, is given by a Binomial draw in the expected number of individuals in bin b, $N_{i,b}$ with $r_{i,b}$ the detection probability within each bin b.

$$N_{i,b} \sim Poisson(\lambda_{i,b})$$

$$n_{i,b} \sim Binomial(N_{i,b}, r_{i,b})$$

We account for spatial variation in the scale parameter of the detection function via η as a log-linear function of sampling effort S_j and of weather condition W_j in transect j: $log(\eta_j) = \alpha_0 + \alpha_1 S_j + \alpha_2 W_j$.

2.4 Bayesian implementation

To highlight the benefit of integrating data for the estimation of bottlenose dolphin density, we compared i) the output of the spatial DS model, ii) the SCR model, and iii) the integrated spatial model. We ran all models with three Markov Chain Monte Carlo chains with 100,000 iterations each in the NIMBLE R package (Valpine et al., 2017). We checked for convergence calculating the R-hat parameter (Gelman et al., 2013) and reported posterior mean and 80% credible intervals (CI) for each parameter. We considered as important the effect of a regression parameter whenever the 80% CI of its posterior distribution did not include 0. We also calculated the predicted density of bottlenose dolphins (i.e. λ). Data and codes are available on GitHub.

3 Results

We detected 536 dolphins through aerial surveys clustered in 129 groups. We identified 927 dolphins over 1707 detections in photo-identification surveys, out of which 638 dolphins were captured only once (68%), 144 were captured twice (15.5%), 149 were captured 3 times and up to 8 times for one individual. The maximum distance between two sightings of the same individual was 302 km and 115 km during the same sampling occasion. We estimated 2450 dolphins (2276; 2631) with integrated spatial model over the study area (Table 1),8470 dolphins (7620; 9329) with the DS model and 1756 dolphins (1645; 1872) with the SCR model (Table 1). Density intercepts of integrated spatial model ($\mu_0 = -0.67(-0.75; -0.60)$) and SCR model ($\mu_0 = -1.01(-1.37; -0.89)$) were lower than intercept of DS model ($\mu_0 = 0.6(0.50; 0.71)$). In the integrated spatial model, estimated abundance increased when bathymetry increased ($\mu_1 = 0.43(0.37; 0.48)$, Table 1), suggesting a preference for low-depth seafloors (Fig. 2). DS model also estimated a positive effect of bathymetry ($\mu_1 = 0.34(0.28; 0.39)$, Table 1), while the SCR model did not detect any effect of bathymetry on density ($\mu_1 = 0.02(-0.73; 0.83)$, Table 1). Then, integrated spatial model and DS models predicted higher densities of bottlenose dolphins in the coastal seas than in the pelagic seas, whereas the SCR model did not predict any variation in density between coastal and pelagic waters (Fig. 2). We detected a positive effect of aerial sampling effort on detection probability in both DS model ($\alpha_1 = 0.61(0.54; 0.67)$) and integrated spatial model ($\alpha_1 = 0.47(0.36; 0.57)$). Boat sampling effort exhibited a positive effect on detection probability for both the SCR model ($\beta_1 = 0.84(0.73; 0.96)$, $d1 = 0.76(0.71; 0.81)$) and the integrated spatial model ($\beta_1 = -0.22(-1.34; 0.76)$, $d1 = 0.70(0.65; 0.75)$, table 1). For the integrated spatial model and the DS model, the detection probability increased when the weather condition improved (integrated spatial model: $\alpha_2 = 0.30(0.18; 0.42)$, DS: $\alpha_2 = 0.14(0.08; 0.20)$, Table 1).

4 Discussion

4.1 Integrated spatial model benefits from both distance sampling and capture-recapture data

With our integrated spatial model, we estimated bottlenose dolphin abundance within the range of what was found in previous studies in nearby areas (Gnone et al., 2011; Lauriano et al., 2014), and found that densities were more likely to be higher in coastal areas (Bearzi et al., 2009). A striking result was the large differences in abundance estimates between DS and SCR models, which were also found in previous studies analyzing the same datasets in isolation. Using capture-recapture data only, Labach et al. (2021) estimated 2647 dolphins (95% confidence interval: 2059; 3528) inhabiting the French continental coast where our model predicted 2450 dolphins (2276; 2631). Analyzing distance sampling data, Laran et al. (2017) estimated 2946 individuals (95% confidence interval: 796; 11,462) during summer, and 10,233 (95% confidence interval: 4217; 24,861) during winter where our DS model estimated 8470 (7413; 9595) all year long. We see several reasons that might explain these differences. First, the seasonal difference in Laran et al. (2017) DS abundance estimates suggests an issue with the geographic closure assumption that might explain the discrepancy in estimates obtained from SCR and DS models. Although the Mediterranean bottlenose dolphins population is clustered in coastal sub-units (Carnabuci et al., 2016), groups can be encountered offshore (Bearzi et al., 2009). In the DS dataset, large dolphin groups were detected in the pelagic seas at the extreme south of sampling design (Appendix 1). These groups could either be i) occasional pelagic individuals that belong to coastal populations and that are mainly resident outside our study area (e.g. Balearic, South-Western Sardinia), or ii) resident pelagic populations that are not sampled by coastal boat surveys (Louis et al., 2014). Second, DS and SCR models do not estimate the same quantities. While DS models take a snapshot of abundance and density in the study area at the moment of the sampling, SCR models estimate abundance and density of the sampled population, whether or not the individuals are present in the study area during the sampling period (Calambokidis & Barlow, 2004). In our case study, SCR data were restricted to the French continental coast and did not sample dolphin populations that exist elsewhere in the study area, e.g. in Corsica, Liguria, and Tuscany (Carnabuci et al., 2016). Despite this geographic sampling bias in the capture-recapture data, SCR models should predict the existence

Table 1: Parameter estimates for the spatial integrated model (SIM), spatial capture-recapture (SCR) model, and distance-sampling (DS) model. For each parameter, we display the posterior mean and its 80% credible interval (CI).

	SIM		SCR model		DS model	
Parameter	Mean	80% CI	Mean	80% CI	Mean	80% CI
Estimated population size N	2450	2276, 2631	1756	1645, 1872	8470	7620, 9329
Intercept of density μ_0	-0.67	-0.75, -0.60	-1.01	-1.37, -0.89	0.60	0.50, 0.71
Effect of bathymetry on density μ_1	0.43	0.37, 0.48	0.02	-0.73, 0.83	0.34	0.28, 0.39
SCR scale parameter: Intercept β_0	0.23	-0.82, 1.45	0.04	-1.01, 1.12		
SCR scale parameter: Effect of at-sea sampling-effort β_1	0.84	0.71, 0.95	0.84	0.73, 0.96		
SCR p_0 parameter: Intercept d_0	-6.65	-7.05, -6.27	-6.51	-6.93, -6.11		
SCR p_0 parameter: Effect of at-sea sampling-effort d_1	0.70	0.65, 0.75	0.76	0.71, 0.81		
DS scale parameter: Intercept α_0	-5.52	-6.50, -4.34			-7.91	-8.52, -7.24
DS scale parameter: Effect of aerial sampling-effort α_1	0.47	0.36, 0.57			0.61	0.54, 0.67
DS scale parameter: Effect of weather condition α_2	0.30	0.18, 0.42			0.14	0.08, 0.20

of Corsican and Italian populations if the relationship between density and habitat in Eq (1) was correct and consistent throughout the study area. As the capture-recapture survey did not sample the lower range of bathymetry, our SCR model underestimated abundance because the link between density and bathymetry was not correctly specified. Overall, because groups of the Sardinian and Balearic populations and offshore groups can be sampled in the aerial surveys, the DS model drives upward abundance compared to the SCR model that is unlikely to account for animals that are members of the Southern neither the Eastern populations. To perform detailed analysis of the NW Mediterranean bottlenose dolphin populations, one should consider additional environmental covariates to better capture spatial variation in density (e.g., sea surface temperature, distance to coast, or 200m contour, Lambert et al. (2017)). Both DS and SCR data affected the estimates of the integrated spatial model. Using the DS data that were collected in both coastal and pelagic seas informed the slope of the inhomogeneous point process (μ_1), and detected the effect of bathymetry on density. Thus, the DS data informed the integrated spatial model by correcting for the geographic sampling bias in the SCR data. On the other hand, the SCR data brought more information about population size (e.g. more detections, more individuals) that the DS data to inform the intercept of density (μ_0), making the integrated spatial model abundance estimate closer to the SCR model estimate (Table 1). In the integrated spatial model, the SCR data informed the estimated population size and the DS data informed spatial repartition of individuals. Then, the integrating approach helped to correct for the sampling bias of each of the dataset and can improve the ecological inference as illustrated here about bottlenose dolphins.

4.2 Conservation implications for monitoring bottlenose dolphins in the French Mediterranean Sea

To date, the assessment of French Mediterranean bottlenose dolphin population required by the EU are established using the DS data (Laran et al., 2017). Aerial surveys provide crucial information on marine megafauna taxa, and on human pressures to fill several criteria of the Marine Strategy Framework Directive (Lambert et al., 2020; Laran et al., 2017; Pettex et al., 2017). However, funding constraints make the aerial monitoring hardly applicable at a high frequency, and it is planned to be implemented every 6 years. Then, the French agency for biodiversity develop and support locally photo-identification monitoring through the French MPA network to collect detailed data continuously. For bottlenose dolphins, at-sea photo-identification programs collecting detailed

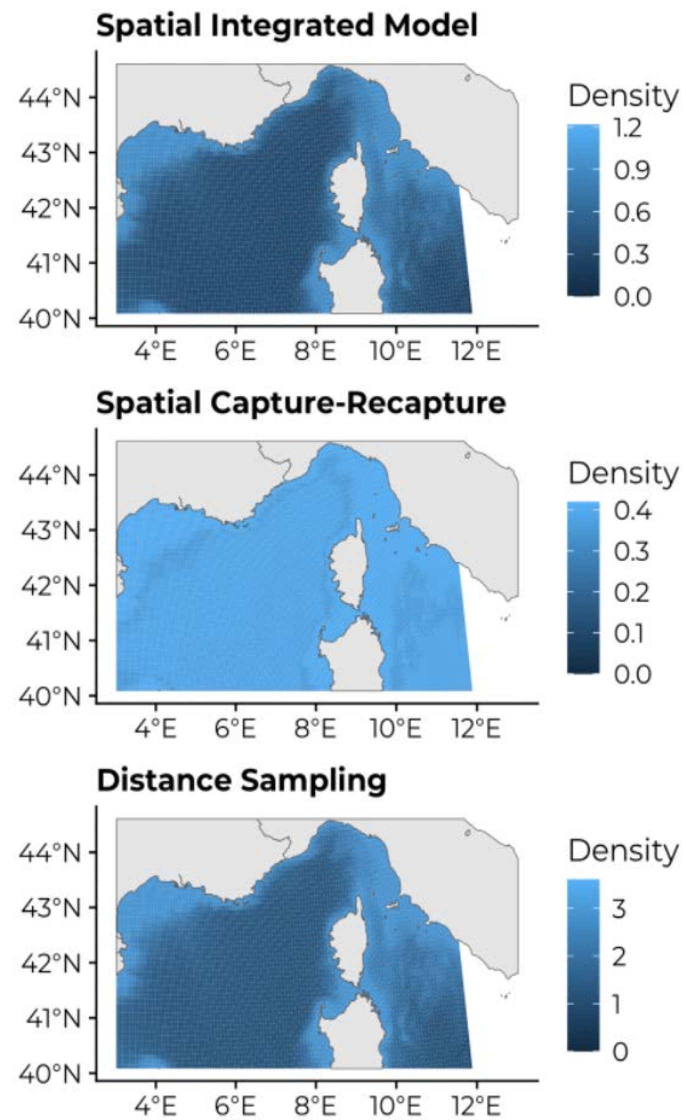

Figure 2: Estimated density surface of bottlenose dolphins (Tursiops truncatus) for the 3 models. Lighter color indicates higher number of individuals per area unit. Both spatial integrated model (SIM) and distance sampling (DS) predicted higher density in coastal seas, while spatial capture-recapture (SCR) predicted homogeneous density across the study area. Note that density scales are different between maps, indicating a higher overall population size for DS model than for SIM, and SCR model.

data are an important asset to inform abundance (Evans & Hammond, 2004). Ecological indicators required by the Marine Strategy Framework Directive for bottlenose dolphins would benefit from integrating aerial line-transect with more data when available (Lauret, Labach, Authier, et al., 2021). In addition, the French Research Institute for Exploitation of the Sea (i.e. IFREMER) collected yearly bottlenose dolphins' data during line transects surveys for pelagic fisheries (Baudrier et al., 2018). Ultimately, several monitoring programs will be available about bottlenose dolphins in the Mediterranean context and integrated spatial models makes possible to include existing datasets that have been discarded so far to inform public policies (Cheney et al., 2013; Isaac et al., 2019).

We acknowledge that our model has limitations and does not provide precise estimates due to several ecological features that we did not account for (e.g. spatial autocorrelation, effect of other environmental covariates). However, we believe that integrated spatial models are highly relevant considering the future monitoring planning by the French biodiversity agency that will perpetuate the coexistence of photo-identification with aerial line-transect. Analyzing the collected data in an integrated framework will lead to a more comprehensive understanding of how the monitoring programs can work together and what exactly it is that they achieve in unison. It is our hope that the ability of integrating different datasets contribute to the ongoing monitoring efforts developed in the Mediterranean context and fit in the scope of what managers expect form statistical developments to inform environmental policies.

Our work provides a promising modelling baseline to deal with the bottlenose dolphin evaluation but also open perspectives for other conservation challenges about marine species that are subject to similar monitoring situations in the French Mediterranean context (e.g. fin whale, seabirds). Last, adding complementary long-term datasets to the aerial-surveys would make possible to access the demographic parameters (e.g. recruitments, survival (Chandler et al., 2018), which would represent a major opportunity for the knowledge about French Mediterranean bottlenose dolphin populations and to produce reliable conservation status. The use of integrated spatial models for the French Mediterranean bottlenose dolphin population also enable to extend the modelling approach exploring seasonality in density, and to measure immigration and dispersal between bottlenose dolphins populations (Zipkin & Saunders, 2018).

4.3 Spatial integrated models as a promising tool for conservation

When establishing species conservation status for large-scale environmental policies, discarding some datasets from the analysis can reduce the reliability of the ecological estimation (Bischof et al., 2016). Using multiple datasets into integrated spatial models help to overcome some limitations present when using separated datasets (e.g. limited spatial or temporal survey coverage, Zipkin & Saunders (2018); Isaac et al. (2019)). However, caution should be taken as integrating data requires additional modelling assumptions (Dupont et al., 2019; Farr et al., 2020; Fletcher et al., 2019; Simmonds et al., 2020). Integrated spatial models are flexible tools that can include more than 2 datasets (Zipkin & Saunders, 2018), and various type of data that enlarge the scope of usable information (presence-absence Santika et al. (2017)), count data Chandler et al. (2018), citizen science data Sun et al. (2019)). Recent and current developments of SCR models widen perspectives to extend integrated spatial models to account for unidentified individuals, or to better describe animal movement (Jiménez et al., 2020; Milleret et al., 2019; Turek et al., 2020). Over the last decades, the spatial scope of conservation efforts has greatly increased, and the analytical methods have had to adapt accordingly (Zipkin & Saunders, 2018). Integrated spatial models are a promising tool that can be used in multiple situations where several data sources coexist, especially for large scale conservation policies.

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Appendix S1: Data exploration: Spatial Integrated Model

Valentin Lauret, Hélène Labach, Daniel Turek, Sophie Laran, Olivier Gimenez

Contents

In this document, we provide data exploration and results of our analyze of bottlenose dolphins *(Tursiops truncatus)* in the northwestern Mediterranean Sea.

To study bottlenose dolphins, we combined two existing datasets in the French waters :

- aerial line-transects collecting bottlenose dolphins data following a distance sampling (DS) protocol.
- at-sea photo identification collecting indivdiual data about dolphins population.

We built a DS model to analyze aerial data, a spatial capture-recapture (SCR) model to analyze at-sea data, and a spatial integrated model (SIM) to analyze jointly both datasets and to estimate abundance and density.

Hereafter, we provide data exploration and displayed some of the results.

The Data

The objective of this section is to provide supplementary information about bottlenose dolphins data.

About bottlenose dolphins

Bottlenose dolphins *(Tursiops truncatus)* in the North-Western Mediterranean Sea. In the marine world, many species of conservation interest are elusive, and ecological data can be costly to obtain. In particular, the high seas are difficult to access and ecological monitoring is often performed through aerial surveys. However, coastal seas allows performing detailed at-sea monitoring. Besides, many species such as marine megafauna are mobile and occur in both coasts and high seas. Combining monitoring programs that are carried out in each realm (i.e. coasts and high seas) has the potential to provide relevant information about these species.

Figure 1: Bottlenose dolphins in the French Mediterranean Sea

Monitoring programs

We focused on the North-Western Mediterranean, an area of 255,000 km2, which includes the Gulf of Lion and the Ligurian sea, the French coast of Provence, Corsica, and the Northern part of Sardinia (Figure 2). Our study area includes the Pelagos Sanctuary, which is a transboundary marine protected area for Mediterranean marine mammals covering an area of 90,000 km2 between Italy, France and Monaco.
The North-Western Mediterranean Sea is a critical habitat for many cetaceans species. Due to its coastal behaviour, bottlenose dolphins suffer from several anthropogenic pressures (e.g. collisions, fisheries bycatch, pollution, or acoustic perturbations), which raise concerns about their coexistence with human activities. The Mediterranean population of Bottlenose dolphins is considered "vulnerable" by the IUCN Red List and is one of the two cetacean species listed on Annex 2 of the European Habitats Directive (92/43/EEC). The protected status of this species within the French seas led to the development of specific programs to monitor Mediterranean bottlenose dolphins within the implementation of the European Marine Strategy Framework Directive (2008/56/EC; MSFD).

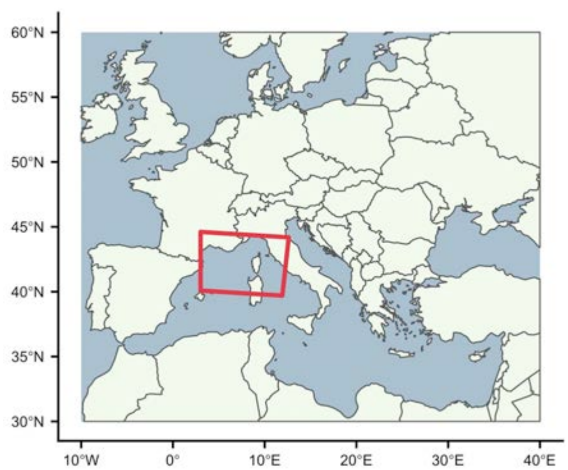


Figure 2: Location of study area in the Mediterranean basin.

At-sea monitoring

We used data from the first large-scale study of Bottlenose dolphins in the French Mediterranean Sea. Four NGOs and one marine reserve performed at-sea surveys over 21,464 km of the French continental shelf including the Gulf of Lion, the French Riviera, and Corsica (Figure 2). Observers performed monitoring aboard small sailing and motor boats to locate and photo-identify bottlenose dolphins all year long between 2013 and 2015 (observers collected group size, behaviour, and took pictures of the dorsal fin of each individual in the group when possible). Such surveys with small vessels are expected to recorded detailed information while being limited to coastal area. Between summer 2013 and summer 2015, at-sea surveys detected 129 bottlenose dolphin groups located in 89 different grid-cells. The sampling effort of at-sea surveys was heterogeneous in space (i.e. between 1 and more than 500 km prospected per sampled grid-cell), and time (i.e. higher prospection in spring and summer than in autumn and winter). At-sea surveys did not include repeated visits. Some sites have been visited once, and others have been visited 50 times.

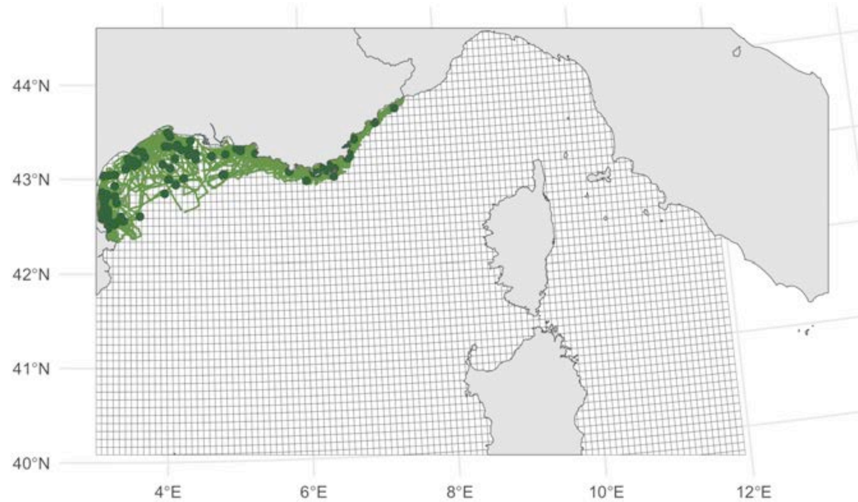


Figure 3: Boat surveys (GDEGeM program) prospected 21,646 km of of the French continental shelf. Darkgreen dots are detection locations.

Aerial pelagic and coastal monitoring program

Data were collected during aerial surveys targeting the main taxa of marine megafauna within the French Exclusive Economic Zone (EEZ) including the Pelagos Sanctuary. The survey covered 24,624 km of line-transect performed by scientific institutional partners of the French Biodiversity Office and sampled 1336 grid-cells (i.e. 30.67% of the total number of grid-cells, Fig. 1). Two trained observers collected cetacean data following a distance sampling protocol (i.e. recording species identification, group size, declination angle). Aerial surveys were conditional on a good weather forecast and were performed using high-wind aircrafts with bubble windows. Sampling effort for aerial surveys was homogeneous over the studied area with three or four replicates per line-transect between November 2011 and August 2012. While aircrafts surveyed large area quickly, the limited temporal coverage may reduce overall number of detections. In the future, this survey will be conducted every six years to inform the MSFD (for more details).

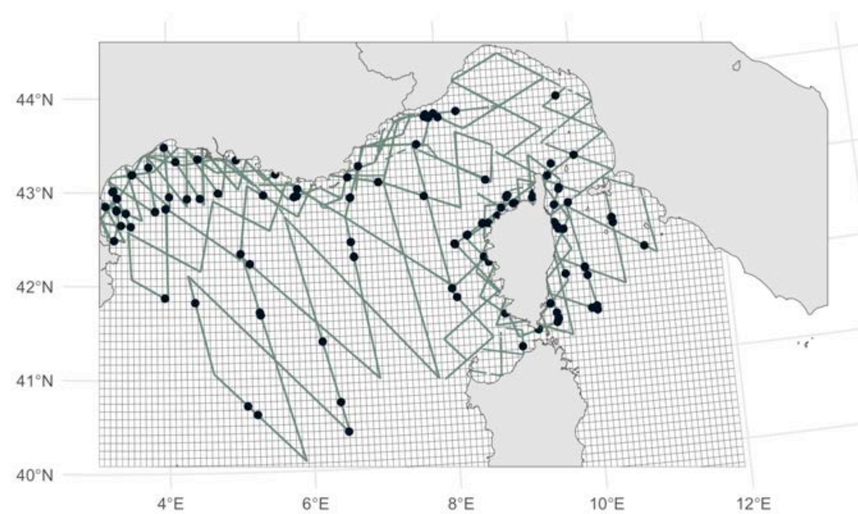


Figure 4: Aerial surveys (SAMM program) prospected 24,624 km of both sea shelf and high seas, darkblue dots are detection locations.

The two monitoring programs collected either photo-identification or distance sampling data. For both programs, we used the locations of bottlenose dolphins encounters and the survey tracks.We used two environmental covariates to estimate the space-use of bottlenose dolphins: i) bathymetry, and ii) sea surface temperature (SST).

Results: comparison between models

About population size

We built the density surface λ from the Inhomogeneous Point Process in every site of the study area from the estimated parameters μ_0 and μ_1.

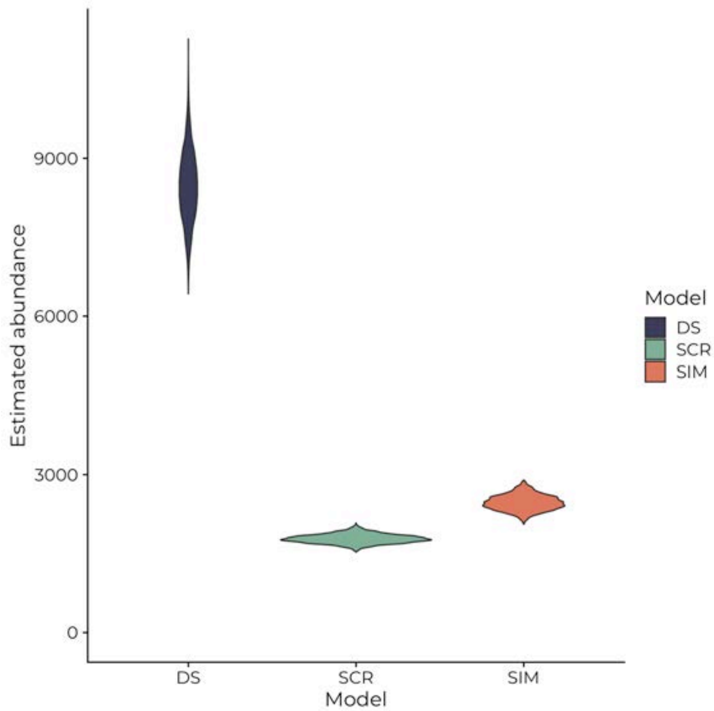


Figure 5: Abundance estimated by DS model, SCR model, and SIM

Density maps

Density maps are built projecting λ in every site of the study area.

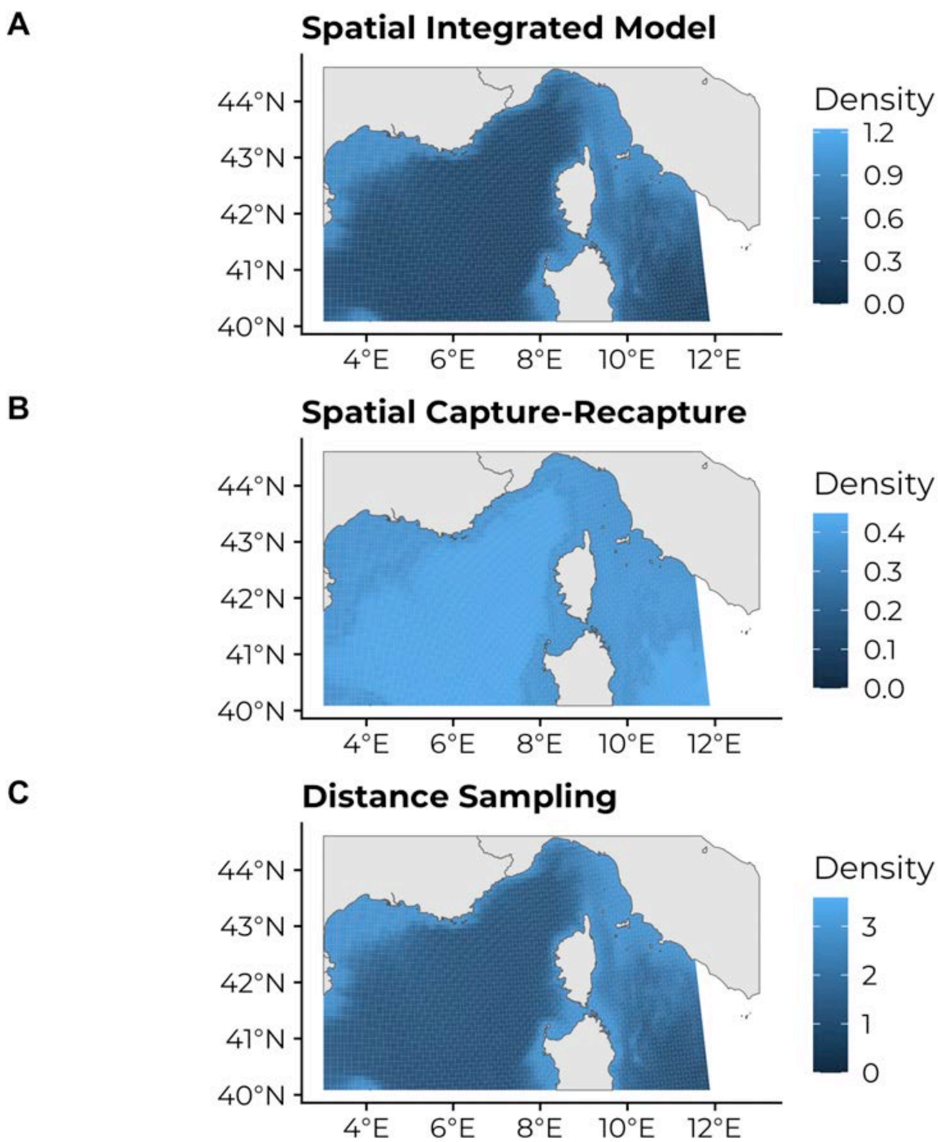
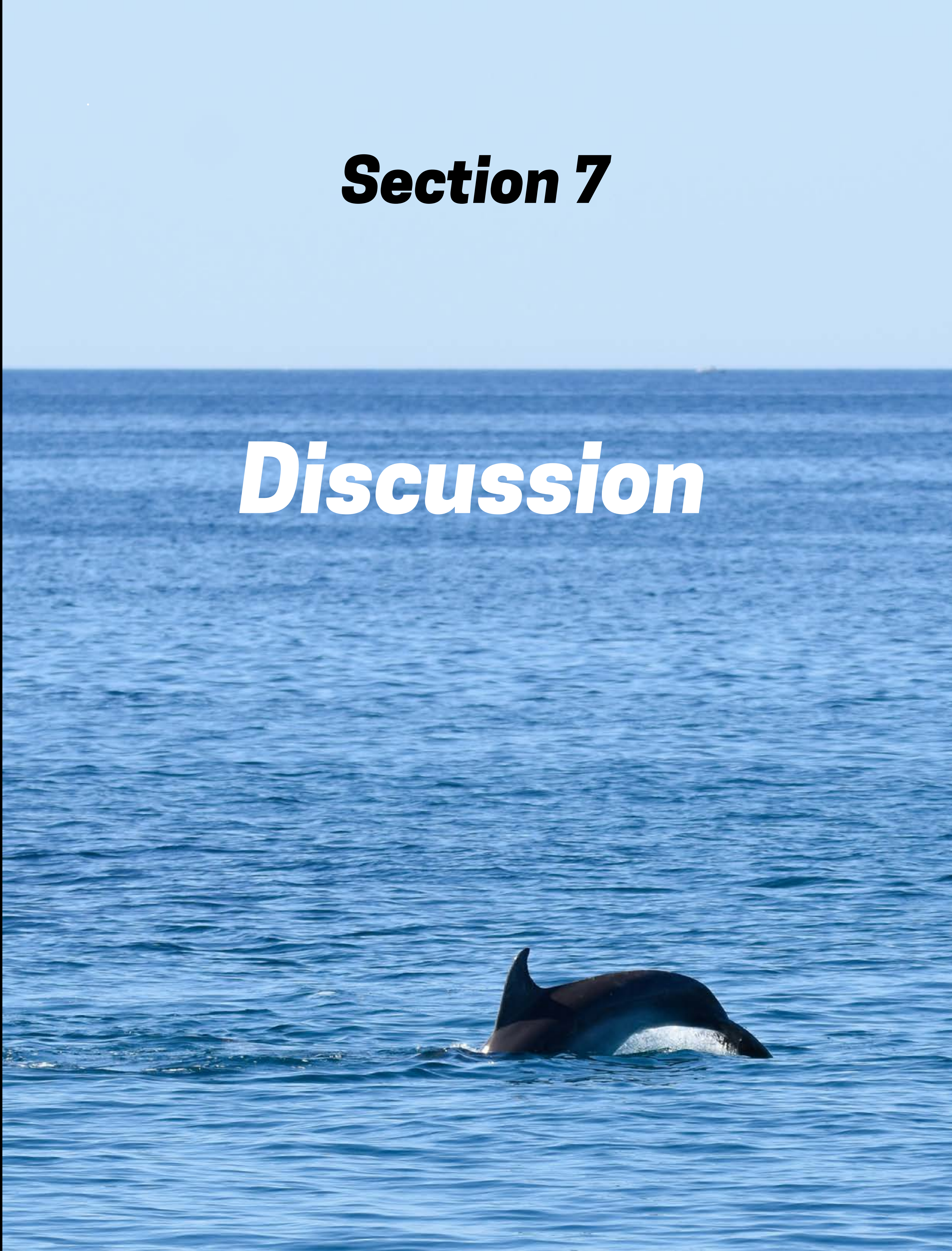


Figure 6: Density of bottlenose dolphins estimated by DS model, SCR model, and SIM

Section 7

Discussion



7 DISCUSSION

7.1 Relevance of the thesis for the ecological monitoring of bottlenose dolphins in the French Mediterranean Sea

The challenge of coordinating ecological monitoring between global and local scales

The interviews (Section 4) and the dialogue with biodiversity professionals emphasized that the construction of ecological indicators is one of the main institutional challenges in the Mediterranean Sea. Several issues have been identified when estimating ecological indicators. The differences of ecological monitoring scales raise concerns to conciliate i) MPAs that require to monitor at a local scale, and ii) OFB that require to produce ecological indicators at the scale of the Mediterranean coastline. For bottlenose dolphins, the ecological indicators of distribution and abundance are mandatory to inform, on one hand, to the MSFD, and on the other hand, to the MPAs management dashboards. However, the large-scale ecological indicators of the MSFD do not meet the needs of the MPAs that are willing to establish high-resolution indicators at a local scale. For example, about aerial surveys for marine megafauna, an OFB agent indicates:

> *"Large aerial surveys are often criticized because MPAs say they can't do much with them. You produce ecological assessments at the scale of the entire EEZ. And even if you do habitat modeling, we're just a little pixel or cell in the middle of a map but it doesn't inform us at all."*

In some cases, ecological indicators produced by large-scale monitoring programs are not compatible with data collected by MPAs because monitoring protocols are different (for example, between large-scale count data and local photo-identification data). Large-scale monitoring protocols are sometimes too coarse and can produce erroneous results according to MPAs. One example concerns Posidonia (*Posidonia oceanica*) meadows, for which meadows are mapped at the scale of the Mediterranean coastline. The definition of zones where boats are forbidden to anchor is based on these maps, but MPAs contest their accuracy; for example, an MPA agent emphasized:

> *"At the local scale, when it does not fit, we are compelled to say so. For example, when they placed seagrass beds where there are none. This has consequences on biodiversity management."*

Sometimes, ecological monitoring is difficult to coordinate at the scale of the MPA network. Discrepancies between MPAs objectives and those at the scale of the French Mediterranean coastline highlight operational and political issues. Conciliating ecological data collected at both spatial scales would be a major asset, as explicitly stated in the interviews by the same OFB manager, who was aware of the problem.

> *"Since the beginning, the idea has been to successfully develop monitoring programs that meets both MPA and large-scale needs and we know that this is not easy to reconcile."*

The statistical models I developed during this thesis are not able to tackle the issue of coordination of protocols in MPAs, but they offer a promising basis for the integration of ecological data from various monitoring protocols, which is especially relevant in the current institutional context in the French Mediterranean. According to managers, monitoring guidelines for bottlenose dolphin in the French Mediterranean Sea are to develop photo-id monitoring in the MPAs and, in parallel, to continue with aerial surveys at the EEZ scale. The two types of data used for the development of the statistical models in Sections 5 and 6 (aerial surveys and photo-id) are likely to be collected recurrently in the French Mediterranean Sea, which reinforces the usefulness of the modeling tools investigated during this thesis.

Integrated models as an operational tool for the MPA network

Using integrated models can be relevant at both local and global scales. First, within an MPA, several monitoring protocols can coexist. As the French Marine Natural Parks are very large MPAs, aerial surveys help to monitor pelagic areas, but coastal monitoring is also performed in parallel for photo-identification of bottlenose dolphins. For these types of large MPAs, the use of integrated models will be useful to inform ecological indicators necessary to feed their management dashboard. Managers of the Marine Natural Park of Cape Corsica and Agriate, and those of the Marine Natural Park of the Gulf of Lion have already contacted us to express their interest in these statistical methods allowing data integration at the scale of their MPA. At the scale of the Mediterranean coastline, OFB is working to centralize ecological data from MPAs (TURSMED program, MIRACETI (2019)). Integrated modeling will allow to jointly analyze the information provided by MPAs and that provided by large-scale aerial surveys, which are planned to be continued every 6 years. From a modeling point of view, since photo-id protocols are performed at a fine scale within MPAs, the resolution of the ecological process could be high enough to simultaneously meet the detailed MPAs requirements and to establish ecological indicators at the coastline scale. Thus, OFB has the opportunity to develop an integrated framework for estimating bottlenose dolphin ecological indicators by bridging local and global scales.

To inform MPA managers of the availability of integrated statistical tools, we will organize a feedback meeting in some MPAs, which could not be done during the thesis due to public health conditions. We are looking forward to present the statistical tools we developed and to discuss their mobilization for inferring ecological indicators in MPAs and at the level of the coastline by the OFB. We also have planned to organize a meeting at the OFB Mediterranean delegation, and another during the Mediterranean Technical Workshops that bring together MPA managers to discuss technical issues. Besides, we are willing to restitute the results of the social science study to MPA agents in a format to be defined.

Perspectives for other ecological monitoring programs in the French Mediterranean Sea

Whereas aerial surveys and photo-identification data are predominant for bottlenose dolphins in the French Mediterranean Sea, other datasets could be considered for integration when estimating ecological indicators. First, we see candidates in the line transect protocols for small pelagic fisheries stock estimation (PELMED program - Baudrier et al. (2018)) or for aerial overflights for tuna (Ifremer, 2015). In this case, data integration would be done via a distance sampling observation process as SAMM data are used for the estimation of abundance (see Section 6). In passing, I thank Claire Saraux for sending us the observations of marine megafauna observed during the scientific fishing campaigns of the PELMED protocol. From a preliminary exploration of the PELMED data, we only count a few detections of bottlenose dol-

phins each year (15 detections in 2015). Moreover, the sampling design is limited to the Gulf of Lion area. However, the annual recurrence of the PELMED protocol and the sampling design allow to have recurrent data off the Gulf of Lion, in areas that are usually rarely monitored. Similar interest applies to data from "tuna surveys": annual recurrence, few detections of bottlenose dolphins, data only in the Gulf of Lion but including the pelagic sea. To assess the added value of these datasets to the ecological estimates of the bottlenose dolphin, one can integrate the line transect data from PELMED and the tuna overflights between 2010 and 2015 to the models developed in Sections 5 and 6, and hence quantify the contribution of this information to the ecological inference.
Marine mammal strandings are a significant source of biological data about cetacean populations (Bouchard et al., 2019; Peltier et al., 2012). Necropsies provide information about possible pollution, about the impact of anthropic activities, but also about the ecology and behavior of cetaceans (e.g. diet). Since the 1970s, the National Stranding Network – NSN (Réseau National Échouage, in French, or RNE in short) monitors the complete French coastline to detect and act promptly when strandings occur (Dars et al., 2020). Stranding data could provide relevant information on mortality at sea, as well as on relative abundance, species richness and distribution of cetaceans (Peltier et al., 2012). Then, the NSN constitutes a long-term marine mammal monitoring program that provides appealing outlook for the use of strandings data into ecological indicators (Dars et al., 2020; Peltier et al., 2012).

Along with standardized monitoring protocols, the amount of opportunistic data is increasing in the French Mediterranean Sea. Some MPAs record observations that are shared by non-profesionnal on social networks. We also note the emergence of digital platforms for recording of ecological data, such as BioObs for observations made during scuba diving activities (https://bioobs.fr/) or the mobile application ObsenMer, which allows marine users (citizens, professionals) to record observations of marine megafauna during their excursions. Since 2015, ObsenMer has included more than 400 opportunistic detections of bottlenose dolphins in the French Mediterranean Sea, which constitutes a significant resource for bottlenose dolphin data. Besides, many sightings were recorded in the Gulf of Aigues-Mortes and in the Camargue area, where standardized monitoring programs are scarce. However, when including opportunistic data, it is crucial to take into account the methodological difficulties generated by the absence of explicitly measured sampling effort. Methods exist for estimating ecological indicators from opportunistic data by taking into account sampling biases ((Derville et al., 2018; Louvrier, 2018).
On a broader scale, using integrated models can be relevant for other species

in the French Mediterranean. During this thesis, we had discussions with the World Wildlife Fund (WWF) Mediterranean to use integrated models to estimate abundance and densities of fin whale (*Balaenoptera physalus*) in the French Mediterranean Sea. Data would include i) detections from SAMM aerial surveys, with ii) a capture-recapture dataset collected by WWF since the 2000s off the coast of Provence (WWF, 2020). The integrated spatial model would be equivalent to that developed in Section 6. The temporal extent of the capture-recapture dataset allows to extend to an open population model to estimate fin whale demographic parameters (Chandler et al., 2018). The use of integrated models could also be applied to other species for which the spatial coverage of current monitoring protocols is limited. This is the case for several seabird species that are sampled by SAMM aerial surveys, by boat transects (as in the Parc Naturel Marin du Golfe du Lion), and that are subject to ringing programs at nesting sites resulting in capture-recapture data (e.g., on Yelkouan shearwaters Puffinus yelkouan at the Port-Cros National Park, Bourgeois & Vidal (2008)). Seabirds are the target of several monitoring objectives in MPAs and at the national level in the DCSMM. Conservation issues about seabirds are currently important in the Mediterranean with the planning of offshore wind farms known to have impact on these populations (Furness et al., 2013). Combining datasets with the models developed in this thesis would make sense to refine ecological indicators on several seabird species.
Beyond the context of the Mediterranean Sea, many data collected on marine mammals worldwide come from photo-identification programs and line transects (Evans & Hammond, 2004). For example, in Scotland, recurrent photo-identification monitoring is performed on bottlenose dolphin populations, in parallel with the aerial surveys of SCANS campaigns (Cheney et al., 2013; Hammond et al., 2013). Scottish monitoring of bottlenose dolphin experiences a similar situation to the one studied in the French Mediterranean Sea. It is likely that the models presented in this thesis could turn out to be relevant to the study of several marine mammal populations already sampled via line-transects and photo-id protocols (Cheney et al., 2013; Pirotta et al., 2015).

At a time when ecological datasets are increasing, integrated models can be particularly relevant conservation tools for estimating ecological indicators, even outside the marine environments of course (Kéry & Royle, 2020; Zipkin et al., 2021). Thanks to recent technological advances, new types of observations have enriched the ecological databases. The emergence of new sampling techniques such as metabarcoding, bioacoustics, and remote sensing allow to obtain qualitative and quantitative ecological information in a non-invasive way (Lahoz-Monfort & Magrath, 2021; Tosa et al., 2021). The simultaneous contribution of advances in Next Generation Sequencing and bioinformatics have democratized these ecological monitoring techniques that can now be included into the planning of environmental studies (Tosa et al., 2021). Environmental DNA methods are being explored for marine mammal detection (Foote et al., 2012). These new technologies have an increasing influence in ecological monitoring programs, especially in conservation (Lahoz-Monfort & Magrath, 2021). The contribution of new sources of ecological data reinforces the relevance of integrated models to combine several complementary protocols during ecological studies.

7.2 Future ecological challenges and methodological developments

Refine the modeling of ecological processes

Statistical tools developed during this thesis provide a methodological basis for the estimation of ecological indicators through the combination of several datasets. However, we have not sufficiently detailed the influence of ecological variables. Our models used a single ecological variable, bathymetry. Incorporating other environmental covariates that influence bottlenose dolphin distribution and density would increase the part of explained variance, and hence precise the inference of the ecological process. To meet the requirements of policies guidelines or to inform MPA dashboard, one would require to produce additional modeling effort to better apprehend the latent ecological process when using the modeling tools developed in this thesis. Several environmental covariates need to be tested to specify the species' use of space, or to characterize the density of individuals. Fine-scale studies of bottlenose dolphin habitat highlighted the influence of distance from the coast, seabed slope, distance to the 100m isobath, surface water salinity (Cañadas et al., 2002; Ingram & Rogan, 2002; Marini et al., 2015). Using higher trophic level variables such as prey availability is not necessarily relevant to study bottlenose dolphin distribution because i) preys availability is only a proxy of the feeding behavior, ii) preys density estimations are often variable to high uncertainty (Torres et al., 2008), iii) bottlenose dolphins displayed a very generalist diet (Bearzi et al., 2009). Modeling habitat suitability of bottlenose dolphin is challenging given the ecological plasticity of the species and the difficulty of defining a marine habitat (Cribb et al., 2015). Nevertheless, the detailed study of environmental covariates at the scale of our study area would allow for more accurate ecological pattern when inferring bottlenose dolphin distribution and density indicators.

Inferring ecological dynamics through open population models

Modeling tools presented here fill the requirements of the DCSMM ecological indicators and those of the MPAs: abundance and distribution. Distribution and abundance allow us to infer the ecological patterns of a population, a snapshot at a given time, but do not give access to the mechanisms that govern ecological dynamics. From the successive estimation of abundance or distribution of a population over time, we can infer a trend, but we do not uncover the ecological processes that underlie population change. For example, what about survival rate of individuals or reproduction rate that affects temporal changes in population dynamics? When planning ecological monitoring, one question arises: do we need to have access to the ecological mechanisms? Identifying ecological mechanisms is of particular interest for management to determine threats and policy leverages to be mobilized to protect species. However, inferring ecological mechanisms requires datasets with long temporal extent, hence more expensive to obtain. To date, most ecological indicators have focused on "static" estimates, and detecting a population trend with certainty is already a methodological challenge when data are limited (Authier et al., 2020). When ecological data are abundant, we can extend integrated models developed in Sections 5 and 6 to explicitly infer the ecological mechanisms driving population dynamics. Dynamic occupancy models estimate local colonization and extinction rates when studying species distribution (Louvrier, 2018; MacKenzie, 2006). Based on the work by Richard Chandler and colleagues (Chandler et al., 2018), distance sampling and SCR data can be combined to estimate population dynamics and calculate individual reproduction and survival rates. Extension to dynamic models requires datasets with significant temporal coverage. For now, these datasets do not exist on bottlenose dolphins in the French Mediterranean Sea, but hopefully such developments will be possible in the future if the collection of standardized data by photo-id and aerial surveys continue as planned in the strategic documents (MIRACETI, 2019).

Exploring the impact of anthropic threats with multispecies models

Identifying threats to marine ecosystems and species is one of the objectives of the MSFD monitoring program. Interactions between marine species and human activities is real in the Mediterranean Sea, the busiest sea on Earth (Coll et al., 2012; Giakoumi et al., 2017). The coastal ecology of bottlenose dolphins and the depredation pressure they put on fishing stocks lead them to regular interactions with human recreational activities and fisheries (Bearzi et al., 2009; Leone et al., 2019; Queiros et al., 2018). Characterizing human-animal interactions is complex, but multispecies modeling tools permit the explicit inference of interaction probabilities and the estimation of the influence of each species on the other (Quéroué et al., 2021; Rota et al., 2016). Bottlenose dolphins are often observed in close proximity to fishing activities, and depredation or bycatch interactions raise conservation concerns (Lewison et al., 2004). Although depredation remains rare in the French Mediterranean Sea, we explored the relevance of a multispecies occupancy model to estimate the probability of spatial co-occurrence between trawlers and bottlenose dolphins in the Gulf of Lion (Appendix 1). We combined bottlenose dolphin and trawler data from SAMM aerial surveys and GDEGeM monitoring in the Gulf of Lion. Our approach is preliminary but we suggest that more advanced implementation of multispecies models could help to study the interactions between human activities and bottlenose dolphins in the French Mediterranean Sea. Overall, considering human activities into multispecies models is a promising perspective to identify and quantify the threats of anthropic pressures on the environment (Marescot et al., 2019).

Spatio-temporal optimization of ecological monitoring programs using adaptive monitoring

Most ecological monitoring programs performed in MPAs sometimes suffer from incompatibilities in terms of schedule and available staff to implement the protocols (see Section 4). In response, MPA managers start thinking about the temporal optimization of protocols. At what time step should the protocols be performed so that all the monitoring programs can be compatible with the working schedule of managers? An MPA agent states:

> *"We would like to look at the temporality of certain monitoring programs, such as for the European shag, we have 10% of the world population and we monitor it every year. To focus on the bottlenose dolphin, we will perhaps monitor the European shag only every 3 years."*

Coming from adaptive management theory, adaptive monitoring methods allow statistical optimization of monitoring protocols based on the iterative evaluation of collected data. The underlying idea is that all stages of ecological monitoring (definition of objectives, data collection, analyses, and protocol design) evolve together while maintaining the compatibility of previously collected data (Lindenmayer & Likens, 2009). Ecological monitoring protocols are adapted as new information is collected that reduces the uncertainties about ecosystem functioning, or as new monitoring questions or monitoring capacity emerge (Lindenmayer & Likens, 2009; Lyons et al., 2008; Runge et al., 2011). Thus, a central challenge in adaptive monitoring is to adapt monitoring protocols while maintaining compatibility among datasets. In Appendix

2, we illustrated the principles and functioning of adaptive monitoring through a simulation study, and we discuss its interest for ecological monitoring in MPAs. Moreover, because MPAs face financial constraints, tools that allow to make ecological monitoring more efficient could be of great interest for MPAs. One manager states:

> *"Often, management plans are very difficult to evaluate and evaluation tool must be designed. We have built indicators that allow us to evaluate the actions. We are somewhat obliged to take into account the optimization of monitoring. Depending on the teams available and the funding. we can't do all monitoring programs every year, we have to organize ourselves to deal with all protocols"*

The implementation of adaptive monitoring as a tool for planning ecological monitoring would be an important asset in terms of rationalizing costs, the schedules of MPA managers, and for the analysis of ecological data. However, the planning of ecological monitoring programs in the French Mediterranean MPAs using a global adaptive monitoring approach would require a level of coordination between institutions that is difficult to achieve given the current situation. To make the parallel with adaptive management, a critical analysis has pointed out the difficulties in overcoming the lack of political will to produce effective decision-making, and the administrative overload linked to the coordination of management and experimental monitoring protocols (Walters, 2007). Similarly, the implementation of adaptive management, human and political constraints are currently important in the conservation institutions of the French Mediterranean Sea, which are hampering the ambitions for the coordination of ecological monitoring.

7.3 Critical analysis of French policies to protect marine biodiversity

The lack of coordination and exchange within the French Mediterranean MPA network

The social science study in Section 4 highlighted structural problems in funding marine biodiversity policies in the French Mediterranean Sea. While the MPAs within a network should operate in a cooperative and synergistic way (Meehan et al., 2020), coordination is lacking in the French Mediterranean Sea. Networking is complicated and communication between the different MPAs is limited. However, the agents highly value the exchanges between MPAs to share experience, advice, or to discuss about different protocols. An agent from a Marine Natural Park explains:

> *"We don't have much discussion [between MPAs], it's a shame. Because we*

would save time. Even if it means spending one day or two to talk. I went to the Parc National des Calanques to train agents on police intervention techniques, and it was great. I came back with a lot of stuff. I had brought back a document that I gave on to the manager in charge of biodiversity monitoring. Otherwise, we would have had to create a lot of new protocols when they already exist somewhere else, and it's better to work in the same way. It is clear that these exchanges are not a waste of time."

The managers' schedules being already saturated, the self-organization of exchanges between MPAs is complicated. Organization and animation of the exchanges must be formally organized, which would be particularly expected to save time and to consult each other when setting up monitoring protocols. On the contrary, the amount of discussions between MPAs has been reduced since the recent institutional transformations that led to the transition from the AFB to the OFB at the beginning of 2020. The former Marine Protected Areas Agency (MPAA) has been dissolved and the different MPAs must now refer to regional agencies of the OFB that are concerned with both terrestrial and marine areas. The loss of the specificity of an organization dedicated to the management of MPAs has affected the coordination dynamics that existed around the marine environment and is generating misunderstandings. The dialogue between MPAs and regional biodiversity agencies, which are largely focused on the terrestrial environment, can be complicated because of the specific nature of marine laws.

"How can the OFB be consistent with itself? Knowing that at MPAA, everyone was under the same banner. At AFB, the Marine Natural Parks have already been separated from the department that was in charge of the MSFD. And now at the OFB, each Park, each Sea agency, is in a different department. The marine biodiversity actors are in 10 different administrative departments. So there will need a lot of internal work that all these people don't go in all directions."

MPA agents fear that the technical workshops of the Mediterranean coastline, or the inter-Marine Natural Parks seminars that brought together the different MPAs during exchange days will be suppressed with the new organization of the OFB. MPA managers try to organize communication and exchange informally via social networks but this is not steady, which probably reduces its effectiveness and impact. Furthermore, lack of coordination also affects the construction and the understanding of ecological indicators and monitoring protocols. Although the MSFD is supposed to be the cornerstone of marine management policies in France, it remains obscure to MPA agents.

> *"Following the 2018 assessment, PELAGIS presented the results a lot but to my knowledge it's not really organized. It's up to goodwill to communicate or not. And there may have been misunderstandings, the 2018 assessment returned for example almost nothing on marine mammals in the Mediterranean Sea, it is all gray. There is nothing to evaluate. Many actors in the Mediterranean Sea had data and may have been a little surprised by this result. It must be understood that the MSFD is a very structured process. Perhaps the Mediterranean stakeholders have not been sufficiently involved. But on other subjects it is even worse. Sometimes, there are assessments that have been done without taking into account other scientific work…"*

Another manager notes:

> *"The issue is that it's pretty much locked down by the Ministry, and it's a big machinery. It should be up to the Ministry to organize the return but there's no website, no communication. It's a huge system, and it's all done in a rush and nobody ever takes the time to explain to people what it is. If you're not involved in it, it's really opaque and it seems like nothing comes out of it when a lot of things are done. We're going to try to improve all of these in the 2nd cycle."*

Because of the lack of coordination, the MSFD may be perceived as ineffective by MPA workers. More broadly, it is the financial support for biodiversity policies that is not at required the level for the MSFD objectives. However, despite the limited budget, attempts are made, the TURSMED programs funded by OFB coordinate the monitoring of bottlenose dolphins by the MPA network (MIRACETI, 2019). However the objectives are limited, the centralization and the analysis of collected data are not funded, and, although extendable, the 3-year funding makes the operational structures financially unstable and reduces the capacity for long-term planning. Better coordination would be a path to follow to improve the situation, and OFB agents and MPA managers are unanimous in their support for such initiatives. On the one hand, the transmission of information and the animation of exchanges between MPAs should be improved. On the other hand, the technical coordination of protocols and analyzes is often pursued to minimize unnecessary financial and human efforts, and to increase the efficiency of ecological monitoring programs (Morán-Ordóñez et al., 2018). Due to a lack of financial resources, OFB struggles to fulfill its role of coordinator and leader of the MPA network.

International trends regarding the lack of political willingness

The structural lack of resources affects both the OFB and the MPAs. Financial constraints are a global trend toward weakening public services in France, with biodiversity policies not being exempted (Frajerman, 2019; Simonet, 2021). At the international scale, protected areas objectives have deleterious effects on the effectiveness of biodiversity protection when protected areas are paper parks that suffer insufficient allocation of financial and human resources (see Section 1.4). There are concerns about some governments that implement protected areas for communication purposes, or *"Just for show?"* (Magris & Pressey, 2018). What is the situation in France regarding the status of marine conservation policies and MPAs? Natura 2000 marine zones cover large areas, especially offshore, but no financial support is allocated and these areas do not have specific legislation. This is the case of the recent Natura 2000 created in 2018 for the bottlenose dolphin in the Gulf of Lion, which reaches a surface of 491,000 hectares (Figure 1). One manager explains:

> *"Marine conservation is not funded for Natura 2000. This is completely inconsistent because OFB is supposed to manage the Natura 2000 MPAs but they cannot because one person is in charge of 4 or 5 different areas"*

Similar to Natura 2000, the recent Marine Natural Parks contribute to achieve the MPA surface objectives in French waters but are underfunded and do not necessarily contain legislation (see Section 4), which is somewhat comparable to the criticisms formulated against the paper parks. A Marine Natural Park agent wonders:

> *"A WWF report showed that there is a large area in terms of percentage of MPAs. I believe that we are within the objectives [of the surface that has to be covered] but in the end, is it really protected? We are a marine natural park, so yes, we do ecological monitoring. But for the moment there is nothing more protected than Calvi where there is no marine park. So restrictive protections are good, they are needed. And we need a little more of these in the MPAs."*

Behind the communication effort (Figure 3), one may wonder about the willingness of the French government considering the insufficient resources allocated to biodiversity conservation. While the trends of underfunding are international, Western countries including the European Union implement a series of policies that align biodiversity conservation within a neoliberal framework of budget reduction and public disinvestment (Apostolopoulou et al., 2014). Neoliberalism is a term commonly used to describe the shift toward the shrinking of the government responsibility and the increasing role of civil society, markets, and market mechanisms in the delivery of services (Holmes, 2011). Increasingly apparent in conservation, neoliberal conservation

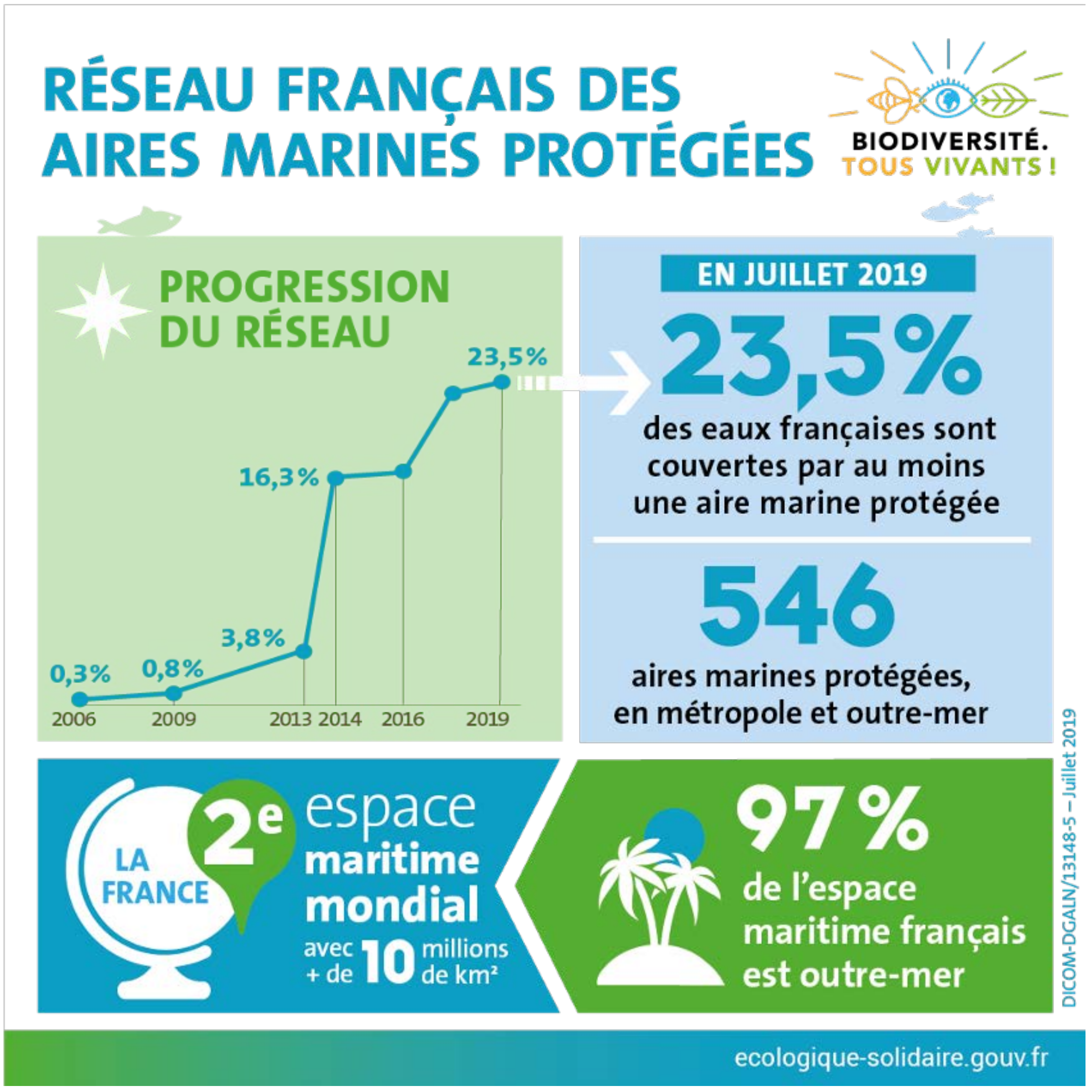


Figure 3: Infographic from the French Office of Biodiversity highlighting the progress of the French MPA network. Source : https://www.ecologie.gouv.fr/patrimoine-marin-et-aires-marines-protegees-francaises

is illustrated by the retreat of state from biodiversity decision-making (sometimes to the benefit of non-governmental organizations), the devolution of conservation management to local institutions, the increase in public-private partnerships for biodiversity management, along with a discourse of deliberative and consensus-based approaches (Igoe & Brockington, 2007). We observed some of these dynamics in marine biodiversity policies in France (see Section 4, Mazurek et al. (2019)). Social sciences and *"political ecology"* allow, among other things, to disentangle the different trends that drive biodiversity governance (Mathevet, 2013; Nuno et al., 2014). The discipline of political ecology sheds light on how biodiversity policies take place within the economic and socio-ecological context specific to the dominant production model [Mathevet (2013). Especially in the actual era of intensifying neoliberalism, I believe there is a greater need to expose the contradictions embedded in the relationship between biodiversity policies and neoliberalism (Apostolopoulou et al., 2014).

7.4 Feedback on collaborative and interdisciplinary research

We built this thesis around a double objective: first, to conduct a work in collaboration with the world of biodiversity management; second, to continue to train myself in social sciences. The alliance between ecology and social sciences for the study of biodiversity management practices quickly became the scientific framework of my thesis, which I wanted to be interdisciplinary.

The value of working collaboration with biodiversity managers

Collaborations between researchers and biodiversity managers are long-standing, due to the role of researchers in the creation of some protected areas and their implications in protected areas governance such as scientific councils (Arpin et al., 2019). Thus, several researchers developed applied research that makes them frequently collaborating with managers, whether they are ecologists, statisticians, sociologists, or geographers. On the one hand, skills complementarity and exchange of experience constitute the value of the collaboration, which makes it "productive". On the other hand, differences in goals and methods can be a potential obstacle to collaboration (Arpin et al., 2019). Collaborating comes at a cost and involves risks that may be unevenly distributed among participants, especially during a thesis when the investment is significant for the PhD student (Chassé et al., 2020). During my thesis, the collaboration with managers was clearly beneficial to the construction of the research project. From a methodological perspective, the adaptive monitoring models we considered initially would have had no application in the current context of French Mediterranean MPAs, in contrast to the integrated models for which several MPAs have already expressed interest. Early collaboration with MPA managers and OFB helped to propose relevant statistical tools, but also to highlight the challenges of coordinating ecological monitoring between MPAs and hence to motivate social sciences study.

Interdisciplinary thesis: a personal, scientific and critical enrichment

Doing an interdisciplinary thesis mobilizing social sciences in parallel with statistical ecology has been rewarding from a personal, scientific, and ethical perspective.

a) Personal asset There is a large gap between statisticians/ecologists' researchers and biodiversity managers. Both communities neither share neither the scientific culture and its rigor, nor the naturalist culture and its pragmatism (Besnard, 2013). Coming from statistical ecology and mobilizing social sciences into an interdisciplinary approach allowed me to partially bridge this gap. I started to understand marine conservation and MPA community. I discovered some of the tasks of protected area managers. I developed a better understanding of French marine conservation policies and their institutional context. Doing an interdisciplinary thesis can be complicated by unsuitable scientific environment and by the difficulties linked to the assimilation of the less mastered scientific methods, social sciences in my case (Chassé et al., 2020). During the thesis, I was lucky enough to benefit from a scientific context that was very favorable to the emergence of interdisciplinary approaches. I worked in an interdisciplinary research team at CEFE (HAIR team) with the complementarity of Nicolas Lescureux, ethnologist, to oversee the methods of semi-structured interviews, Aurélien Besnard, ecologist/statistician who collaborates very closely with protected areas managers and who contributed to some of the thoughts developed in this manuscript, and Olivier Gimenez whose skills in modeling, experiences of collaboration with the biodiversity managers, and awareness of the social sciences allow him to guide the development of statistical tools adapted to the needs of the managers while having a sharp view of the whole interdisciplinary project. The scientific framework is paramount for the emergence of interdisciplinary practices, emulation and for the dialogue between different disciplines.

b) Scientific asset Scholarly, the social science study illustrated the consequences and contradictions that affect biodiversity workers when collecting ecological data. Statistical ecology helped to develop an advance in the consideration of multiple datasets by providing tools adapted to conservation contexts. The thesis was interdisciplinary in the sense that we tried to bring together the scientific disciplines involved

(Létourneau, 2008). There was a transfer of results from the social sciences toward statistical ecology as the interviews helped to adapt the methodological developments. However, the outcomes of interdisciplinarity are not very apparent in the scholar productions of my thesis. The scientific papers of Sections 4, 5, 6 (and even those in Appendices 1 and 2) are mono-disciplinary, either in statistical ecology or in social sciences. Benefits of interdisciplinarity mainly push toward a better applicability of research to "the real world" (Chassé et al., 2020). I hope that my work will illustrate the value of the dialogue between social sciences and statistical ecology to produce ecologically effective and socially relevant conservation tools.

c) Ethical asset about the researcher's place in the public debate The multi-disciplinary nature of conservation sciences offers a global vision of biodiversity conservation linking the ecological processes to the socio-economic and political context. Engaging in a multi-disciplinary approach also allows the ecological researcher to step back from the scope of his or her study. The outreach of social sciences provides a wider view of the processes in place in conservation. Understanding the political and societal drivers is crucial in my opinion for two reasons. First, scientists can better target their research topics to maximize their ecological and societal utility. On the other hand, researchers are able to comment on or evaluate the decision-making process and the policies measures. Conservation is an oriented scientific discipline that incorporates explicitly subjective values (Robinson, 2006). Thus, conservation sciences blur the classical distinction between science and policy by integrating scientific practices into the policy process, as illustrated by the scientific advisory organization that assist public policy (e.g. IPBES, IPCC, scientific councils of protected areas). While ensuring the need to distinguish science and form environmentalist activism, conservation sciences must be recognized having a central place and a societal duty in the production of knowledge and in the evaluation of public policies. Crossing scientific disciplines provides a wide and sharp viewpoint of environmental issues that would enable conservation sciences to become increasingly involved in the scientific analysis of public policies (Robinson, 2006). In an era where scientific misinformation is reaching prominent societal topic in alarming proportions (e.g. misinformation about climate change, vaccination campaigns, or misuse of quantitative data political purposes, West & Bergstrom (2021)), the independence and democratization of public scientific research has never been more urgent to collectively and intellectually strengthen ourselves.

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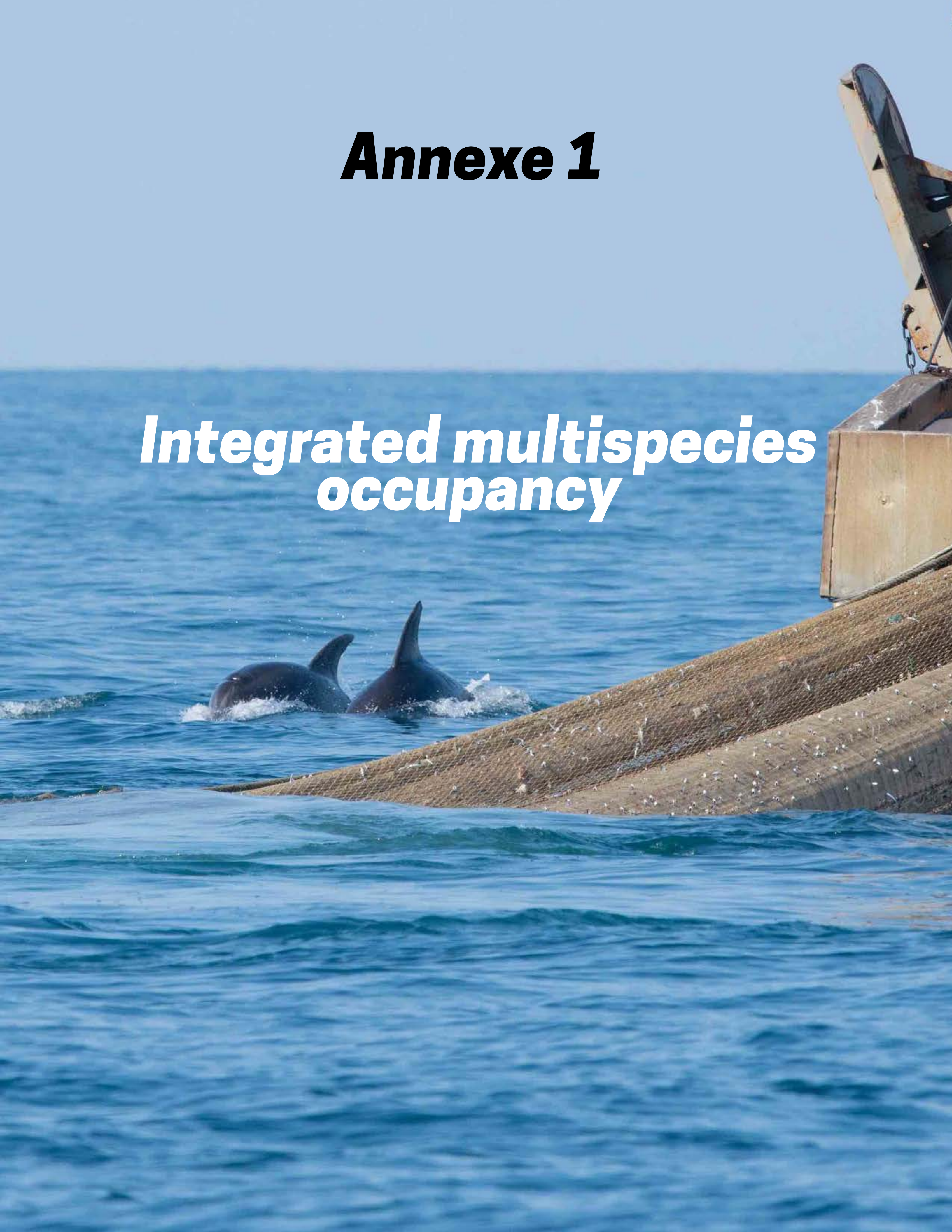
Annexe 1

Integrated multispecies occupancy



Quantifying co-occurrence between bottlenose dolphins and fisheries in the Gulf of Lion, French Mediterranean Sea with multispecies integrated occupancy models

Target journal: Short communication in Marine Ecological Progress Series

Valentin Lauret, Hélène Labach, Léa David, Matthieu Authier, Olivier Gimenez

Abstract

In the Mediterranean Sea, interactions between marine species and human activities are prevalent. The coastal ecology of bottlenose dolphins and the depredation pressure they put on fishing stocks lead them to regular interactions with fisheries. Mapping the risks of interactions is a preliminary step in managing anthropic pressures. However, quantifying interactions is hampered by the issue of false negatives whereby dolphins and trawlers may go undetected despite being present and co-occurring. Here, we develop an integrated multispecies occupancy model to quantify spatial co-occurrence between trawlers and bottlenose dolphins in the Gulf of Lion, French Mediterranean Sea. We combined bottlenose dolphin and trawler detections from both aerial surveys and boat surveys in the Gulf of Lion. Multispecies modeling opens promising avenues in the study of interactions between human activities and marine mammals.

Contents

1 Introduction

Identifying threats to marine ecosystems and species is one of the objectives of ecological monitoring programs (Lindenmayer & Likens (2010)). The Mediterranean, being the busiest sea on Earth, is especially affected by anthropic pressures (Coll et al. (2012), Giakoumi et al. (2017)).In particular, there are increasing interactions between marine species and human activities.

Among other species, the coastal ecology of bottlenose dolphins (*Tursiops truncatus*) and the depredation pressure they put on fishing stocks lead them to regular interactions with human recreational activities and fisheries (Queiros et al. (2018), Bearzi et al. (2009), Leone et al. (2019))). Bottlenose dolphins are often observed in close proximity to fishing activities, and depredation or bycatch interactions pose conservation concerns (Lewison et al. (2004)).

Mapping interactions is a preliminary step to better understand and manage human-animal interactions. This is usually achieved by calculating the overlap between a species distribution map and a map of human pressure. This approach raises two issues. First, when modelling species distribution, failure to account for interspecific interactions between co-occurring species may lead to biased inference, which arise when modelling only abiotic and habitat associations (Rota, Wikle, et al. (2016)). Second, another challenge when quantifying species interactions is to account for imperfect detection, e.g. when species do co-occur but one or several of the species involved go undetected by sampling (Rota, Ferreira, et al. (2016), Fidino et al. (2019)). Ignoring imperfect detection leads to underestimation of species distribution and imprecise quantification of species interactions (MacKenzie (2006)).

To account for these issues, multispecies occupancy models have been developed to estimate occupancy probabilities of two or more interacting species while accounting for imperfect detection (Rota, Wikle, et al. (2016)). One caveat of multispecies models is that they require substantial data to produce robust ecological inference(Clipp et al. (2021)). To overcome data scarcity, several authors have suggested to combine multiple datasets into an integrated modelling framework (see Kéry & Royle (2020) for a review). In that spirit, we previously developed a single-species integrated occupancy model to study common bottlenose dolphins (Lauret et al. (2021)).

Here, we extend this single-species integrated occupancy model to an integrated multispecies occupancy models to study interactions between common bottlenose dolphins and fisheries in the Gulf of Lion (French Mediterranean Sea). Our main objective was to provide a statistical framework for maping co-occurrence between fisheries and bottlenose dolphins. Our second objective was to test, based on field observations, the hypothesis that dolphins are likely to be more detected where fishing boats are active.

2 Material and Methods

2.1 Data

We combined bottlenose dolphin and fisheries data extracted from SAMM aerial surveys and from GDEGeM monitoring restricted to the Gulf of Lion (see Thesis manuscript Section 2.3).

We used GDEGeM data collected by EcoOcean Institut https://ecoocean-institut.or in the Gulf of Lion between 2013 and 2015. We extracted detections of common bottlenose dolphin (Tursiops truncatus), and that of trawlers which we considered as a proxy of fisheries. We used data on fishing trawlers only as we focused on fishing areas and not traveling routes between harbour and fishing areas. In parallel, we used detections of bottlenose dolphins and of fishing trawlers from the 2011-2012 SAMM project. We divided the study area into 397 contiguous grid-cells for the statistical analysis. Below, we provide a visualization of the study area, the detections, and the sampling effort for the two datasets (Figure 1).

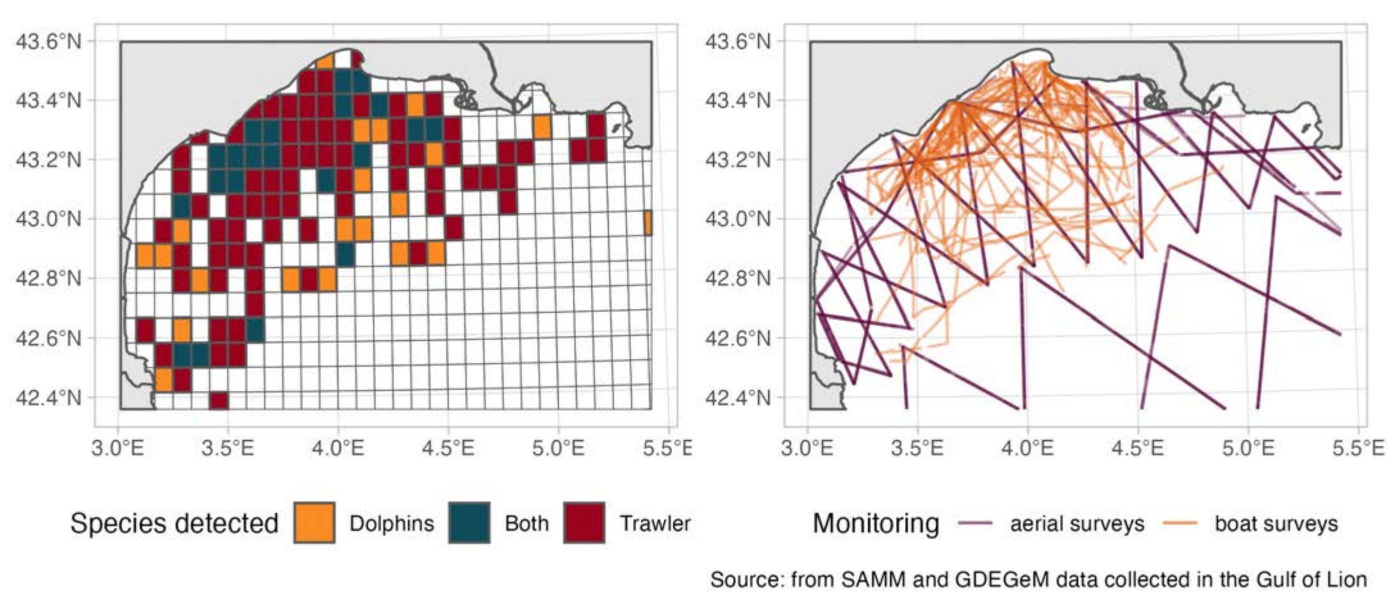


Figure 1: Gulf of Lion detections of bottlenose dolphins and trawlers by aerial surveys (SAMM) and boat surveys (GDEGeM) along with the sampling effort for each monitoring program.

To describe spatial variation in occupancy of bottlenose dolphins and trawlers, we used two environmental covariates:

- Bathymetry
- Sea Surface Temperature (SST) averaged monthly between 2011 and 2015

Below, Below, we represent the value of each covariate in space (Figure 2).

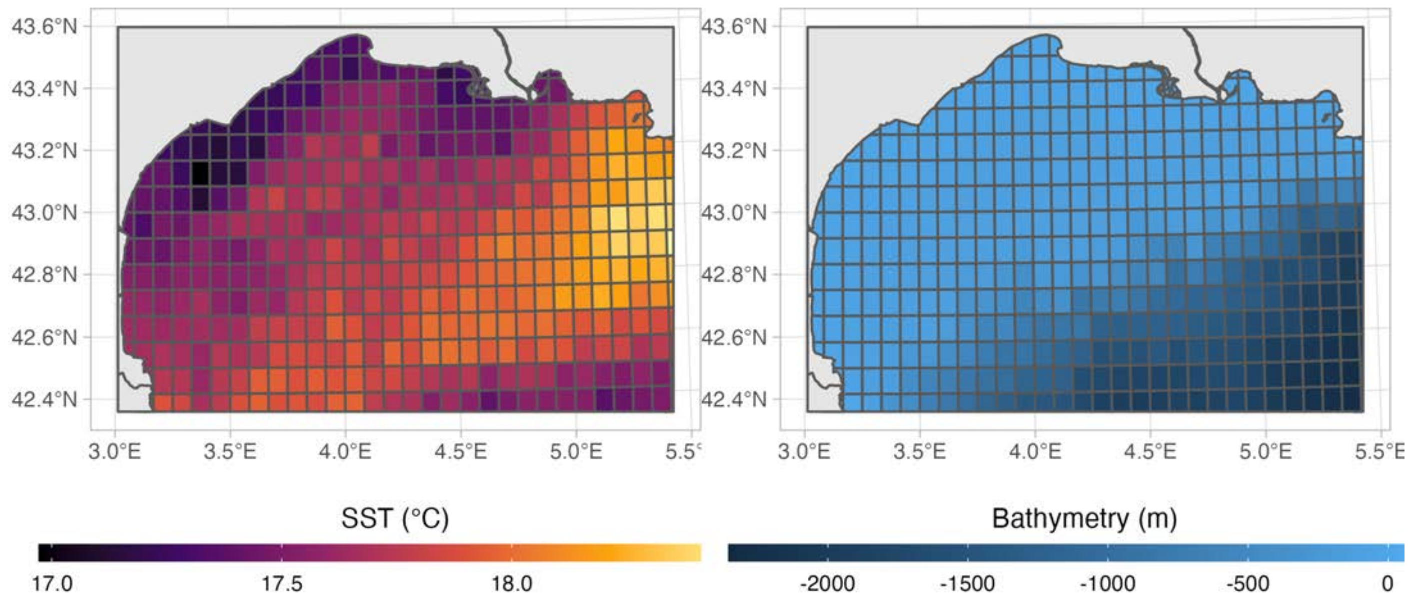


Figure 2: Spatial variation in bathymetry and Sea Surface Temperature (SST) over our study area

2.2 Multispecies occupancy

We consider a two-species static occupancy model à la Rota et al. (2016).

Ignoring the site index, we use the following notation for the occupancy probabilities:

- ψ_{11} is the prob. that species A and species B are both present;
- ψ_{10} is the prob. that species A is present and species B is absent;
- ψ_{01} is the prob. that species A is absent and species B is present;
- ψ_{00} is the prob. that species A and species B are both absent,

with $\psi_{11} + \psi_{10} + \psi_{01} + \psi_{00} = 1$.

The marginal probabilities of occupancy are:

- $\Pr(z_A = 1) = \Pr(\text{species A is present}) = \psi_{10} + \psi_{11}$
- $\Pr(z_B = 1) = \Pr(\text{species B is present}) = \psi_{01} + \psi_{11}$
- $\Pr(z_A = 0) = \Pr(\text{species A is absent}) = \psi_{01} + \psi_{00}$
- $\Pr(z_B = 0) = \Pr(\text{species B is absent}) = \psi_{10} + \psi_{00}$

And the conditional probabilities (reminder: $\Pr(\mathrm{A}|\mathrm{B}) = \Pr(\mathrm{A \text{ and } B}) / \Pr(\mathrm{B})$):

- $\Pr(z_A = 1 | z_B = 0) = \psi_{10}/(\psi_{10} + \psi_{00}) = \Pr(\text{species A is present given species B is absent})$;
- $\Pr(z_A = 1 | z_B = 1) = \psi_{11}/(\psi_{11} + \psi_{01}) = \Pr(\text{species A is present given species B is present})$;
- $\Pr(z_B = 1 | z_A = 0) = \psi_{01}/(\psi_{01} + \psi_{00}) = \Pr(\text{species B is present given species A is absent})$;
- $\Pr(z_B = 1 | z_A = 1) = \psi_{11}/(\psi_{11} + \psi_{10}) = \Pr(\text{species B is present given species A is present})$.

2.2.1 Dolphins detection probability conditional on trawlers presence

Our second objective was to test whether trawlers presence would affect dolphins detection probability. This hypothesis comes from at-sea observations. People performing at-sea monitoring of marine mammals in our study area reported that dolphins were often detected following fishing trawlers. In statistical terms, this could be translated in dolphins detection would be higher at grid-cells where trawlers are present. To formally assess the relationship between trawlers presence and dolphins detection in the multispecies occupancy model, we proceed as follows. While detection probabilities for both dolphins and fishing boats depend on the sampling effort (sites and occasions), we built another multispecies occupancy model in which dolphin detection probability was a function of presence or absence of fishing boats. To do so, we used the formulation in Waddle et al. (2010):

$$\text{logit}(\Pr(\text{dolphin is detected}|\text{dolphin is present})) = \beta_1 z_{\text{fishing boats}} + \beta_2(1 - z_{\text{fishing boats}}) + \beta_3 \text{sampling effort}$$

where the β's are unknown regression parameters to be estimated, with β_1 capturing the effect of the presence of boats, and β_2 their absence. We provide the results of this test in the Supplementary results (see Figure 8).

2.3 Integrated mutlispecies occupancy model

Here, we extend the multi-species occupancy model of Rota, Ferreira, et al. (2016) to integrate two datasets in the spirit of Lauret et al. (2021). We consider dataset S (e.g SAMM aerial line transects), and dataset G (e.g. GDEGeM boat search-encounter program). Both monitoring collected detection / non-detection about species A (i.e. bottlenose dolphin) and B (i.e. trawlers). Then, each species has a different detection probability depending on the monitoring program considered. For example, p_A^G is the probability of detecting species A by monitoring program 'g'. Then, 16 observation 'events' can occur. We coded them as follow:

- `1` for none species detected neither by G nor S
- `2` for species A detected by G, nothing by S
- `3` for species B detected by G, nothing by S
- `4` for both species detected by G, nothing by S
- `5` for none species detected neither by G, species A detected by S
- `6` for species A detected by G, species A detected by S
- `7` for species B detected by G, species A detected by S
- `8` for both species detected by G, species A detected by S
- `9` for none species detected neither by G, species B detected by S
- `10` for species A detected by G, species B detected by S
- `11` for species B detected by G, species B detected by S
- `12` for both species detected by G, species B detected by S
- `13` for none species detected neither by G, both species detected by S
- `14` for species A detected by G, both species detected by S
- `15` for species B detected by G, both species detected by S
- `16` for both species detected by G, both species detected by S

From the 4 ecological states (in rows) and the 16 observation events (in columns), we get the observation process with the following (transposed) 4x16 matrix.

$$t(\theta) = \begin{bmatrix}
1 & (1-p_A^G)(1-p_A^S) & (1-p_B^G)(1-p_B^S) & (1-p_B^G)(1-p_B^S)(1-p_A^S)(1-p_A^G) \\
0 & p_A^G(1-p_A^S) & 0 & (1-p_B^S)(1-p_A^S)p_A^G(1-p_B^G) \\
0 & 0 & p_B^G(1-p_B^S) & (1-p_B^S)(1-p_A^S)p_B^G(1-p_A^G) \\
0 & 0 & 0 & (1-p_B^S)(1-p_A^S)p_A^G p_B^G \\
0 & p_A^S(1-p_A^G) & 0 & p_A^S(1-p_B^S)(1-p_A^G)(1-p_B^G) \\
0 & p_A^G p_A^S & 0 & p_A^S(1-p_B^S)p_A^G(1-p_B^G) \\
0 & 0 & 0 & p_A^S(1-p_B^S)p_B^G(1-p_A^G) \\
0 & 0 & 0 & p_A^S(1-p_B^S)p_A^G p_B^G \\
0 & 0 & 0 & p_B^S(1-p_A^S)(1-p_A^G)(1-p_B^G) \\
0 & 0 & p_B^G p_B^S & p_B^S(1-p_A^S)p_A^G(1-p_B^G) \\
0 & 0 & 0 & p_B^S(1-p_A^S)p_B^G(1-p_A^G) \\
0 & 0 & 0 & p_B^S(1-p_A^S)p_B^G p_A^G \\
0 & 0 & 0 & p_A^S p_B^S(1-p_B^G)(1-p_A^G) \\
0 & 0 & 0 & p_A^S p_B^S p_A^G(1-p_B^G) \\
0 & 0 & 0 & p_A^S p_B^S p_B^G(1-p_A^G) \\
0 & 0 & 0 & p_B^G p_B^S p_A^G p_A^S
\end{bmatrix}$$

We estimated 4 occupancy probabilities for each cell of the study area :

- the prob. that only bottlenose dolphins use the cell, `psi1`

- the prob. that only trawlers use the cell, `psi2`
- the prob. that both dolphins and trawlers use the cell, `psi3`
- the prob. that neither dolphins nor trawlers use the cell, which correspond to the probability that none of the previous events occur, `psi0`.

Probabilities `psi1`, `psi2`, and `psi3` are modelled as logistic functions of environmental covariates (bathymetry and SST) as in:

$$logit(\psi) = \theta_0 + \theta_1 Bathymetry + \theta_2 SST$$

Data and code may be found on GitHub at https://github.com/oliviergimenez/human-tursiops-twospeciesoccupancy.

To address our two objectives, first we estimated the relationship between occupancy and environmental covariates (bathymetry and SST). We displayed on a map an estimate of `psi3` the probability of having both species using a cell. Second, to get a better understanding of the observation process, we estimated detection probability of trawlers and dolphins which we made monitoring program-specific and a function of sampling effort.

3 Results

3.1 The latent ecological process

We found that the probability of having neither species was independent of bathymetry, while co-occurrence increased with decreasing depth (Figure 3). Dolphins and trawlers displayed an important overlap in their occupancy according to these simple results (Figure 3).

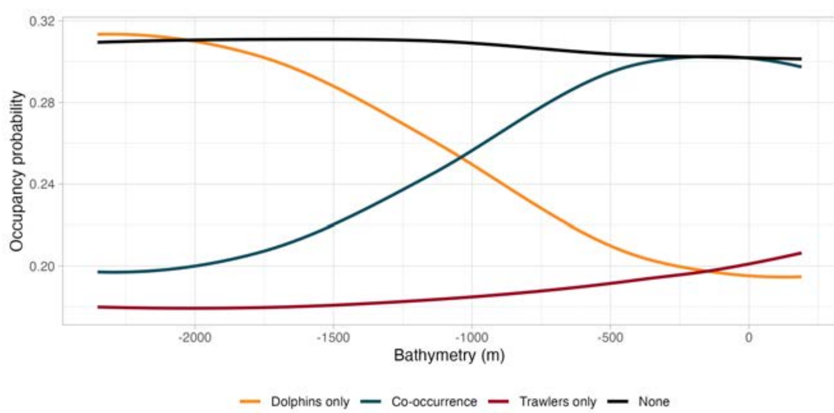


Figure 3: Occupancy probabilities estimated from the integrated multispecies model as function of bathymetry. For better readibility, we do not represent credible intervals here, but see Figure 4

This latter pattern is confirmed in Figure 4, which shows that co-occurrence probability is mainly driven by bathymetry.

3.2 Probability of detecting dolphins and trawlers

Both dolphins and trawlers detection probabilities increased when sampling effort increased. Boat surveys had higher detection probabilities than aerial surveys (Figure 5).

4 Discussion

We predicted a high co-occurrence probability throughout our study area (Figure 4). The Gulf of Lion waters are of critical importance for French fisheries and for bottlenose dolphins. However, fishing pressure is not homogeneous over the study area, a pattern that did not transpire in our data. Despite combining two datasets, we still miss data to produce precise estimates of trawlers occupancy. Including more data about trawlers would be valuable to better delineate fishing areas and hence better estimates of co-occurrence probability. Our results also underline that bathymetry drives co-occurrence but it is likely that more environmental variables contributed to spatial variation in occupancy (e.g. prey availability, distance to coast, salinity). A more detailed analysis of the ecological process would allow to better investigate potential interactions.

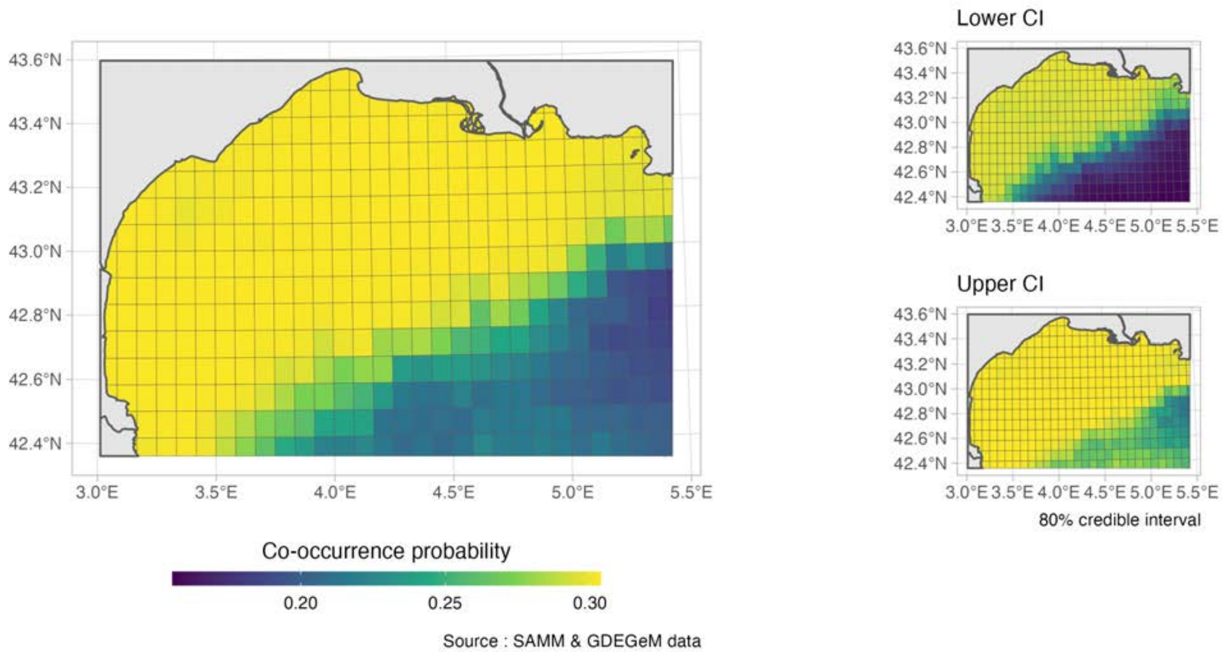


Figure 4: Co-occcurence probability between dolphins and trawlers. Left panel shows estimated probability and right panels display lower and upper bounds of 80% credible intervals.

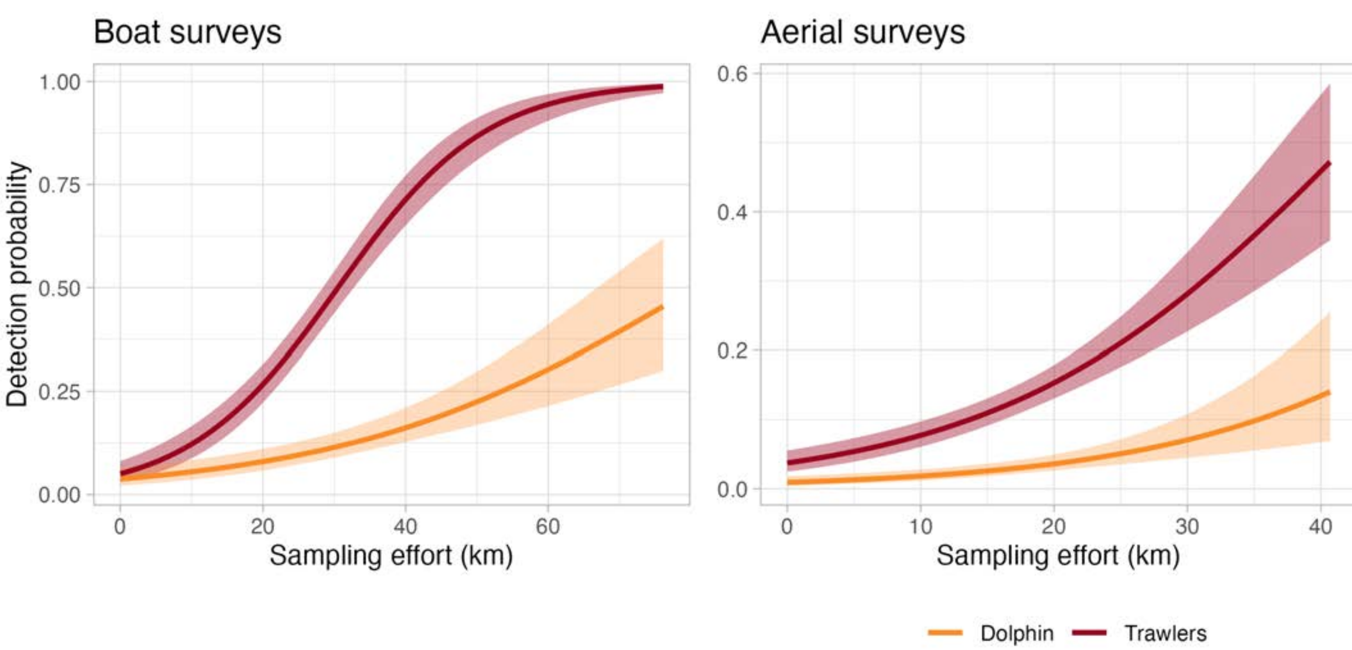


Figure 5: Estimated detection probability of dolphins and trawlers as function of sampling effort of each monitoring program. We provide posterior medians (solid line) and 80% credible intervals.

Several assumptions need to be valid to safely apply multispecies occupancy models (similar assumptions to those of the single-species occupancy) : i) geographic and demographic closure, ii) independence of the detections over space and time, iii) accurate identification (i.e. no misidentification). In our case study, dolphins and trawlers obviously moved in and out grid-cells during the sampling period making the geographic closure unlikely to be respected. Thus, we are interpreting the occupancy as "space-use", that is the probability that the species uses the grid-cell given it is present in the study area, hence reflecting the usage a species makes of the different components of the study area.

Overall, our results suggest that an integrated multispecies occupancy modelling approach could contribute in the study of the interactions between human activities and bottlenose dolphins in the French Mediterranean. Our approach echoes recent work integrating human activities into multispecies models to identify and quantify threats of anthropic pressures on the environment (Marescot et al. (2019)).

5 Supplementary results

First, we display in Figure 6 and Table 1 estimates of the regression parameters θ's for probabilities `psi1`, `psi2`, and `psi3`.

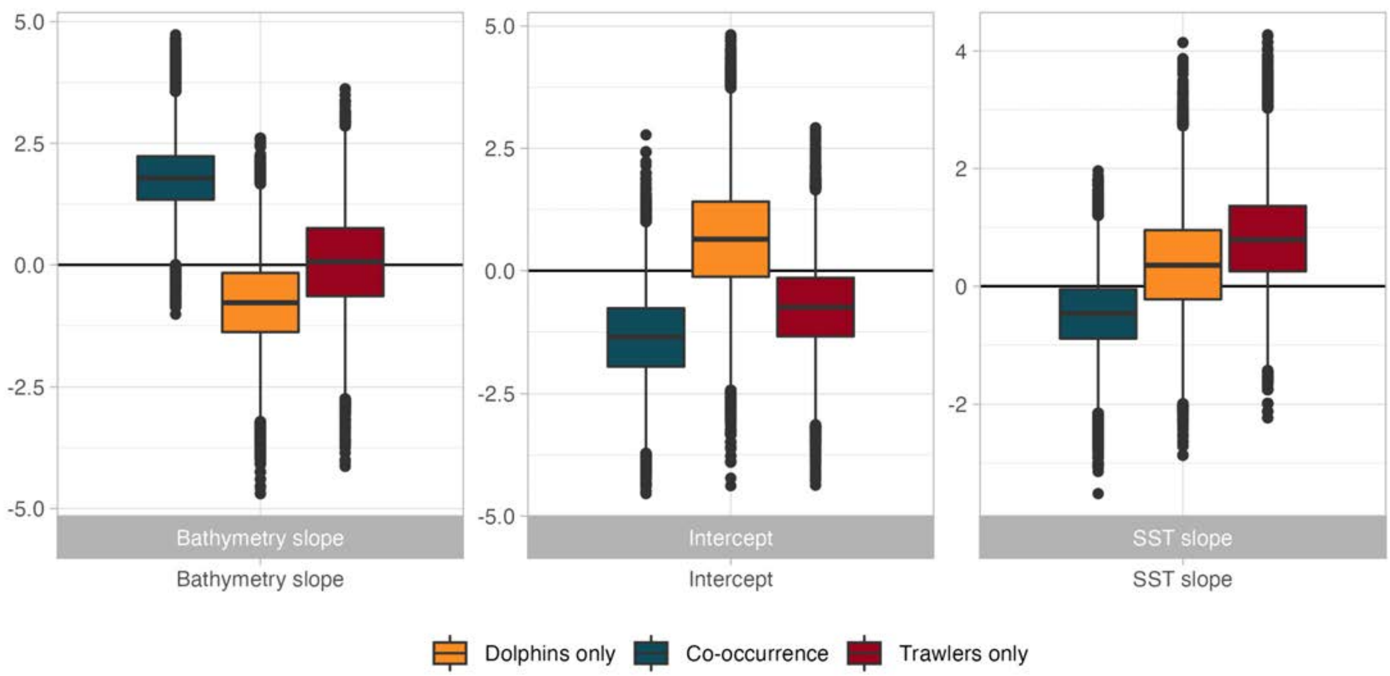


Figure 6: Parameters of the logistic regression relationships for occupancy probabilities for the integrated multispecies occupancy model between dolphins and trawlers.

Table 1: Values represent the mean estimates and its 80% associated credible intervals.

Parameter	Dolphins only ψ_1	Trawlers only ψ_2	Coocurrence ψ_3
Intercept θ_0	0.633 (-0.83; 2.10)	- 0.74 (-1.90; 0.40)	- 1.35 (-2.46; -0.23)
Bathymetry effect θ_1	- 0.77 (-1.95; 0.41)	0.06 (-1.27; 1.39)	1.79 (0.94; 2.65)
SST effect θ_2	0.37 (-0.72; 1.475)	0.82 (-0.22; 1.89)	- 0.48 (-1.30; 0.30)

Second, to look at the occupancy probability of dolphin (or trawlers), we used `psi1 + psi3` (or `psi2 + psi3`). In Figure 7, the maps reflect the influence of bathymetry on dolphins and trawlers occupancy.

Finally, we provide in Figure 8 the detection probabilities of dolphins and trawlers obtained from the integrated multispecies occupancy model with the Waddle et al. (2010) parametrization to test for a dependence between dolphins detection and trawlers presence. With the conditional parametrization of the observation process, the ecological process is the same as displayed in the Results section (Figure 3 & Figure 4).

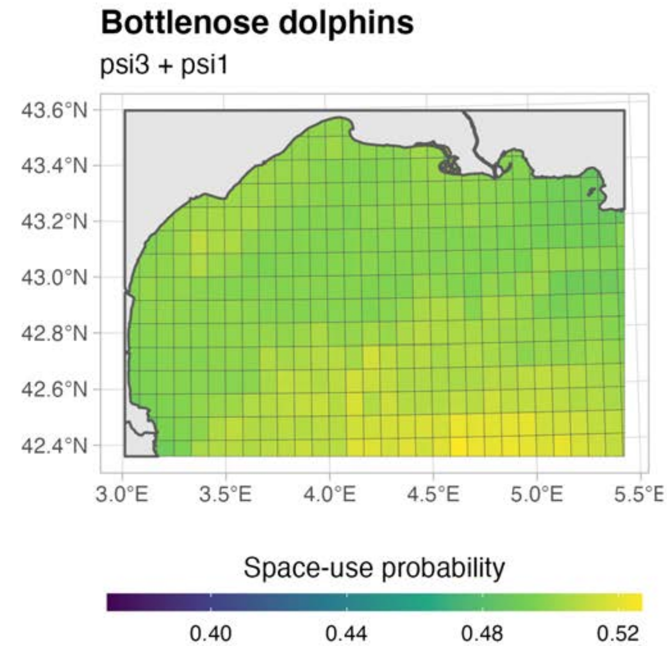


Figure 7: Occupancy probability of dolphins and trawlers estimated from the integrated multispecies occupancy model

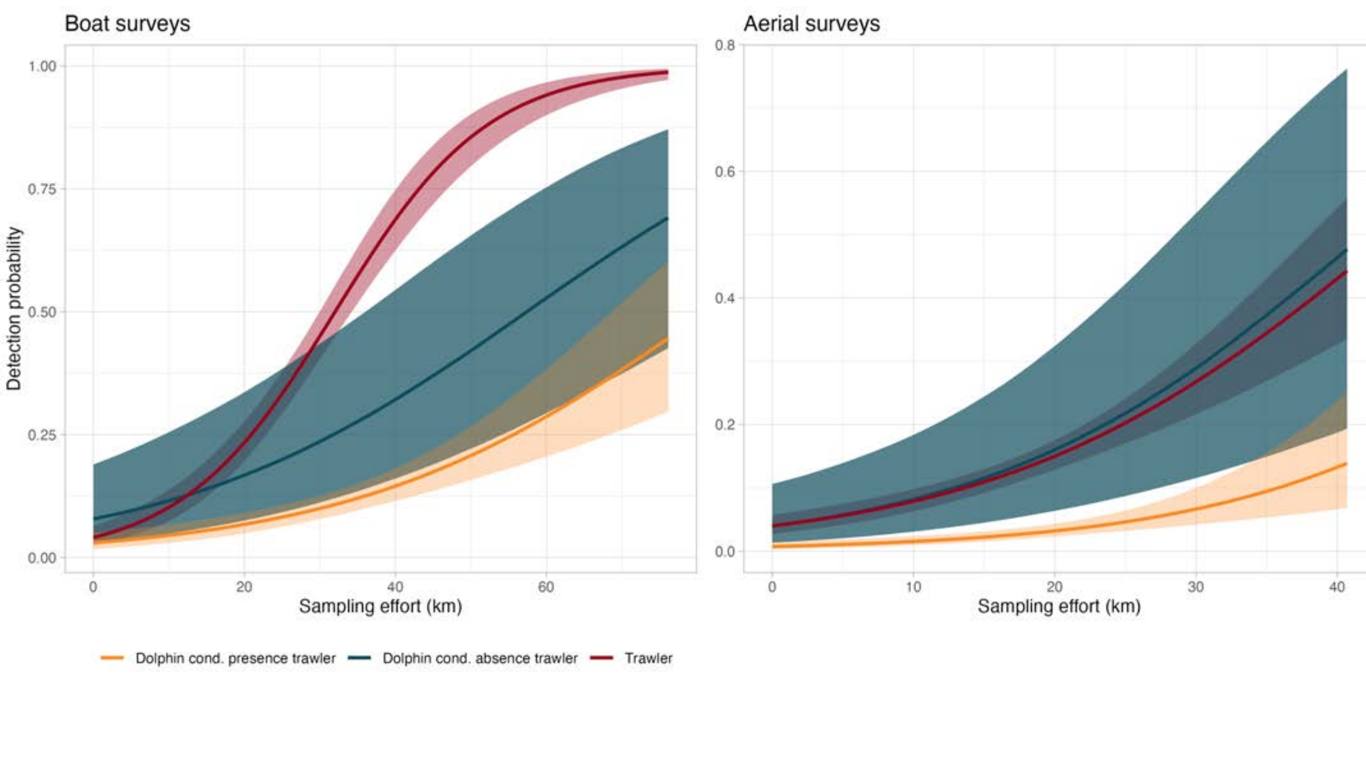


Figure 8: Estimated detection probability of dolphins and trawlers as function of sampling effort for each monitoring program in the case where dolphins detection is conditional on trawlers presence or absence. We provided posterior medians (solid line) and 80% credible intervals.

Our results showed no effect of trawlers presence on dolphins detection. We see several reasons for this result. First, detections of dolphins remain scarce despite trawlers and dolphins being predicted to occur widely throughout the study area (Figure 7). Indeed, there are many grid-cells where $z_{trawlers} = 1$, $z_{dolphins} = 1$ and $y_{dolphins} = 0$, hence negatively driving dolphins detection probability conditional on trawlers presence. Second, we had insufficient data to correctly specify the link between dolphins detections and trawlers presence (see Discussion section).

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Annexe 2

Exploring adaptive monitoring

Towards adaptive monitoring in protected areas, a toolkit.

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Abstract: Ecological monitoring programs are needed to inform biodiversity management. However, in a conservation context, efficient monitoring is challenging due to ecological uncertainties and economic constraints. Here, we showcase adaptive monitoring (AM), a conceptual framework that aims to identify an optimal monitoring strategy conditional on the predicted state of the system, with predictions based on previous monitoring inputs. We describe the key steps of AM and use simulations to illustrate the implementation of AM targeting a species of interest in a conservation context. To be successful, AM requires co-construction between stakeholders, biologists, and modelers to define the objectives and quantify the costs and benefits of monitoring actions.

Introduction

Cost- and time-effective monitoring programs are urgently needed to inform decision-making about biodiversity management (Aylesworth et al., 2017; Fraschetti et al., 2002; McCauley et al., 2015). Monitoring programs will be most useful if developed with full consideration of the ecological uncertainties and for how the resulting information will be used. Therefore, careful thinking about the expected return on investment for monitoring efforts is especially important, where return on investment can be measured in terms of the management objectives, thereby focusing the role of monitoring on addressing the needs of managers (Gibbs et al., 1999; Lindenmayer & Likens, 2010; Nichols & Williams, 2006; Runge et al., 2011). Monitoring is critical for evaluating the efficacy of management (Fulton et al., 2015; Gibbs et al., 1999) and for improving the identification of optimal policies (Baxter & Possingham, 2011; Williams et al., 2018). Monitoring for conservation in a protected area is typically performed in a cost-constrained environment with limited funding and human resources. Furthermore, it is common for a monitoring objective to be multi-faceted, i.e., to have several objectives in a single monitoring plan.

In real-world ecological monitoring, many species of interest are elusive, and data can be costly to obtain (Authier et al., 2017; Aylesworth et al., 2017; NRC, 2001). To be effective, monitoring needs to be flexible enough to adapt to changes in the ecological system being monitored, and to changes in management objectives and monitoring abilities (Authier et al., 2017; Heylen, 2017; Williams, 2011). For example, it is not uncommon for funding availability to change over time. In this context, several studies have promoted a framework in which monitoring adapts in response to the dynamics of ecosystems and to socio-economic changes (Lindenmayer & Likens, 2009; Nichols & Williams, 2006). The notion of adaptive monitoring (AM) is increasingly used in wildlife management to optimize the design of monitoring efforts (Lindenmayer et al., 2011; Lindenmayer & Likens, 2009, 2010). The underlying idea is that all steps of the monitoring approach (e.g., objective setting, data collection, data analyses, and statistical design of surveys) evolve jointly without threatening the usefulness of previously collected data. Monitoring is adapted as newly collected information reduces uncertainties about ecosystem functioning, or when new questions or monitoring conditions emerge (Baxter & Possingham, 2011; Costello et al., 2010; Lyons et al., 2008). A main challenge is to adapt monitoring while maintaining the overall value of the data series.

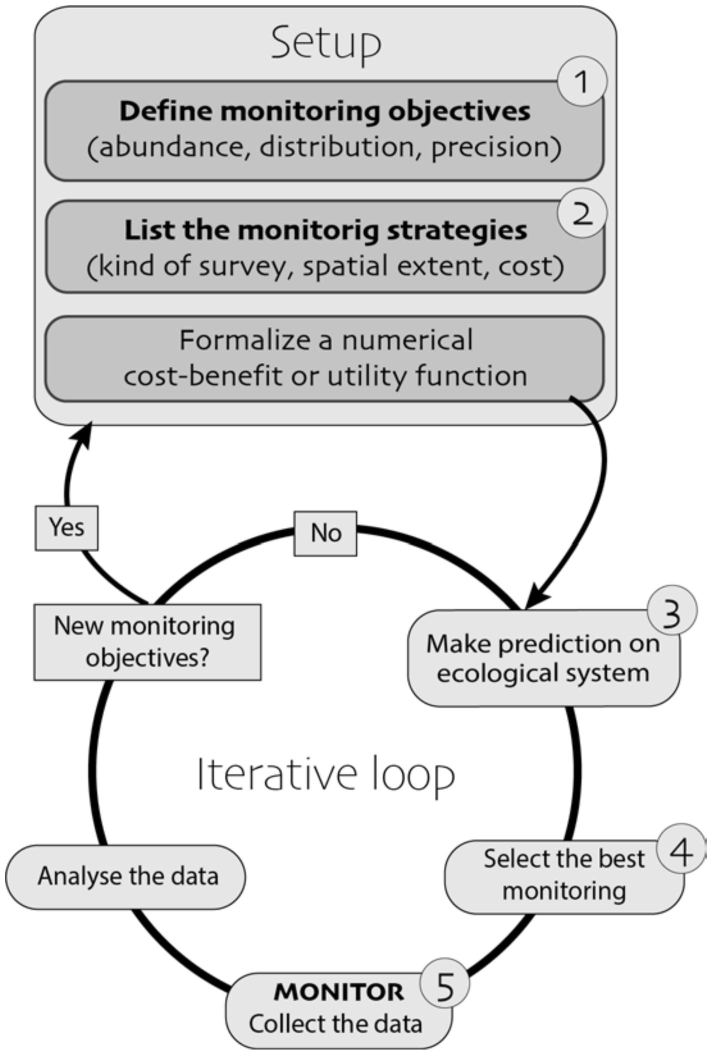

Figure 1: Adaptive monitoring schematic. We distinguish a set-up phase that includes 1) defining the monitoring objectives explicitly, as well as 2) the sampling protocols and spatial and temporal limits of the study. Both are combined in a numerical function called ‘utility’. Then, the adaptive loop runs iteratively. At each time step, 3) we model the ecological system according to the available knowledge, 4) we perform simulations of monitoring strategies and select the most relevant one according to our objectives. Then, 5) monitoring is carried out and data are collected. Finally, we analyze the new data and select the monitoring strategy for the next time step.

The management of protected areas is economically costly and the structure and functioning of wildlife populations remain the source of many uncertainties (McIntosh et al., 2018). AM has the potential to lead to substantial management benefits in protected areas systems (Fulton et al., 2015; McIntosh et al., 2018). AM has been effective in broad-scale monitoring of terrestrial ecosystems (Lindenmayer et al., 2011; Ringold et al., 1996), and for rare plant species (Pacifici et al., 2016), terrestrial wildlife (Gibbs et al., 1999), and partially terrestrial marine species (McIntosh et al., 2018; Williams et al., 2018).

To our knowledge, there has been no attempt to formalize the implementation of AM through precise example, and ecological monitoring programs have sometimes been characterized as AM only post hoc. Likely explanations for the dearth of fully conceptualized AM programs is that these programs are more technically challenging to implement than non-adaptive monitoring, because of a lack of familiarity with AM in the management community, and because monitoring itself is sometimes treated as an afterthought rather than as a key part of management. Here, we showcase the implementation of AM to assist protected area management with marine realms in mind.

As a potential candidate for AM implementation, the EU Marine Strategy Framework Directive (MSFD 2008/56/EC) requires that all EU member states reach a 'good environmental status' in their marine waters by 2020, and further mandates ongoing assessment of the status of these waters (Authier et al., 2017; Baudrier et al., 2018; Marine Strategy Framework Directive, 2008). In this context, marine monitoring programs of the MSFD are being developed across European seas to inform and guide marine management strategies (Baudrier et al., 2018; Lehtiniemi et al., 2015; Van Hoey et al., 2010). The functioning of MSFD is based on iterative cycles every 6 years, and aims to reevaluate the monitoring and management practices based on information collected during previous cycles.

Methods

We used a virtual ecologist approach to illustrate AM and evaluate its performance. This approach is increasingly used in the ecological literature to assess the performance of sampling designs and modeling tools (Zurell et al., 2010). We simulated a species occurring in a restricted area – the ecological system – and mimicked the detection of this species through monitoring

– the observation process. Then, based on these simulated ecological data, we evaluated the performance of different monitoring strategies (Zurell et al., 2010). Adopting a virtual ecologist approach through simulations allows the analyst to have perfect knowledge about the fictive species and hence to draw solid conclusions about the effectiveness of sampling and modelling methods (Zurell et al., 2010).

We illustrate an AM approach built following a structured decision-making process (Gregory et al., 2013; Martin et al., 2009). We distinguished a setup phase, and an iterative loop (Figure 1). During the setup phase, 1) we formulated monitoring objectives and defined the time horizon within which the monitoring is performed, and 2) we listed the components of the monitoring strategies that could be used to reach the objectives: where to monitor, which monitoring methods (aerial survey, boat survey, etc), and what sampling effort (frequency, labor forces, working hours). Then, the iterative phase runs through successive time steps. At each time t: 3) we analyzed ecological data with statistical models, 4) we selected the monitoring strategy that best fits with the predicted species status at time t+1, then 5) we implemented the selected monitoring strategy and collected the data.

Below, we introduce the AM framework in more details. We consider a fictive area of 400 contiguous sites within which the target species occurs. Spatial habitat heterogeneity in the study area is implemented through a continuous site-specific covariate that varies over fictive unit ‘m’ over a range of 0 to 2000 m across the study area; this is a simplification of what is often a more complex relationship between species presence and multiple environmental covariates for purposes of illustration. We assumed a quadratic relationship between the covariate and species presence – with maximum occupancy at intermediate values of the covariate around 1000 m – but we allowed the parameters of the quadratic relationship to change over the course of the monitoring period (thus changing the value of the covariate at which occupancy probability is maximized, simulating a dynamic ecological system). Once this underlying system model was in place, we simulated a presence-absence dataset with an optimum of presence around 1000m over 3 seasons. Then, to get the idea that adaptive monitoring can deal with changing ecological conditions, we changed the relationship between the covariate and occupancy probability adjusting the optimum of species occurrence around 1500 m from season 3 to season 5. We displayed the two ecological preferences of the fictive species in Figure 2. This 5-season presence-absence dataset is the ‘true’ ecological data upon which AM strategies are to be determined.

Step 1: Defining the monitoring objective

Here, we showcase monitoring objectives that we believe to be relevant and common when monitoring in protected areas. Defining monitoring objectives should be the result of a consultative process involving multiple stakeholders, managers, statisticians. The monitoring objective in our fictive protected area is to maximize the precision of the estimated species distribution. We also assume that monitoring resources are fixed, such that no more than 100 sites can be monitored at each sampling occasion.

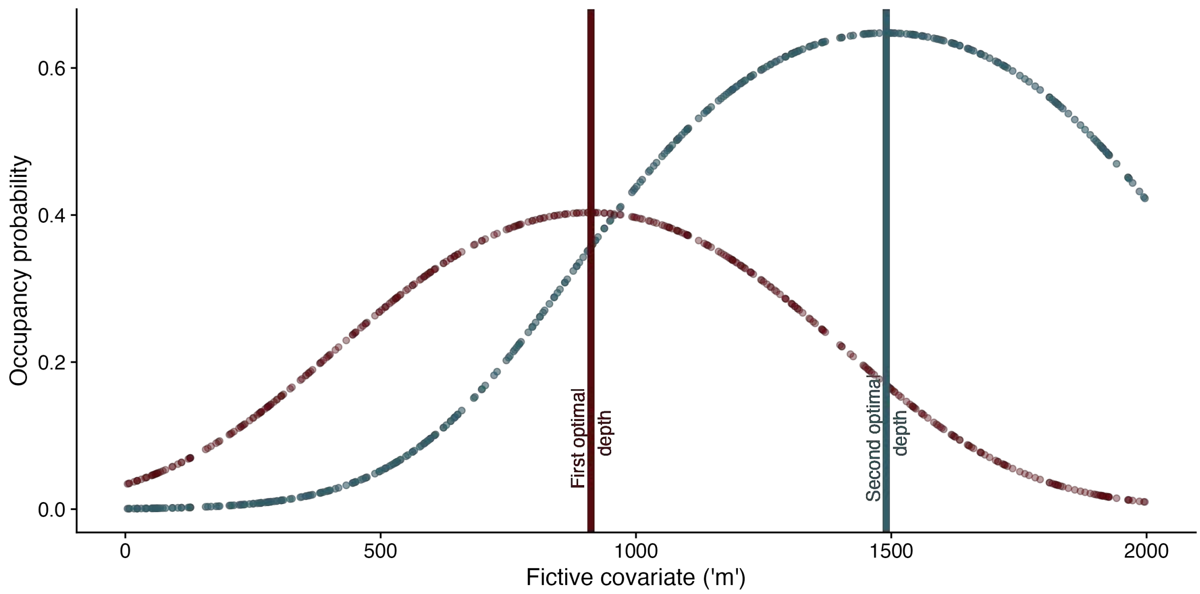

Figure 2: Two sets of quadratic relationship between occupancy probability and a fictive covariate (‘m’) simulated in 400 sites. The first set of occupancy probabilities is simulated according to an optimum of 100m, the second set with an optimum of 1500 m.

Step 2: Defining the monitoring strategies

To meet the monitoring objective, managers can survey 100 of the 400 sites in the study area at each survey. At the beginning of each monitoring season, managers decide which sites they will monitor that season. Chosen sites will be sampled 3 times during the sampling season to mimic the repeated visits needed when monitoring for occupancy modelling. Over the 100 sites to be monitored, managers chose to monitor 50 sites where the species is most likely to occur, and 50 sites randomly. After each monitoring season made of 3 sampling per site, data will be analyzed, species distribution predicted, and sampling effort re-allocated following the same rule but according to the new prediction of species distribution.

Step 3: Modeling the ecological system

We modeled the ecological system with a dynamic species distribution model in which each site can be either occupied or unoccupied by the species. Accounting for imperfect detection while estimating species distribution, which is especially relevant for monitoring elusive species (Issaris et al., 2012; MacKenzie et al., 2003), can be accomplished with occupancy models (Mackenzie et al., 2002). The occupancy status of each site (i.e., occupied or unoccupied by the species) changes between seasons through local colonization and extinction events. We estimated model parameters – the proportion of sites occupied and the probabilities of colonization and extinction – using the R package ‘unmarked’ (Fiske & Chandler, 2011). We fitted occupancy models considering 3 possible ecological relationships between occupancy and the environmental covariate, i.e., a null model, a linear model, and a quadratic model. We compared the occupancy models using the Akaike Information Criterion - AIC (Akaike, 1998). We model-averaged the estimated occupancy parameters across the 3 occupancy models and used these to predict species distribution.

Step 4: Decision-making: selecting the monitoring strategy

After each monitoring season, we added the last 3 sampling occasions to the dataset from the previous sampling season. We analyzed this new dataset with the modeling process described in Step 3 and used the prediction to choose the monitoring strategy to apply during the subsequent season. To select the monitoring strategy for next season, we identified the sites in which the species was most likely to occur and allocated 50% of the sampling effort to these sites and the remaining 50% randomly.

Run the monitoring and evaluate monitoring strategy

We illustrated the AM process based on 5 seasons of true ecological data, which correspond to 5 monitoring seasons with 3 sampling occasions per season. As detailed above, during the three first monitoring seasons, the preferred ecological condition of the species is around 1000 m, while for the monitoring seasons 4 and 5 the preferred ecological condition is around 1500m (Figure 2). To assess the precision of the predicted occupancy, which is the monitoring objective defined in Step 1, we estimated the Root Mean Square Error (RMSE) and the Relative Bias (RB) of the predicted occupancy probability versus the true occupancy.

We assumed that between seasons 1 and 3, the species is known to have an ecological preference for 1000 m of the covariate, hence the first monitoring strategy corresponds to the allocation of 50% of sampling effort around 1000 m (and 50% randomly, see Step 2). Then, from monitoring season 1 to 3, monitoring was performed indistinctly between non-adaptive and adaptive approaches because no ecological changes occurred that can motivate the reallocation of sampling effort. Between season 3 and season 4, the species distribution shifted from 1000 m to 1500 m.

To illustrate the benefit of adapting the sampling strategy, we applied a 4^{th} round and a 5^{th} round of monitoring after the change in ecological condition. During these new rounds of monitoring, we compared i) an adaptive monitoring approach that can reallocate the sampling effort according to the prediction of occupancy probabilities (following the allocation rule defined in Step 4), and ii) a non-adaptive approach in which we keep the same sampling design for monitoring seasons 1 to 3. We provide the predicted relationship between occupancy and the fictive covariate, and the RMSE and RB for each monitoring season and for each of the monitoring strategy in Figure 3.

Results

Across the 3 first monitoring seasons, RMSE and RB decreased. This increase in precision is likely due to the augmentation of data time series. However, after ecological conditions changed between seasons 3 and 4, the adaptive strategy (reallocating sampling effort) exhibited higher precision than the non-adaptive strategy (same sampling effort allocation) (Figure 3). In the adaptive approach, the reallocation of the sampling effort to sites where the species is likely to occur increase the number of detection when monitoring, which is known to have a positive influence on the precision of occupancy estimates (MacKenzie, 2006). The adaptive approach allows to better sample the species distribution to increase the precision of the ecological inference, which is the monitoring objective defined in this fictive process (Step 1).

Discussion

With our simulations, we intended to illustrate the benefit of an adaptive monitoring framework through an explicit formulation of the analytical process. We pointed out that if ecological conditions changed, the iterative analysis of the ecological system and the reallocation of the sampling effort allow to increase precision in ecological estimates while maintaining the integrity of collected data. To date, we are uncertain this is sufficient to highlight an effective adaptive monitoring implementation. The current work is still ongoing and clarifications and precisions have to be added.

A limitation of our study lied in the explicit formulation of the monitoring objectives and strategies under ecological uncertainty, which should be the result of a consultative process (Lindenmayer & Likens, 2009). To simulate a 'naïve' decision-making in the face of uncertainty, we had to design imperfect monitoring strategy on purpose, which was unrealistic as we had access to 'perfect knowledge' through the simulation.

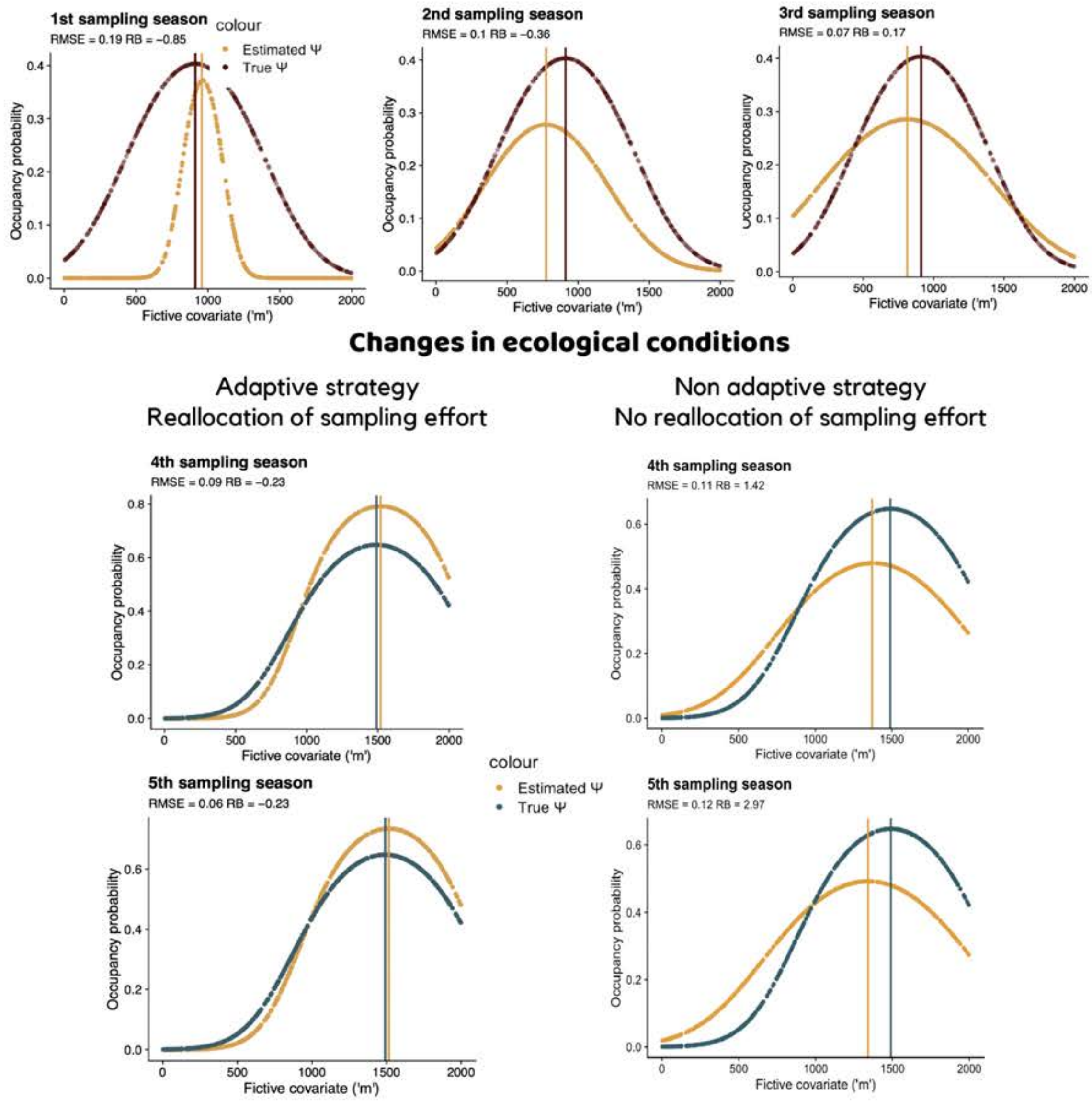

Figure 3: During the three first monitoring seasons, the preferred ecological condition of the species is around 1000 m (dark red dots and lines), while for the monitoring seasons 4 and 5 the preferred ecological conditions is around 1500m (dark blue dots and lines). From monitoring season 1 to season 3, monitoring was performed indistinctly between non-adaptive and adaptive approaches because no ecological changes occurred that can motivate the reallocation of sampling effort. Between season 3 and season 4, the species distribution shifted from 1000 m to 1500 m.

For seasons 4 and 5, we compared i) an adaptive monitoring approach that can reallocate the sampling effort according to the prediction of occupancy probabilities (following allocation rule defined in Step 4), and ii) a non-adaptive approach in which we keep the same sampling design as for monitoring seasons 1 to 3. The predicted relation between occupancy and the fictive covariate is displayed with golden dots and lines, and we added the Root Mean Square Error and Relative Bias for each monitoring season and for each of the monitoring strategy.

Overall, defining clear objectives is a critical step of AM (Lindenmayer & Likens, 2009; Ringold et al., 1996). In a protected area, monitoring is one component among a variety of practices (Dunham et al., 2020; Giakoumi et al., 2018; Vimal, 2017), hence management policies should direct targeted monitoring programs (Lindenmayer et al., 2011). Co-construction process between stakeholders, scientists, and modelers (Bolam et al., 2018) would be valuable to ensure sustainability and efficiency of monitoring programs (Lindenmayer et al., 2011; McIntosh et al., 2018).

Adaptive monitoring for wildlife conservation

Monitoring dynamic ecological processes is gaining attention in the literature (Williams et al., 2018) and the production of high quality data with adaptive strategies has been emphasized in ecology and other fields (Hooten et al., 2009; Merl et al., 2009; Shea et al., 2014). However, non-adaptive strategies are widely used in monitoring programs because they are simpler and have lower costs than AM (Hooten et al., 2009; Williams et al., 2018). AM requires planning, preparation, and modeling. Lindenmayer et al. (2009) underlined that many monitoring programs are poorly designed partly because statistical tools are discarded from designing phases, considered as not worthy to include, or hard to access for managers. Hence, non-adaptive monitoring design are often preferred for geopolitical, geographical, or economic considerations (Walters, 2007; Wikle & Royle, 1999). Consultative processes including multiple stakeholders such AM or adaptive management are seldomly applied in real world (Walters, 2007). On the other hand, when resources are limited (as for monitoring protected area), managers and scientists need to optimize monitoring efficiency and in this situation, targeted AM improves the quality of information obtained with limited survey capacity (Hooten et al., 2009; Williams et al., 2018). Moreover, protected area management requirements might fluctuate (e.g., variations of funding or priorities) and these changes should be carefully included in the monitoring process to maintain the integrity of long-term ecological datasets

(Williams, 2011). Another strength of AM is that reframing the monitoring objective continuously allow to better fit with updates in conservation policies.

Overall, monitoring in the wild is complex, involving environmental uncertainties and cost-constrained conservation contexts. AM is an ideal long-term monitoring strategy that can help in protected area management. To be widely adopted, adequate funding and real motivation for consultative approaches in conservation policies are required (Ban et al., 2011; Fulton et al., 2015; McIntosh et al., 2018).

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Résumé

Les suivis écologiques permettent de collecter des données et d'acquérir des connaissances sur les espèces ou les écosystèmes. Les suivis écologiques constituent la base sur laquelle s'organise la gestion de la biodiversité. Aujourd'hui, ces suivis se font dans le contexte d'une diversification des échelles d'analyse des enjeux de conservation, et d'une complexification des dynamiques institutionnelles en lien avec la collecte de données écologiques. En Méditerranée française, une trentaine d'Aires Marines Protégées (AMP) forment un maillage de la façade maritime. Ces AMP collectent des données et œuvrent pour la protection de la biodiversité marine, chacune à son échelle et avec ses moyens. Pour de nombreux enjeux touchant à la protection de la biodiversité marine, l'échelle écologique pertinente est celle de la façade Méditerranéenne. C'est par exemple le cas pour les espèces mobiles comme les mammifères marins.

Dans ce contexte, acquérir des connaissances écologiques à large échelle à partir de données collectées par une multitude d'acteurs soulèvent deux grands enjeux. Premièrement, un enjeu opérationnel et politique consiste à impliquer et coordonner les institutions et les acteurs qui collectent les données écologiques. Deuxièmement, un enjeu méthodologique réside dans la capacité à proposer des outils statistiques pouvant produire des indicateurs écologiques robustes à partir de plusieurs protocoles de suivis écologiques. Durant cette thèse, j'ai souhaité proposer l'étude simultanée de ces deux enjeux, opérationnel et méthodologique, en mettant en place une approche interdisciplinaire mobilisant sciences sociales et écologie statistique. L'analyse est centrée sur les suivis écologiques du grand dauphin (*Tursiops truncatus*) réalisés en Méditerranée française.

En réalisant des entretiens semi-directifs avec les agents des AMP de Méditerranée française, j'ai développé une réflexion sur la place des données écologiques dans le fonctionnement des AMP et dans le quotidien des agents qui y travaillent. Les entretiens et la collaboration avec les professionnels de la biodiversité ont aussi permis d'identifier des besoins méthodologiques pour appuyer le suivi écologique du grand dauphin à l'échelle du réseau d'AMP de Méditerranée française. Ainsi, j'ai développé des outils de modélisation intégrée permettant l'analyse conjointe de plusieurs jeux de données pour estimer la distribution, les effectifs et la densité de grand dauphin à l'échelle de la Méditerranée française.

Mon travail aura permis i) de proposer des outils statistiques adaptés au contexte actuel du suivi écologique du grand dauphin en Méditerranée française, et ii) de mettre en évidence et décrire les enjeux opérationnels et politiques de coordination des suivis écologiques entre les différentes AMP de Méditerranée française. Plus largement, ma thèse constitue une illustration de la pertinence du dialogue entre sciences sociales et écologie statistique pour produire des propositions d'outils de conservation écologiquement efficaces et socialement pertinents.

Mots-clés : aires marines protégées, écologie statistique, grand dauphin, Mer Méditerranée, recherche interdisciplinaire

Abstract

Abstract:

Ecological monitoring allows to collect data and to gain knowledge on species or ecosystems. Thus, ecological monitoring is the basis on which biodiversity conservation is organized. Nowadays, the spatial scales of ecological monitoring and conservation issues diversify, as well as the increased complexity of institutional dynamics related to the collection of ecological data. In the French Mediterranean, a network of thirty Marine Protected Areas (MPA) is operating along the coastline. These MPA collect ecological data and work for the protection of marine biodiversity, each at its own scale and with its own means. For many issues related to the protection of marine biodiversity, the relevant ecological scale is that of the Mediterranean coastline embracing the entire MPA network around the same ecological context. This is the case for mobile species such as marine mammals.

In this context, acquiring ecological knowledge at large spatial scales from data collected by a multitude of actors raises two major issues. First, an operational and policy challenge that consists in involving and coordinating institutions and stakeholders that collect ecological data. Second, a methodological challenge that lies in the ability to propose statistical tools that can produce robust ecological indicators from several monitoring protocols. During this thesis, I wanted to jointly study both of these two issues, operational and methodological, by setting up an interdisciplinary approach mobilizing social sciences and statistical ecology. The analysis is focused on the ecological monitoring of bottlenose dolphins (*Tursiops truncatus*) in the French Mediterranean Sea.

By conducting semi-directive interviews with MPA managers in the French Mediterranean, I studied the place of ecological data in the functioning of MPA and in the working life of the MPA managers. The interviews and the collaboration with biodiversity managers also allowed to identify methodological requirements to support the ecological monitoring of bottlenose dolphins at the scale of the French Mediterranean MPA network. Thus, I developed integrated modeling tools allowing the joint analysis of multiple datasets to estimate the distribution, abundance and density of bottlenose dolphins at the scale of the French Mediterranean Sea.

My work will have allowed i) to propose statistical tools relevant to the current context of the ecological monitoring of bottlenose dolphins in the French Mediterranean Sea, and ii) to highlight and describe the operational and political issues of coordinating ecological monitoring between the different MPA of the French Mediterranean Sea. Overall, my thesis is an illustration of the relevancy of the dialogue between social sciences and statistical ecology to produce ecologically effective and socially relevant conservation tools.

Keywords: bottlenose dolphin, interdisciplinary research, Marine Protected Areas, Mediterranean Sea, statistical ecology