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Camille Ollier

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**Cetacean population monitoring: the
merits and challenges of combining
acoustic and visual data**

Camille Ollier

**PhD thesis
La Rochelle Université 2024**

Under the supervision of Vincent Ridoux, Auriane Virgili and Oliver Boisseau



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THÈSE

présentée par :

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**Cetacean population monitoring: the merits and challenges of combining
acoustic and visual data**

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"A person who is severely impaired never knows his hidden sources of strength until he is treated like a normal human being and encouraged to shape his own life." - Helen Keller

Helen Keller, née en 1880, est devenue sourde et aveugle dès son plus jeune âge. Grâce à la langue des signes, elle a appris à communiquer et, avec sa détermination, a trouvé sa voie. Devenue écrivaine et militante pour défendre les droits des personnes handicapées, elle est une source d'inspiration pour moi.

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Scientific productions

Peer-reviewed publications

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Sol, M., Ollier, C., Boisseau, O., Ridoux, V., Virgili, A. (2024) Temporal patterns in dolphin foraging activity in the Mediterranean Sea: insights from vocalisations recorded during the ACCOBAMS Survey Initiative. *Frontiers in Marine Science*. DOI: 10.3389/fmars.2024.1378524

Ollier, C., Boisseau, O., Ridoux, V., Virgili, A. (in prep.) A comparison of acoustic and visual group sizes in Mediterranean dolphins. *Journal of Cetacean Research and Management*.

Ollier, C., Boisseau, O., Ridoux, V., Virgili, A. (in prep.) Accounting for variable detection biases in an acoustic-visual survey for Mediterranean dolphins. *Biological conservation*.

Conference papers

Poster presentation

Ollier, C., Sinn, I., Boisseau, O., Ridoux, V., Virgili, A. (2023) Matching visual and acoustic detections to estimate detection probability for small cetaceans in the ACCOBAMS Survey Initiative. In 34th European Cetacean Society Conference, O Grove, Spain.

Oral presentation

Ollier, C., Sol, M., Boisseau, O., Ridoux, V., Virgili, A. Diel and lunar cycle variations in acoustic events of small cetaceans in the Mediterranean Sea (in prep.) In 25th Biennial Conference on the Biology of Marine Mammals, Perth, Australia.

Ollier, C., Sol, M., Boisseau, O., Ridoux, V., Virgili, A. Diel and lunar cycle variations in acoustic events of small cetaceans in the Mediterranean Sea (2024) In STEM Sign Language Summit, Washington D.C., United-States.

Teaching

Tutorials in Ecology of Top predators at Master 1 level and practical work on plant physiology at the level of Licence 3 of Life and Health Sciences. Biology Department. La Rochelle Université.

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List of Abbreviations

| | |
|------------------------|---|
| ACCOBAMS | Agreement on the Conservation of Ceatecans of the Black Sea, Mediteranean and contiguous Atlantic Area. |
| AAM | Active Acoustic Monitoring. |
| AIC | Akaike Information Criterion. |
| ARU | Autonomous Recording Unit. |
| ASI | ACCOBAMS Survey Initiative. |
| AU | Assessment Unit. |
| CDS | Conventional Distance Sampling. |
| CU | Conservation Unit. |
| CV | Coefficient of Variation. |
| DS | Distance Sampling. |
| DSL | Deep Scattering Layer. |
| EDA | Effective Detection Area. |
| ESW | Effective Strip Width. |
| FI | Full Independence. |
| GAM | Generalized Additive Model. |
| GBYP | Grand Bluefin Tuna Year Programme. |
| GLM | Generalized Linear Model. |
| HN | Half-Normal. |
| HR | Hazard-Rate. |
| ICCAT | International Commission for the Conservation of Atlantic Tunas. |
| IUCN | International Union for Conservation of Nature. |
| IWC | International Whaling Commission. |
| MCDS | Multi-Covariate Distance Sampling. |
| MLD | Mixed Layer Depth. |
| MR | Mark-Recapture. |
| MRDS | Mark-Recapture Distance Sampling. |
| MU | Management Unit. |
| PAM | Passive Acoustic Monitoring. |
| PBR | Potential Biological Removal. |
| PI | Point Independence. |

| | | |
|--------------|-----------|--|
| PPS | | Porpoise-Positive Seconds. |
| ROCCA | | Real-time Odontocete Call Classification Algorithm. |
| SCANS | | Small Cetaceans in european Atlantic waters and the North Sea. |
| SE | | Standard Error. |
| TMA | | Target Motion Analysis. |
| UAV | | Unmanned Aerial Vehicle. |
| UTC | | Universal Time Coordinated. |
| VES | | Visual Encounter Survey. |
| VHR | | Very High Resolution. |

1

General introduction

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1.1 Population monitoring for conservation efforts

1.1.1 The importance of monitoring the population

In ecology, the term "monitoring" has a broad scope and its interpretation varies depending on the context. It has become a general term covering a spectrum of studies ranging from occasional observation of species to systematic surveillance of biological parameters within an ecosystem (Hellawell, 1991). Yoccoz et al. (2001) defined monitoring as "the process of gathering information about a state variable at different points of time to assess system state and draw inferences about changes in state over time". The state variable is defined as "a variable within the system of interest that is used to characterize the system status" (Yoccoz et al., 2001); it can be, for example, the abundance or distribution of a species. This process spans spatial scales, from local to global, and involves diverse data collection methods, including those conducted by professionals, citizen scientists, commercial entities, satellite remote sensing, and opportunistic observations by the public (Jones et al., 2013). A more precise definition of population monitoring emerged in the context of conservation where Moussy et al. (2022) suggested renaming it as long-term species monitoring and defined it as "the repeated, systematic collection of data with the intention of detecting changes over time in the abundance or distribution of one or more predefined taxa or taxonomic groups". This approach involves long-term research studies using predefined methodologies, focusing on one or more species at a time, using one or multiple methods, and excluding data collected by non-scientists (Moussy et al., 2022). The nuances in defining "population monitoring" can be subtle, and the precise definition depends on the objectives that drive the need for monitoring to make informed management decisions (Witmer, 2005).

There are many different objectives for population monitoring. For example, population monitoring for trends aims to monitor changes in populations or environmental conditions over time (Maas-Hebner et al., 2015). In more specific cases, it is essential to assess populations that pose a threat to agriculture/fisheries or natural resources, such as invasive species. For example, the blue crab, *Portunus segnis*, an invasive species from the Indo-Pacific Ocean, has rapidly colonised the Mediterranean Sea since the creation of the Suez Canal and has become an environmental and economic burden for many Mediterranean countries (Katsanevakis et al., 2014; Shaiek et al., 2021). The proliferation of this species has caused significant socio-economic damage to fisheries in the Gulf of Gabès, as it has not been commercially marketed locally and has frequently been caught in fishing nets (Crocetta et al., 2015). The blue swimming crab has also harmed commercially valuable fish caught in the nets. This invasion has led to a 72% decline in fishermen's income in the region (Khamassi et al., 2019). Monitoring these invasive species helps to estimate their prevalence, the level of damage they cause, and the economic benefits of control measures.

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In other scenarios, monitoring is focused on managing wildlife populations on a sustained-yield basis for recreational activities (hunting game). For example, black-tailed deer (*Odocoileus hemionus columbianus*), the most popular game species in the United States, have declined over the past decade (Macaulay et al., 2020). Macaulay et al. (2020) proposed an approach to estimate deer population abundance using camera traps and natural marking to inform harvest and habitat management decisions. Monitoring also helps manage fisheries. Monitoring fish populations and the harvesting process helps to regulate catches and optimize the exploitation of fisheries (Clark, 1980). Bluefin tuna (*Thunnus thynnus*) is a high-value pelagic species found in the North Atlantic Ocean, and Mediterranean Sea and has been severely overfished (Fromentin & Ravier, 2005). Its importance as a shared fishery resource requires international management. The International Commission for the Conservation of Atlantic Tunas (ICCAT) has established the Grand Bluefin Tuna Year Programme (GBYP) to improve data collection and understanding of the biology and ecology of the species (Alemany et al., 2023). Aerial surveys have been conducted in the Mediterranean to monitor the bluefin tuna population (Di Natale et al., 2018). Monitoring can be used to understand the effects of introducing sustainable energy facilities into the environment. For example, monitoring the impact of offshore wind farms on seabirds can help evaluate and develop mitigation measures to minimize environmental damage, such as temporarily shutting down wind turbines during migration periods (Drewitt & Langston, 2008).

In the context of conservation, population monitoring is essential to protect wildlife in the face of increasing human pressure and environmental change (Salafsky et al., 2001). Collecting data to understand these changes enables specific management actions to be taken (Jones et al., 2013). For example, it helps to assess the status of threatened or endangered species to track their recovery progress, or to determine what measures need to be taken to avoid population decline or collapse. This is the case, for example, with the population of the African penguin (*Spheniscus demersus*), endemic to southern Africa, which has declined by 70% from the early 1900s to the present (Crawford et al., 2011). This population decline can be attributed to a reduction in the availability of prey around their colonies, forcing them to make longer foraging trips (Sherley et al., 2020). In response to this alarming trend, the South African government established a Biodiversity Management Plan for the African Penguin in 2013 (DEA, 2013), to halt the species decline and promote population growth. Although the goals of the plan have not been fully met, numerous actions have been implemented, leading to revisions to the plan over time (Sherley et al., 2020). In particular, recent efforts have included the implementation of fishing restrictions around penguin colony sites, resulting in improvements in demographic characteristics favourable to population growth (Sydeman et al., 2021). Monitoring helps to assess trends in threats and population stability and to identify key threats, their locations and their temporal variations. It also allows the effectiveness of interventions to be tested, ensuring that conservation efforts are effectively directed towards achieving their goals (Jones et al., 2013).

1.1.2 Conservation status assessment helps prioritize species for conservation actions

The classification of species into risk categories is a common practice in conservation decision-making, with significant implications for legal protection, prioritization of conservation efforts and resource use (Rodrigues et al., 2006). Understanding the status of species and ecosystems, whether they are thriving, rare, or declining, is critical to directing conservation efforts to those most in need. Therefore, most conservation efforts are based on categorizing the status of populations, species and ecosystems to determine their current existence or the likelihood of their extinction in the future (Rodrigues et al., 2006). This classification process is based on specific criteria, with the status of species subject to change based on the evolving threats they face. The International Union for Conservation of Nature (IUCN) Red List of Threatened Species is the leading international standard for species classification, with nine categories (Figure 1.1) ranging from "not assessed" to "extinct" (Rodrigues et al., 2006). Of the 157,190 species assessed, 44,016 are considered threatened (IUCN Red List of Threatened Species, December 2023). The IUCN Red List informs several international agreements, such as the Convention on International Trade in Endangered Species (CITES; Dunham et al., 2023). In addition, various countries have their own national or regional assessment systems, such as the New Zealand Threat Classification, which classifies native species or subspecies into 9 groups: Not threatened, Naturally Uncommon, Relict, Recovering, Declining, Nationally Vulnerable, Nationally Endangered, Nationally Critical and Extinct (Townsend et al., 2008). Another example is the Endangered Species List managed by the United States Fish and Wildlife Service (a federal government agency) which classifies species or subspecies as Endangered or Threatened (Listing and Classification | U.S. Fish & Wildlife Service (fws.gov)). These classifications vary between systems due to differences in the definition of categories (Schnittler & Günther, 1999), designated regions, thresholds, methods of parameter assessment, and periodic assessment (Puissauve et al., 2016).

To categorise the species in question, the assessment is based on various parameters that provide an overview of the health and viability of the species (Dunham et al., 2023). One of the most commonly used metrics is population size or trend, which indicates whether or not the population is declining (Mace et al., 2008). This may include estimating the size of the geographic range through the area of occupancy, which indicates the extent of habitat use and distribution, and informing whether these overlap with threats or if the range is limited (Keith et al., 2013; Mace et al., 2008). Some systems consider population demographic characteristics such as sex ratios and survival rates to assess the viability of a population (Volis & Deng, 2020). Assessment of abiotic and biotic degradation also remains critical; for example, examination of remotely sensed sea ice extent data can reveal the retreat of ice masses (Hong & Shin, 2010; Keith et al., 2013). The specific

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indicators chosen depend on the species, habitat and purpose of the assessment (Mace et al., 2008). Vertebrates might be assessed based on population size and structure, while plant assessments might focus on geographic distribution. Invertebrates, on the other hand, could be assessed based on population fluctuations and habitat fragmentation (Mace et al., 2008). Then, by considering the system’s thresholds and aggregating these parameters, experts like scientists or conservationists determine the conservation status of species, facilitating the prioritization of conservation efforts.

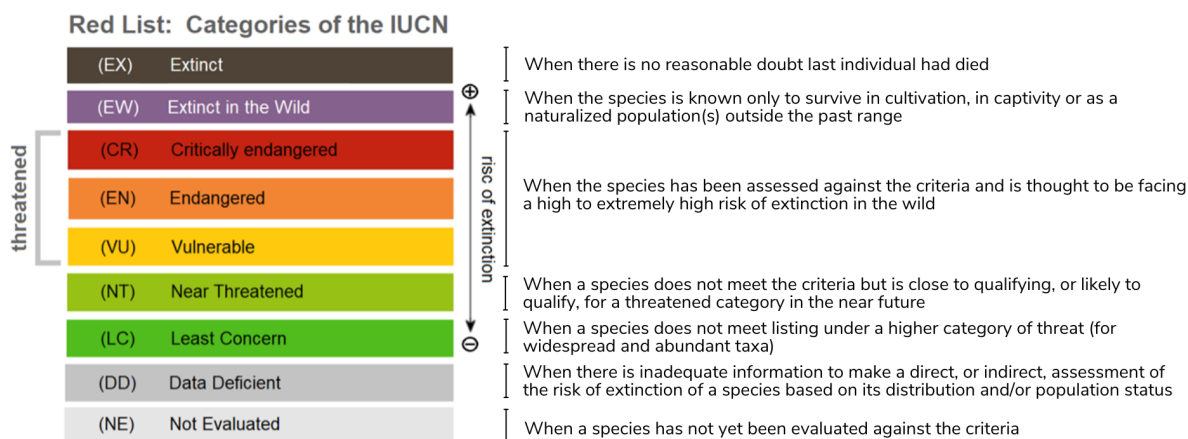


Figure. 1.1: The IUCN Red List categories. Species are classified into one of seven Red List Categories when assessed: Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable, Near Threatened, and Least Concern. If not assessed, species are categorised as either Data Deficient or Not Evaluated. Definitions for each category or group of categories are provided. Adapted from Rodrigues et al. (2006).

Increasing anthropogenic threats to the environment are having a significant impact on ecosystems and species. While the ranking of these threats varies by location, habitat, and species, the major threats to biodiversity include climate change, habitat loss, overexploitation, and pollution (Bellard et al., 2022). As a result, tens of thousands of species are threatened with extinction (Tilman et al., 2017). Given the vast number of species and limited conservation resources (Myers et al., 2000), prioritizing species based on their risk of local extinction can help conservationists and policymakers determine which species need closer monitoring (Davidson et al., 2012). For example, species that occupy high trophic levels, small geographic ranges, small population sizes and large body sizes tend to be more vulnerable to extinction (Purvis et al., 2000; Johnson, 2002). The vulnerability of species to extinction can be shaped by a combination of extrinsic and intrinsic factors (Hernández-Yáñez et al., 2022). Extrinsic factors, which are external to the species itself, include environmental and anthropogenic factors such as climate change, habitat destruction and invasion of non-native species (Pearson et al., 2014). Intrinsic factors relate to the biological characteristics of the species, including its physiology, behaviour and life cycle (Hernández-Yáñez et al., 2022). Albaladejo-Robles et al. (2023) have shown that species with different life history strategies respond differently to environmental changes. Those with

fast-life history strategies, characterised by rapid reproduction and shorter life spans, may be resilient to some disturbances (Gaillard et al., 2016). These species often thrive in areas affected by human activities and may even benefit from global warming (Albaladejo-Robles et al., 2023). Conversely, species with slow-life history strategies that prioritize survival over long periods with lower reproductive output are considered more sensitive to disturbances and global warming (Pacifci et al., 2017; Gaillard et al., 2016), especially when the threats they face directly affect their survival such as over-exploitation (Hernández-Yáñez et al., 2022). With climate change and human activities, slow-life history species tend to be more vulnerable and most conservation efforts focus on these types of species. For example, several cetaceans species or populations, which are highly vulnerable to overfishing and fisheries bycatch, have been identified as at risk of extinction, while many others have not yet been evaluated due to lack of data (Davidson et al., 2012). Their extinction can have significant ecological, economic, social, and political consequences (Davidson et al., 2012).

1.2 Cetaceans as long-lived species under threat

1.2.1 Cetaceans as top predators: their role in the marine ecosystems

Marine ecosystems, which cover about 71% of the Earth's surface, are home to complex assemblages of species adapted to specific environments, ranging from microorganisms to whales. This biodiversity includes microbes, fish, molluscs, crustaceans, corals, anemones, sea turtles, marine mammals and more (Gray, 1997). They live in diverse habitats such as coral reefs, kelp forests, seagrass beds, estuaries and the open ocean, from the poles to the equator and from the surface to over 10,000 m deep (Du et al., 2021; Helm, 2021; Moline et al., 2008). Marine ecosystems are maintained by energy flows from primary producers at the base of food chains to intermediate and higher consumers, and then in the opposite direction through the effects of decomposition or prey consumption (Aebischer et al., 1990; Pinardi et al., 2006; Reid et al., 2000; Baum & Worm, 2009; Roman et al., 2014). Marine communities are therefore biological networks in which the interactions between species are more or less direct. The reduction or increase in the abundance of a species or functional unit can unbalance the food web (Baden et al., 2012). Yet, there is resistance to ecological change as some species can take over the ecological roles of others within the ecosystem due to some degree of functional redundancy (Biggs et al., 2020; Palumbi et al., 2008). Predators play a central role in shaping prey populations and communities (Albouy et al., 2020). This influence is exerted both through direct predation, resulting in prey mortality, and by inducing prey to adopt resource-intensive anti-predator behaviours (Heithaus et al., 2008; Creel & Christianson, 2008). For example, in the Northwest Atlantic Ocean, the decline of large sharks has led to an increase in the abundance of cownose rays (*Rhinoptera bonasus*), with documented increases in catch rates of up to 9% per year. Since cownose rays

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are known to feed on bivalves (Smith & Merriner, 1985), this shift in species dynamics may be linked to the regional decline of bay scallop species (*Argopecten irradians*), which are important resources (Myers et al., 2007). Although the interaction between top predators based on their feeding ecology and the ecosystem as a whole can be complex (Heithaus et al., 2008), the removal of these apex predators can reduce redundancy, thereby affecting ecosystem resilience to ecological change (Rodríguez-Lozano et al., 2015).

Marine apex predators, such as cetaceans, play a critical role in maintaining marine biodiversity. Despite being a relatively small taxonomic group (Pace et al., 2015), their presence is essential for the ecological balance of marine ecosystems, and the potential extinction of cetaceans could have major consequences for ecosystem functioning (Katona & Whitehead, 1988). Cetaceans can also consume significant amounts of prey (Wurtz & Simard, 2007). Consequently, changes in the abundance, distribution, or feeding habits of cetaceans can have cascading effects throughout the entire ecosystem (Baum & Worm, 2009). Mass-balance ecosystem models, such as 'Ecopath with Ecosim', have effectively illustrated the top-down influence of cetaceans on food webs, highlighting their important role in shaping trophic interactions within marine ecosystems (Morissette et al., 2012). However, their importance extends beyond their role as top predators and their top-down influence on lower trophic levels through prey consumption (Baum & Worm, 2009). They also contribute significantly to nutrient cycling through their foraging behaviour. For example, grey whales (*Eschrichtius robustus*) and bottlenose dolphins (*Tursiops truncatus*) dislodge sediments (i.e., bioturbation), bringing nutrients to the surface, to the benefit of seabirds and other organisms (Anderson & Lovvorn, 2008). Nutrient cycling is also stimulated by cetacean faeces. By foraging at depth and releasing nutrients to the surface or to another habitat (e.g., from offshore to inshore) through buoyant faeces, they enrich surface layers, stimulating phytoplankton growth and overall ecosystem productivity (Roman et al., 2014; Kiszka et al., 2022; Gilbert et al., 2023). For example, as deep-diving species, sperm whales (*Physeter macrocephalus*) feed on cephalopods at depths below the Mixed Layer Depth (MLD, i.e., surface layer of the ocean) and release nutrient-rich faeces to the surface, which increases primary production in the photic zone (Whitehead, 2003; Lavery et al., 2010). Mysticetes, while having similar carbon pathways, recycle nutrients from the surface layer because they do not dive as deep to feed (Lavery et al., 2014; Savoca et al., 2021). Cetaceans also contribute to carbon sequestration by storing carbon in their bodies, which is then transported to the deep ocean when they die (Pearson et al., 2023). Their carcasses provide organic matter to deep-sea communities, acting as an "oasis" in the otherwise barren deep-sea environment and significantly impacting these ecosystems (Li et al., 2022). The dynamics of nutrient cycling and carbon sequestration are illustrated in figure 1.2. These multiple ecological roles underscore the importance of cetaceans to marine ecosystems.

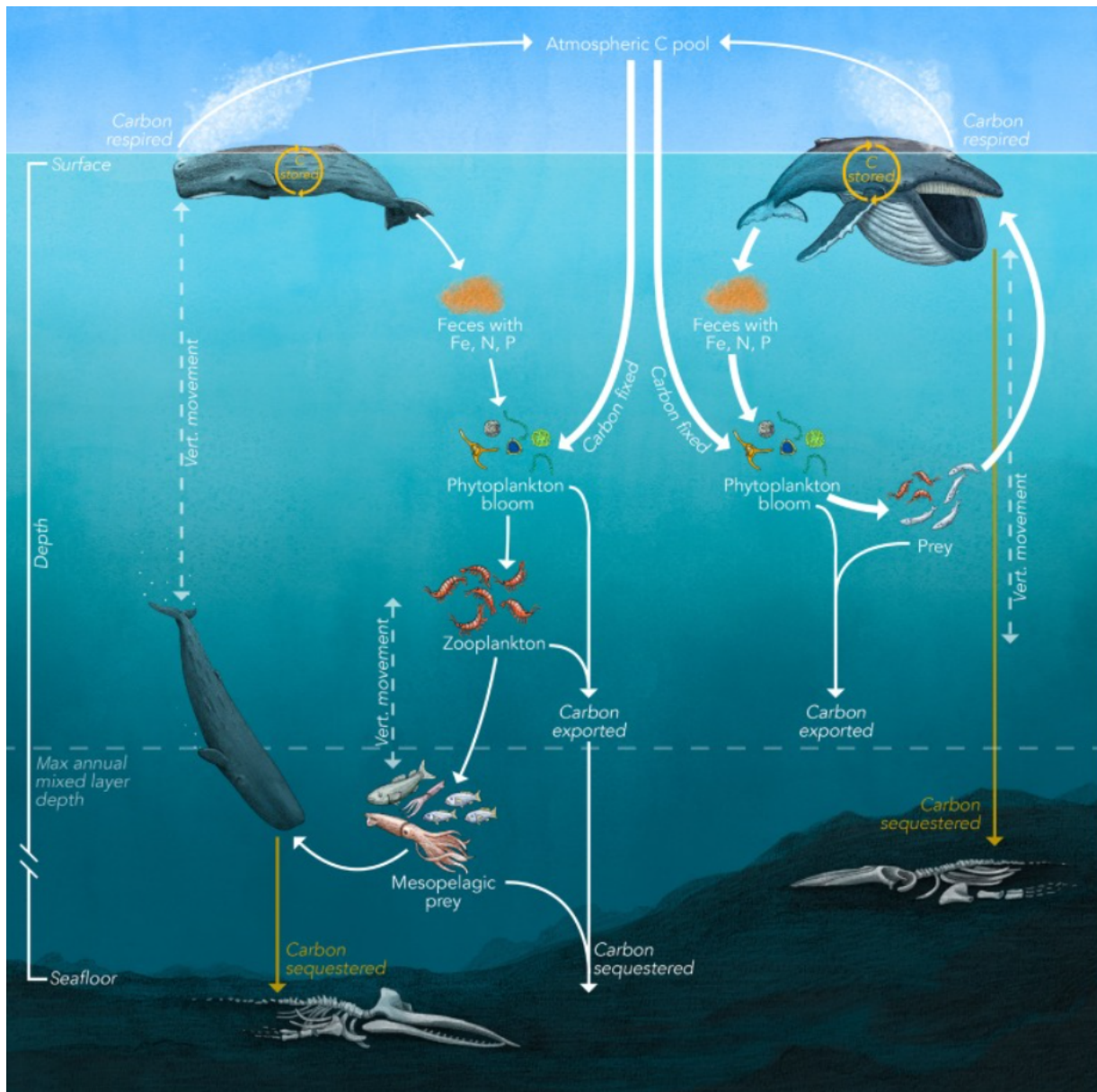


Figure. 1.2: Illustration of the dynamics of nutrient cycling and carbon sequestration by whales. A hypothetical Southern Ocean, demonstrated by two endmembers (deep-diving sperm whale, *Physeter macrocephalus*, left, vs. shallow-diving mysticete, right) that share the same direct carbon pathways (i.e., biomass carbon, whale falls) but differ in their indirect carbon pathways (i.e., the whale pump). Sperm whales, feeding below the mixed layer, release new nutrients at the surface, stimulating new primary production, carbon export and carbon sequestration. Mysticetes, feeding within the mixed layer, release regenerated nutrients at the surface, stimulating recycled primary production and carbon export. Arrow thickness indicates the relative magnitude of the carbon flux. The arrow colour indicates direct (orange) versus indirect (white) pathways. Illustrations by Alex Boersma. From Pearson et al. (2023).

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Cetaceans are considered sentinel or indicator species in marine ecosystems, a role that is becoming increasingly important as the effects of global warming and environmental change escalate (Moore, 2008). Sentinel species act as environmental indicators and are sensitive to changes in their habitat. Their presence or absence can therefore give an indication of the overall health of the ecosystems (Bossart, 2011a). Salvadeo et al. (2010) suggest a possible correlation between rising water temperatures and shifts in the occurrence of Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) in the northeastern Pacific Ocean, suggesting broader climate-related changes in local ecosystems. Assessing ecosystem health also goes beyond monitoring distribution (Bossart, 2011a). Cetaceans such as bottlenose dolphins tend to accumulate contaminants in their tissues, especially in coastal regions with high human densities. This makes them valuable biological models for biomonitoring spatial and temporal trends in contaminants (Bossart, 2011b). By monitoring cetaceans, scientists can detect early warning signs of environmental disturbance or degradation.

The importance of cetaceans extends into cultural and economic sectors as they are widely recognized as charismatic species (Albert et al., 2018) and they attract public, media and political attention (Parsons et al., 2015). Historically, they have had cultural and economic significance due to products such as oil, bones, teeth, and meat. However, perceptions have changed since the 1970s (Mazzoldi et al., 2019). Today, cetaceans contribute significantly to economic growth through coastal tourism (Parsons et al., 2003). The whale and dolphin watching industry alone generates millions of dollars in revenue and has become a major source of income and employment in many coastal areas (Parsons et al., 2003). The decline of cetacean populations could have irreversible consequences for ecosystem functioning and services.

1.2.2 Threats or pressures on cetaceans

Cetaceans, with their long life spans, low fecundity rates and high longevity (McCauley et al., 2015; Sequeira et al., 2019) are particularly sensitive to anthropogenic pressures and therefore face conservation risks (Bossart, 2011b). They face a wide range of anthropogenic threats and cumulative impacts that affect their vital rates and population viability. While the importance of these threats varies by location, time and species, the most important threats for cetaceans include underwater noise, chemical pollution, ship strikes, coastal development, disease, overfishing and accidental entanglement in fishing gears (Simmonds, 2018). As a result, many cetacean populations are in a state of concern. According to the IUCN, a quarter of cetacean species, including whales, dolphins and porpoises (26% of the 92 species assessed), are currently threatened with extinction, and 11% are near threatened (Figure 1.3). Riverine and coastal odontocetes are the most endangered cetaceans (Braulik et al., 2023). Given their limited resilience, their recovery may take decades, and their current conservation status reflects the effects of historical pressures from the last century,

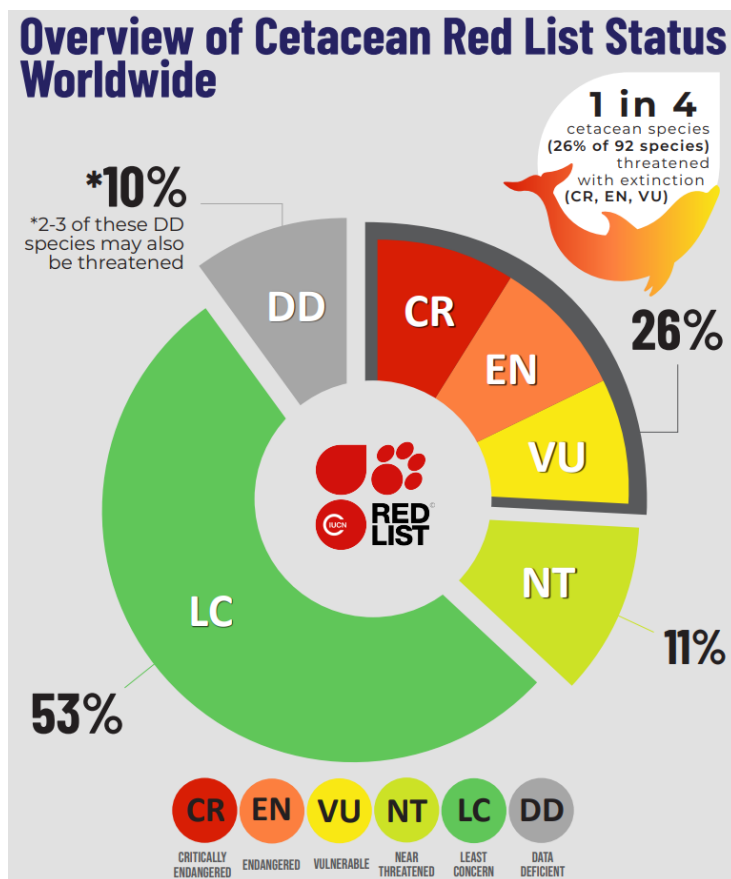


Figure. 1.3: Red List status and extinction risk of cetaceans worldwide. Of the 92 cetacean species assessed, including whales, dolphins and porpoises, 26% are threatened with extinction, 11% are near threatened, 53% are of least concern, and 10% were not assessed due to lack of data. This information is illustrated in an infographic by Daria Blackwell, available at <https://iucn-csg.org/>, based on the 2023 analysis by Braulik et al. (2023).

combined with current threats (Lotze et al., 2011). Since anthropogenic pressures on cetaceans are numerous (Avila et al., 2018), and rather than categorizing them according to the type of human activity involved, it seems preferable to group them according to their impact on animals (Figure 1.4, Authier et al., 2017). Primary pressures, such as incidental and intentional capture and collisions, directly cause additional mortality. In the Bay of Biscay, Peltier et al. (2016) estimated a high level of bycatch of stranded common dolphins, ranging from 3,650 to 4,700 dolphins per year. Secondary pressures, such as chemical pollution and overexploitation of food resources, induce physiological stress that negatively affects the health and condition of the animals, which directly reduces individual fitness and therefore affects overall population dynamics (Authier et al., 2017). Previous research has reported the potential effects of exposure to contaminants such as PCBs (Polychlorinated biphenyls) on the survival of bottlenose dolphin offspring, specifically reducing first-year calf survival and annual population growth (Bossart, 2011b; Zanuttini et al., 2019; Hall et al., 2006). Tertiary pressures (e.g. noise exposure or disturbance) alter animal behaviour, driving animals into less suitable habitats and interrupting crucial activities that affect

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vital functions (Bejder et al., 2006). These pressures may indirectly affect population dynamics. Pirotta et al. (2015) quantified the effects of boat disturbance on bottlenose dolphin foraging activity in the Mediterranean Sea. Their results indicate that foraging activity was reduced by 49% with the physical presence of boats. Assessing the conservation status of cetacean populations requires up-to-date data on abundance, distribution, health status and identification of pressures. These data need to be collected in a standardized manner through the implementation of cetacean population monitoring programs.

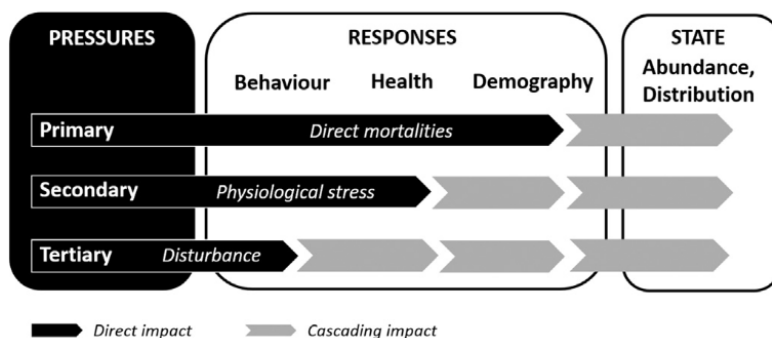


Figure. 1.4: Typology of pressures based on their effect on marine megafauna. Primary pressures directly cause additional mortality. Secondary pressures induce physiological stress that negatively affects the health of the animals. Tertiary pressures alter animal behaviour. From Authier et al. (2017).

1.3 Monitoring cetacean for conservation efforts

1.3.1 What indicators for monitoring cetacean populations?

The core of cetacean conservation research focuses on understanding and identifying the threats that cetaceans face in their natural habitats in order to protect them. A critical aspect of this research is understanding population dynamics, which is essential for assessing factors that threaten the viability of cetacean populations and for improving conservation efforts (Morris & Doak, 2002). This involves understanding how many individuals are present and how they are distributed in space and time. To achieve this, a range of metrics are used to assess population dynamics (Evans & Hammond, 2004).

Population size is a widely used metric in cetacean research and conservation efforts (Wilson et al., 1999; Williams et al., 2011). Estimating the size of a population in a defined geographical area serves as a baseline for assessing its conservation status and identifying temporal trends (Hammond et al., 2021a). For example, the European Union's Habitats Directive requires member states to conduct regular monitoring of cetacean species and to submit reports every six years to assess conservation status and the effectiveness of conservation measures. Four surveys called Small Cetaceans in European Atlantic Waters

1.3. Monitoring cetacean for conservation efforts

and the North Sea (SCANS) have been conducted since 1994 (Hammond et al., 2002; Hammond et al., 2013; Hammond et al., 2021b; Gilles et al., 2023). These surveys aim to estimate the abundance and distribution of cetaceans in European Atlantic waters to facilitate the detection of any trends in the abundance of species in these regions and to assess anthropogenic impacts (Gilles et al., 2023). In addition, spatial predictions of density or probability of occurrence based on abundance data can be used to assess risks in specific areas (Nichol et al., 2017; Pennino et al., 2017).

Monitoring population size is often coupled with monitoring distribution, as these two metrics are density-dependent and are typically collected using the same method. In addition to knowing how many there are, it is also essential to understand the spatial and temporal distribution of cetaceans. Cetaceans can exhibit habitat-specific behaviours/utilizations, showing preferences for particular areas for breeding, feeding and social interactions, often on a seasonal basis (Nowacek, 2005; Zein et al., 2019). Examining the relationship between distribution and environmental factors can provide valuable information on their habitat use, enable conservation efforts to be prioritized in areas where cetaceans may face anthropogenic threats and even help to establish marine protected areas to protect species (Hooker et al., 1999). In the face of increasing climatic changes, van Weelden et al. (2021) reviewed the impact of climate changes on cetacean species, highlighting spatial shifts in distribution and migration timing caused by increasing sea surface temperatures and changes in sea ice extent (Heide-Jørgensen et al., 2010). Monitoring population size or distribution alone does not provide sufficient information for management if the causes of the decline are unknown (Caughley, 1994).

Another approach is to monitor demographic parameters such as survival rates, reproduction rates and recruitment, which are critical to understand the mechanisms behind population growth and decline (Norris, 2004). Declines in population growth rates or changes in vital rates can be warning signs of increased extinction risk (Caughley, 1994; Mosnier et al., 2015). Murphy et al. (2009) emphasized the importance of estimating life history parameters to assess the status and dynamics of exploited populations, based on data from captured and stranded individuals. They reported a low annual pregnancy rate in the eastern North Atlantic common dolphin (*Delphinus delphis*) population, which may affect population dynamics by slowing population growth, reducing recruitment of new individuals, and potentially leading to long-term population declines (Murphy et al., 2009; Murphy et al., 2021). By incorporating accurate life history data into population models, conservationists can improve their ability to predict population trends, identify vulnerable populations and evaluate the effectiveness of management strategies (IJsseldijk et al., 2020).

Social structures are less studied but have a significant impact on population dynamics, as individuals in a population can form associations or exhibit more fluid social structures.

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Social structure can shape how populations respond to environmental changes and serve as a relevant indicator (Louis et al., 2015). Within a population, groups of individuals may have different foraging success and thus different fitness levels depending on environmental conditions (Whitehead & Rendell, 2004). For example, Lusseau et al. (2006) identified two distinct social groups within a resident bottlenose dolphin population in Scottish waters characterised by limited social interactions. This finding suggests that the separation into two groups may lead to differences in resource use, which can affect overall population dynamics. Incorporating social relationships into population analyses provides a deeper understanding of population dynamics and allows for targeted management strategies for different segments of the population. It is recommended that social dynamics be considered when assessing abundance trends (Lusseau et al., 2006).

Among these metrics, population size (abundance) remains the most important parameter to estimate, and several methods to collect data on a species abundance within a given area have been developed for this.

1.3.2 How to monitor cetaceans?

1.3.2.1 Monitoring with visual observation methods

Visual observation is one of the methods used to detect cetaceans and is carried out from a variety of platforms, including aerial and vessel-based surveys and fixed stations. While each platform provides specific degrees of coverage, aerial and vessel surveys are the most common (Evans & Hammond, 2004). However, the financial resources required can vary depending on the platform chosen, with effectiveness influenced by factors such as objectives, questions, area and target species (Evans & Hammond, 2004; Verfuss et al., 2018).

Surveys conducted from moving platforms, whether aerial or vessel-based, have been widely used for the last three decades, with many studies incorporating data from aerial (Kingsley & Reeves, 1998; Panigada et al., 2011) or vessel-based surveys (Barlow, 1995; Forcada et al., 1994; Hansen et al., 1995), either independently or in combination (Forney & Barlow, 1998; Holt & Powers, 1982; Hammond et al., 2002). Aerial-based surveys have the advantage of covering large areas efficiently. They can cover large areas in a short period of time thanks to their speed, generally between 90 and 100 knots and offer good flexibility in response to weather conditions (Dawson et al., 2008; Laran et al., 2017). However, aerial surveys provide a snapshot view, with limited temporal resolution to capture seasonal distribution; additionally, species identification can be difficult due to platform altitude and in the limited observation time (Laran et al., 2017). Indeed, observers from a plane often have difficulty distinguishing between species that share similar physical characteristics, such as the striped dolphin (*Stenella coeruleoalba*) and the common dolphin, which are

often grouped together in a lower taxon such as 'small delphinids' (Laran et al., 2017). Vessel-based surveys can also cover large areas but over longer times (generally below 10 knots), allowing surfacing animals to be detected for longer periods of time (Dawson et al., 2008). In addition, using a vessel as a platform allows for the collection of different types of data, including photo-identification, genetic and oceanographic data (Dawson et al., 2008). However, compared with aerial surveys, vessel-based surveys may be subject to movement bias such as the attraction or repulsion of animals to the vessel (Verfuss et al., 2018; Buckland et al., 2001).

Another approach is to collect visual observations from fixed stations, either on land (e.g., headlands) or at sea (e.g., oil platforms), allowing for continuous monitoring. Although this method does not provide quantitative measures for assessing population change, it does provide basic data collection at a low cost. Fixed stations can effectively focus attention on specific geographical areas or seasons. They are particularly suitable for areas where little is known, or for studies focusing on habitat use, and are well suited to behavioural studies (Evans & Hammond, 2004). For example, Hastie et al. (2004) used this method from a fixed station on land to study dolphin surfacing behaviour and whether it varied with bathymetry. However, this method is less commonly used due to its limited coverage and the need to be close to the animals to collect data (Evans & Hammond, 2004).

In visual surveys, accurate species identification depends on experienced observers and prolonged periods of observation can lead to fatigue, potentially affecting data collection (Evans & Hammond, 2004). Technological developments, such as unmanned aerial vehicles (UAV) or satellites, can assist visual observations (Guirado et al., 2019; Ferguson et al., 2018). These technologies capture high-resolution images, allowing observers to spend as much time as necessary reviewing each image, assessing animal presence, identifying species, and determining group sizes. However, manual analysis of these images can be very labor- and time-intensive (Ferguson et al., 2018). While the use of new technologies shows great promise, it is too early to say that UAVs can completely replace traditional aerial surveys for estimating abundance (Ferguson et al., 2018).

Visual surveys from either platform are limited by weather conditions, particularly visibility, sea state and glare (Barlow, 2015; Evans & Hammond, 2004). Most surveys are conducted when the Beaufort scale is 4 or less to ensure good to excellent detection conditions (Laran et al., 2017; Hammond et al., 2021a; Panigada et al., 2011). For harbour porpoises (*Phocoena phocoena*), which are more difficult to observe, Evans and Hammond (2004) recommend not exceeding Beaufort scale 2.

From a financial point of view, visual observation from fixed stations can be cost-effective if the goal is to collect basic information, such as detecting the presence of a species but

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it provides access to only a limited proportion of the population home range (Evans & Hammond, 2004). An alternative approach is to use platforms of opportunity, such as ferries, fisheries research vessels, or whale-watching boats which are also cost-effective because the monitoring program has low logistical costs (Evans & Hammond, 2004). However, these platforms do not provide control over vessel speed and trajectory, and as they are typically confined to a limited part of a population's home range, are not suitable for estimating metrics such as abundance. Conversely, dedicated surveys (aerial and vessel-based surveys) are both financially and logistically costly but allow for the implementation of a representative sampling design. Vessel-based surveys, especially those covering large areas requiring larger vessels, are more expensive than aerial surveys (Dawson et al., 2008) but can be combined with acoustic methods, which is not possible with aerial surveys.

1.3.2.2 Monitoring with acoustic methods

In addition to visual observations, acoustic monitoring is increasingly being used because of its many advantages. Acoustic methods are particularly effective over visual methods for detecting cetaceans when weather conditions or time of day are not favourable for visual observation and/or when animals do not surface frequently, such as deep-diving species (sperm or beaked whales, Verfuss et al., 2018; Mellinger et al., 2007). Acoustic monitoring is typically divided into two methods: Active Acoustic Monitoring (AAM) and Passive Acoustic Monitoring (PAM).

AAM involves emitting sounds into the water that are reflected by objects such as marine animals. These reflections allow the detection of animals and are captured by hydrophones (Verfuss et al., 2018). AAM has the advantage of being able to detect silent animals. However, when using AAM systems, the emitted signals at high source levels can fall within the hearing range of marine mammals, potentially affecting them and their behaviour (Stein, 2011). AAM is most commonly used to monitor fish or zooplankton (Simmonds & MacLennan, 2005; Godø et al., 2013).

The second approach, PAM, is widely used for cetacean monitoring (Mellinger et al., 2007). Unlike AAM, PAM does not emit sounds, but instead uses hydrophones to capture sounds emitted by animals and relies on the vocalisations of the animals for detection. Cetaceans produce sounds for a variety of purposes, including communication (Madsen et al., 2002), orientation (Payne & Webb, 1971), prey location and capture (Au et al., 2004), and social interaction (Janik, 2009). Variations in acoustic behaviour according to species include the bandwidth of vocalisations, with large whales (mysticetes) emitting low-frequency sounds that can be detected over greater distances, while odontocetes typically emit higher-frequency sounds (Mellinger et al., 2007, figure 1.5). Cetacean vocal behaviour can also

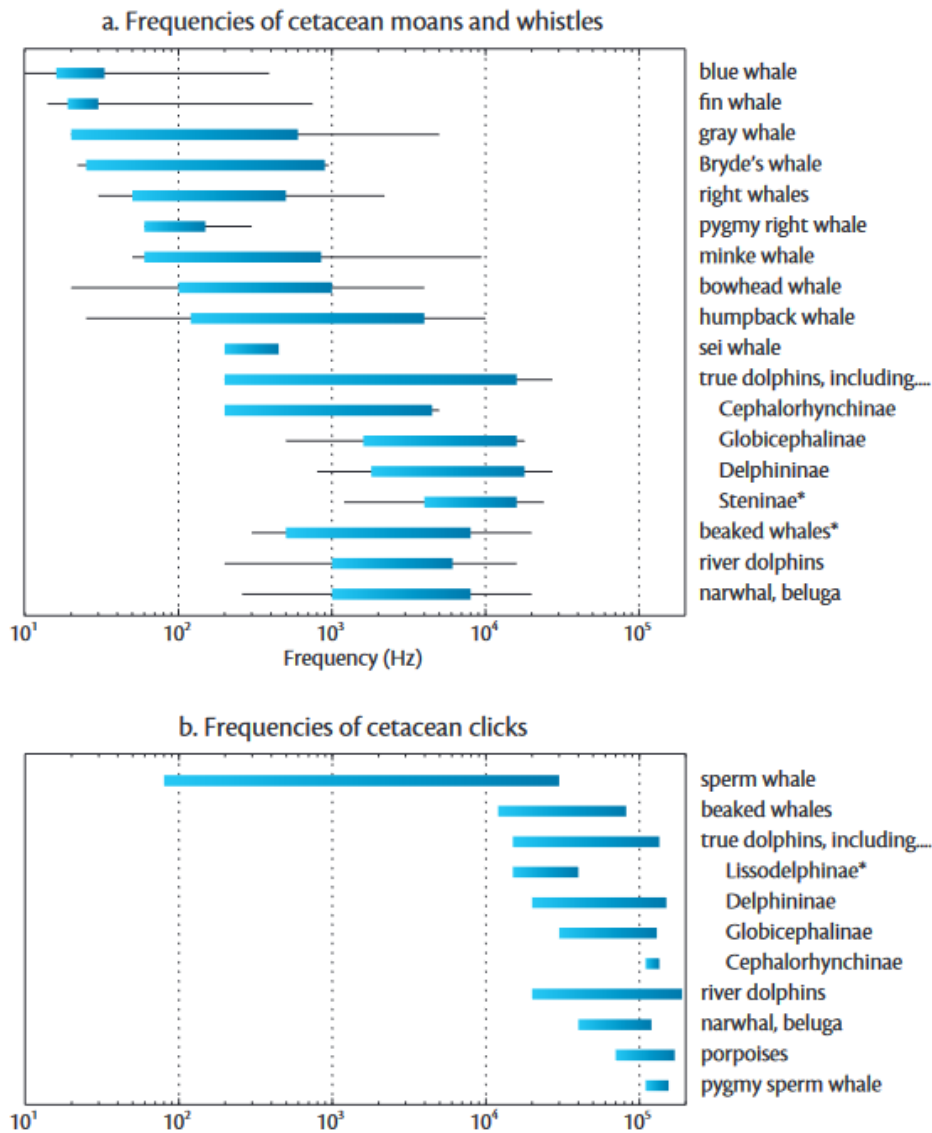


Figure. 1.5: Known frequency ranges of cetacean sounds. Large whales are listed by species, while toothed whales are grouped into families. The thick bar shows the range of the most common types of vocalisations, while the thinner line shows recorded extremes of frequency. An asterisk (*) indicates that the upper frequency is unknown because of recording equipment limitations. **(A)** Tonal sounds—moans and whistles—with most baleen whale species shown separately. **(B)** Echolocation clicks. Baleen whales do not produce high-frequency echolocation clicks, while some toothed whales, dolphins and porpoises do not produce tonal sounds. From Mellinger et al. (2007).

1. General introduction

vary with sex, season and age (Mellinger et al., 2007). The sounds produced by cetaceans are often characteristic and loud, making them readily detectable and often identifiable. PAM can be operated from a variety of platforms, the three most common being towed hydrophone arrays, autonomous underwater or surface vehicles as moving platforms and seafloor hydrophones as fixed platforms (Figure 1.6). Each type of platform has its advantages and disadvantages. Fixed PAM stations, similar to visual surveys, provide detailed information within a given area, allowing the study of seasonal patterns (Mellinger et al., 2007). Fixed stations also allow for longer monitoring periods, up to several years (Van Parijs et al., 2021) in remote areas (Širović et al., 2004). However, while they can be less costly than moving platforms, their spatial coverage is limited (Van Parijs et al., 2021). Autonomous underwater vehicles or gliders are efficient at surveying large geographic areas for extended periods of time, with the ability to access the recordings in real time (Wiggins et al., 2010; Van Parijs et al., 2021). However, such equipment is expensive and the noise generated by the glider can be a challenge for audio analysis, especially when monitoring low-frequency baleen whales (Mellinger et al., 2007). Towed hydrophone arrays provide extensive coverage, but the logistics involved such as the need for boats and associated costs, can be quite significant. However, their use in parallel with visual observation can greatly improve research efforts and results (Andriolo et al., 2018). They also help to improve cetacean sound classification (Oswald et al., 2003) and can even contribute to abundance estimates through various approaches such as distance sampling (discussed in chapter 2).

1.3.3 The challenges of detecting cetaceans in the marine environment

Monitoring, whether by visual or acoustic methods, remains challenging due to the difficulties associated with detecting all animals within a study area (Buckland et al., 2001). Detection of animals can be affected by availability bias and perception bias (Marsh & Sinclair, 1989). Together these biases are known as visibility bias (Marsh & Sinclair, 1989). The term "visibility bias" refers specifically to visual surveys. To cover both acoustic and visual surveys, I suggest using the term "detection biases" instead. Availability bias corresponds to the unavailability of animals for detection, either because they are below the sea surface, which depends on the time spent at depth and the speed of the platform, or because they are not acoustically active, which depends on the vocalisation rate of the species (Marques et al., 2009). Availability bias can differ between platforms. For example, in visual vessel-based surveys, availability bias is a significant challenge when studying deep-diving species such as sperm or beaked whales. This challenge is even more significant in aerial surveys, where the high speed of the aircraft reduces the time available to observe any given point at sea (Laake et al., 1997). As a result, a significant proportion of animals may go undetected in such surveys. For example, according to Laake et al. (1997), about 70% of harbour porpoises would not be available to observers in a fixed-wing aircraft.

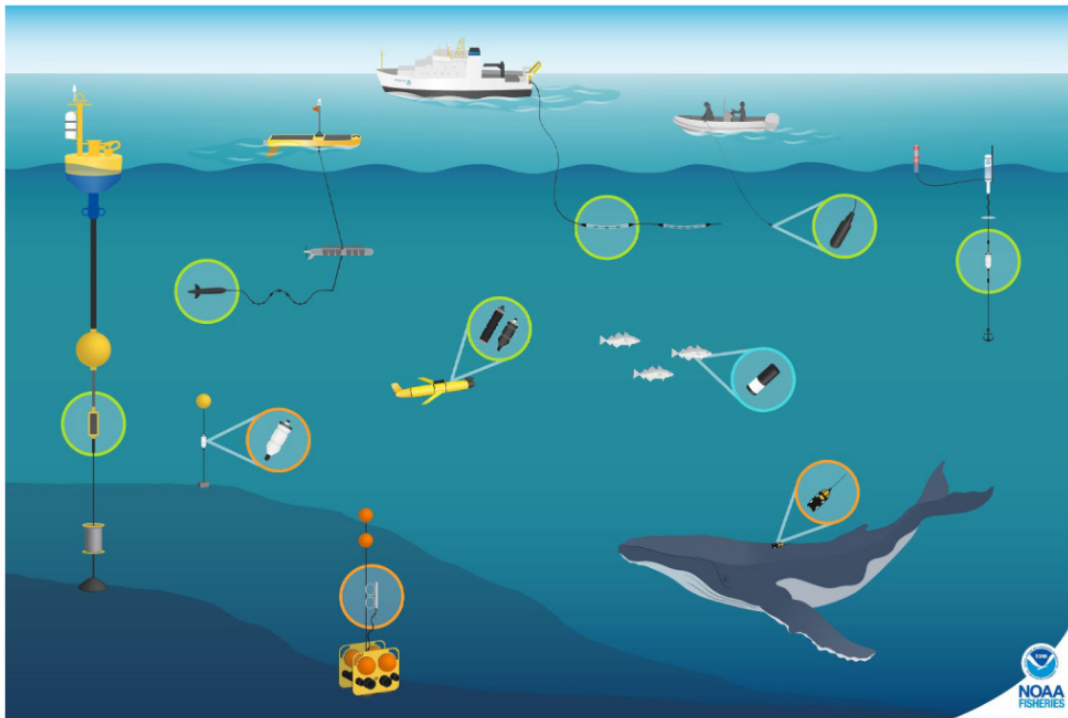


Figure 1.6: Illustration of different types of acoustic technologies. From left to right, the illustration shows a moored surface buoy, wave glider, SoundTrap on the seafloor, bottom-mounted acoustic recorder (High-frequency Acoustic Recording Package [HARP]), Slocum glider, NOAA ship towing a hydrophone array, tagged Atlantic cod, humpback whale with an archival tag, drop hydrophone deployed from a small boat, and autonomous, free-floating acoustic recorder (Drifting Acoustic Spar Buoy Recorder [DASBR]). The different technologies are highlighted with coloured circles that show a zoomed-in view of the instruments and colours that represent the type of data collected: green for real-time data capabilities, orange for archival data and blue for active acoustics. From Van Parijs et al. (2021).

Some studies have used dive recording systems to model diving behaviour and estimate the availability bias from the proportion of time spent at the surface (Barlow, 1999; Heide-Jørgensen & Laidre, 2023). Perception bias accounts for the non-detection of available animals by observers or recorders due to imperfect observer vigilance or unfavourable conditions for detection (e.g., glare, low visibility, poor sea state) or acoustic limitations such as background noise masking the acoustic signal or directional characteristics of certain vocalisations (Au et al., 1978). For example, species that occur in large groups with distinctive features, such as killer whales with large dorsal fins, are typically easier to detect than smaller species such as harbour porpoises (Barlow & Forney, 2007). These biases are critical to consider, as they can significantly affect density-dependent estimates such as distribution or abundance (Saavedra et al., 2018), and consequently affect conservation management strategies (Sucunza et al., 2018). Therefore, numerous studies have focused on the probability of detecting individuals and how to quantify this probability in population abundance and density surveys (Akamatsu et al., 2008; Buckland et al., 2001; Lambert et al., 2019).

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Several studies have compared acoustic and visual methods and found them to be complementary (Dalpaz et al., 2021; Gridley et al., 2020; Duporge et al., 2023; Akamatsu et al., 2001; Verfuss et al., 2018). Acoustic methods have the advantage of detecting cetaceans when they are submerged and not visible at the surface, a limitation of visual observation. On the other hand, visual detection allows species identification and estimation of group size, aspects that remain challenging for acoustic methods despite ongoing efforts in species classification (Oswald et al., 2003; Rankin et al., 2017). Combining both methods often leads to higher detection rates per species, as demonstrated by Dalpaz et al. (2021). Their study pooled data from four simultaneous passive acoustic (towed hydrophone) and visual line transect surveys conducted annually over four years in Brazilian waters. The results showed that the acoustic method detected a greater range and number of animals compared to the visual method, but had difficulty identifying species. Conversely, the visual method was more effective at identifying species (Figure 1.7). They also matched events and found that only 35% of events were duplicated, suggesting that acoustic and visual methods are complementary rather than redundant (Dalpaz et al., 2021). Using complementary methods improves overall detection efficiency (Verfuss et al., 2018). However, few studies have used both methods to estimate abundance or distribution (Gerrodette et al., 2011; Martin et al., 2020). Combining two methods, each with its own strengths and weaknesses can be more complex when trying to achieve more than a simple comparison of methods. This leads to the central question of this study: can the strengths of both acoustic and visual surveys be exploited to improve cetacean detectability and what would be the implications for abundance, a widely used metric?

1.4 Research objectives and outline of the thesis

1.4.1 Context and research objectives

The research objectives of this thesis are:

1. To develop a method for using combined acoustic and visual data to estimate detection probability,
2. To investigate the parameters related to the behaviour of small cetaceans that may affect the detection probability,
3. To assess the effects of variability in detection probability on abundance estimates.

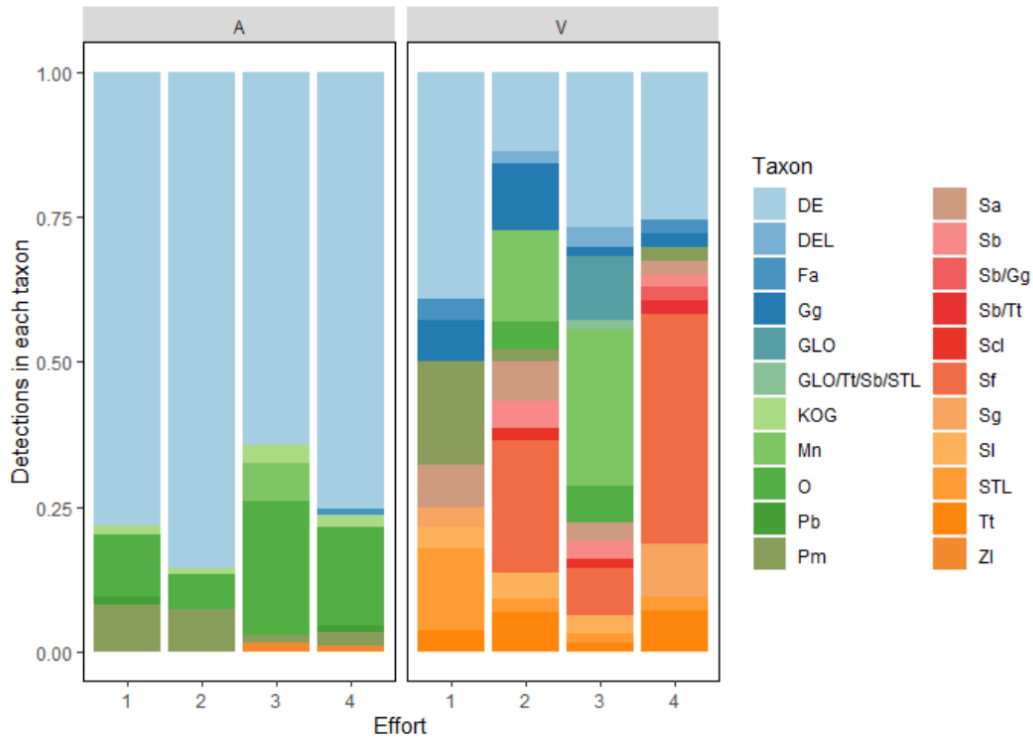


Figure 1.7: Percentage of taxa composition identified by each method in each survey. Percentage of taxonomic composition of acoustic (left) and visual (right) detections throughout each cetacean survey (four in total) in the Santos Basin, Brazil. Taxonomic identification corresponds to the most specific taxa that each method attributed to each event, and include: DE (Delphinidae), DEL (*Delphinus* spp.), Fa (*Feresa attenuata*), Gg (*Grampus griseus*), GLO (*Globicephala* sp.), KOG (*Kogia* sp.), Mn (*Megaptera novaeangliae*), O (Odontoceti), Pb (*Pontoporia blainvillei*), Pm (*Physeter macrocephalus*), Sa (*Stenella attenuata*), Sb (*Steno bredanensis*), Scl (*Stenella clymene*), Sf (*Stenella frontalis*), Sg (*Sotalia guianensis*), Sl (*Stenella longirostris*), STL (*Stenella* sp.), Tt (*Tursiops truncatus*), ZI (Ziphiidae). Events with more than one taxon (GLO/Tt/Sb/STL, Sb/Gg and Sb/Tt) correspond to mixed groups that were visually identified. From Dalpaz et al. (2021).

1.4.2 Thesis outline

This thesis is methodologically oriented, with the primary objective of improving conservation efforts, especially for cetaceans in a specific region, the Mediterranean Sea. The thesis is divided into 7 chapters (Figure 1.8).

Chapter 1 describes the importance of monitoring cetacean populations with an emphasis on the usefulness of acoustic and visual monitoring methods and leads to the statement of the research objectives.

Chapter 2 is a comprehensive literature review of the problems associated with estimating abundance and efforts to combine visual and acoustic data.

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Chapter 3 describes the research material (species, area, season. . .) and provides an overview of the data obtained in the Mediterranean Sea. This chapter also presents the methods used to process and treat the acoustic and visual data used in the following chapters.

Chapter 4 aims to estimate detection probabilities using data collected during transects using both acoustic and visual platforms. The process involved the construction of a decision tree to identify duplicate events between the acoustic and visual platforms.

Chapter 5 aims to identify parameters associated with animal behaviour that may influence the acoustic detection probability. This study used transects where acoustic data were collected to investigate variations in the number of events per unit of time during the nycthemeral cycle. Parameters that might influence the number of events were modeled to understand their relationship.

Chapter 6 focuses on investigating different methods for accounting for detection biases inherent to acoustic and visual platforms. Abundance estimates were derived using different datasets (visual and/or acoustic) and different scenarios accounting for detection biases. In addition, abundance was estimated for each scenario and compared with corrected aerial abundance estimate from blocks surveyed by both components.

Chapter 7 include a general discussion and conclusion.

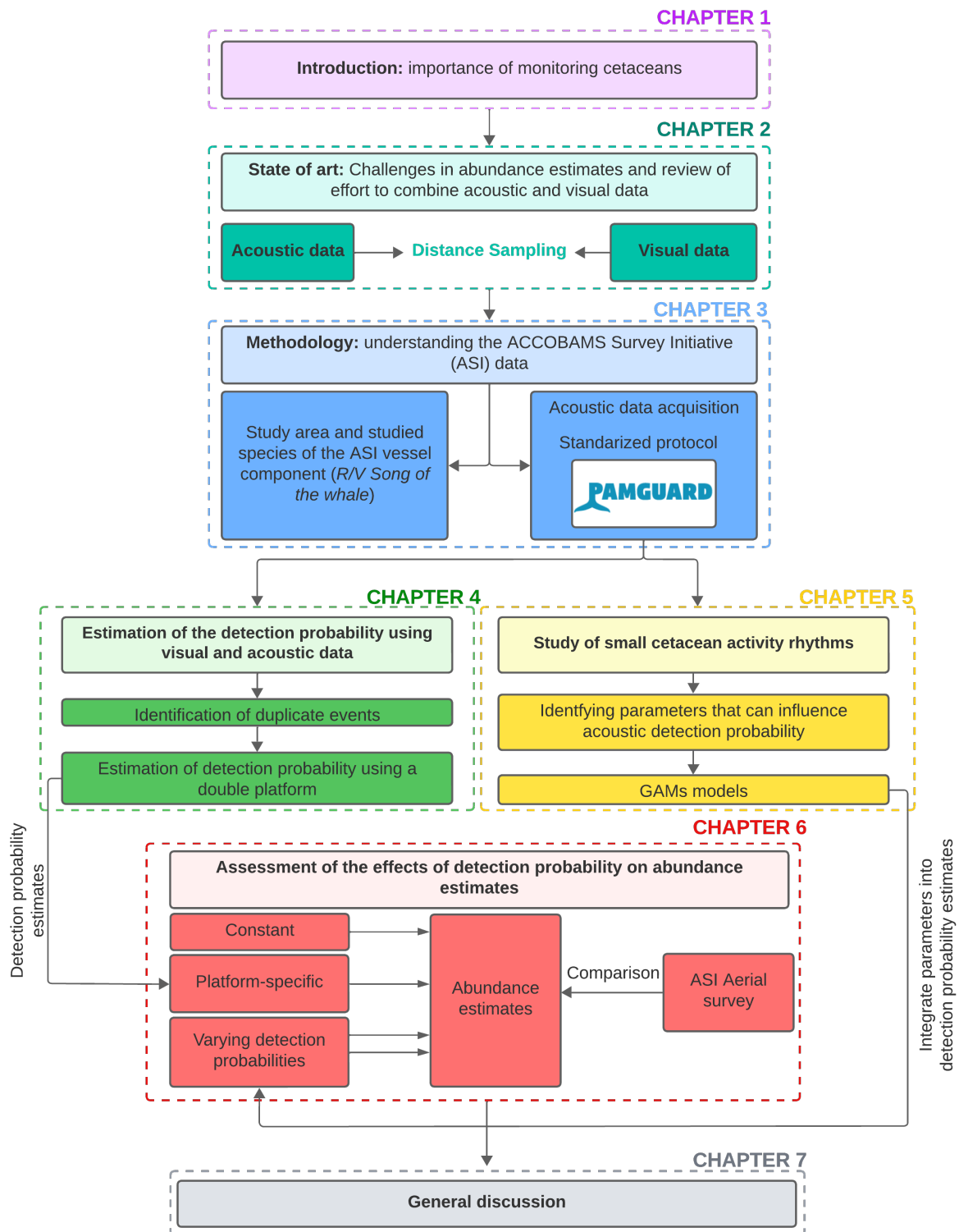


Figure. 1.8: Flowchart of the PhD dissertation.

2

Combining passive acoustic and visual methods for cetacean abundance estimates: a review

Combining passive acoustic and visual monitoring can be beneficial for cetacean studies, as each method is subject to different biases and can complement each other. While the use of both methods is becoming more common, it is still rare to merge datasets to produce a final output, such as an abundance estimate utilising both datasets. The purpose of this chapter is to review the challenges associated with abundance estimation and to review efforts to combine methods, highlighting different degrees of integration between visual and acoustic datasets.

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2.1 What is abundance?

2.1.1 General principles

Abundance refers to the size of a population, but the term "population" can convey different meanings. A common definition of a population is the set of individuals of a given species living and interbreeding in the same space, as described by Cole (1957): "*a biological unit at the level of ecological integration at which it is meaningful to speak of a birth rate, a death rate, a sex ratio and an age structure in describing the characteristics of the unit*". In this context, population refers to a group within a specific area, not to a wider biological population (Hammond et al., 2021a). However, defining a population in a marine area is challenging. A population can refer to individuals that use the study area, including those that migrate out at certain times of the year and those that stay (Hammond et al., 2021a). They are still considered to be the same population (Calambokidis & Barlow, 2004). A population can also refer to animals present in an area at a given time, as defined by Krebs (1972): "*a group of organisms of the same species occupying a given space at a given time... [its] boundaries... both in space and time are vague and, in practice, are usually arbitrarily fixed by the investigator*".

Policy makers need to understand the boundaries of the population they wish to protect and implement appropriate management strategies for those specific populations (Fraser & Bernatchez, 2001; Allendorf & Luikart, 2010). Populations can be defined as Conservation Units (CUs), with the resolution of these units depending on the conservation objectives. Management Units (MUs) are used for short-term management purposes, often related to resource exploitation. For example, the International Whaling Commission (IWC) manages whaling on the basis of defined management stocks, where each whale stock is treated as a single unit for conservation and sustainable use. This is similar to the concept of "stocks" in fisheries biology (Palsbøll et al., 2007; Hammond et al., 2021b). Assessment Units (AUs) are used to assess the status of a species. For example, in the OSPAR monitoring program, data collected during SCANS surveys allow the abundance and distribution of harbour porpoises to be estimated in 5 AUs in the Northeast Atlantic Ocean (Gilles et al., 2023). Overall, the definition of a population depends on the objectives, and it is crucial to establish a clear definition of the "population" to which abundance estimates refer (Hammond et al., 2021a).

Abundance, or population size, refers to the number of animals. However, it is not possible to count all individuals of any cetacean population because the whole area of their distributions cannot be scanned exhaustively and because cetaceans spend much of their time underwater (availability bias). To obtain a measure of the number of individuals in cetacean populations, abundance must be estimated. This involves sampling data and

2. Combining passive acoustic and visual methods for cetacean abundance estimates: a review

using statistical models to extrapolate the results to the entire study area (Hammond et al., 2021a). For example, as illustrated in Hammond et al. (2021a), if a study area A is 450 km² and a smaller surveyed area a is 50 km², and if 35 animals are counted (n) in a , the density can be calculated as $n/a = 35/50 = 0.7$ animals per km². This density can then be extrapolated to the entire study area A , resulting in an abundance (N) calculated as $D \times N = 0.7 \times 450 = 315$ individuals. Because N is an estimate, it is subject to uncertainty and provides an approximation rather than an exact count.

2.1.2 Estimation errors

An abundance estimate is associated with a degree of error. Two terms related to error in estimates are uncertainty and precision. Uncertainty refers to how close the estimate is to the true value and represents the variability in the estimate that is unknown (Li & Wu, 2006). This uncertainty is somewhat unavoidable in modeling due to the stochastic nature of ecological processes, the complexity of systems due to spatial heterogeneity and nonlinear relationships, the unreliability and unavailability of data, and imperfections in models (Li & Wu, 2006). For example, when observers measure the distance to animals from a boat, there are inherent measurement errors from the binoculars used. Variability in the measurement of the parameter contributes to the uncertainty (Marques et al., 2006). Another example is uncertainty due to the misclassification of acoustic events by a classifier (Caillat et al., 2013). Uncertainty in modeling can be quantified using bootstrap and resampling methods (Davison & Hinkley, 1997).

Precision, on the other hand, measures the consistency and reproducibility of the measurements. It indicates the degree to which estimates would vary if calculated from multiple sets of sample data (Hammond et al., 2021a). Typical measures of precision include the standard error (SE) and the coefficient of variation (CV) which can be expressed as a proportion or a percentage and is estimated by dividing the SE by the estimate. Higher precision leads to higher statistical power, which provides greater confidence in the results (Buhl-Mortensen, 1996) and facilitates more informed decision making.

An abundance estimate with high precision (low CV) does not necessarily mean that the estimate is unbiased. An estimate is unbiased if the assumptions inherent in the sampling method are met and the estimate is therefore centered on the true population parameter. If these assumptions are violated, the estimate becomes biased and systematically deviates from the population parameter. Even an accurate estimate derived from a large amount of data can be biased if these assumptions are violated, which is particularly problematic for informing conservation and management decisions because it does not represent true abundance (Hammond et al., 2021a). As highlighted in chapter 1, cetacean detection is challenging, and failure to account for detection biases can lead to biased abundance estimates. Nevertheless, there are several methods for quantifying population size.

2.1.3 Relative *versus* absolute abundance

There are two parameters used to represent population size: absolute abundance and relative abundance, each with its own implications for understanding spatio-temporal patterns. Absolute abundance refers to the total number of individuals within a population present in a given area; it aims to estimate the "true" population size of a species (Hammond et al., 2013, figure 2.1). However, such estimates are often subject to error and uncertainty, influenced by factors such as species rarity, detectability or sampling intensity, and it is extremely difficult to estimate absolute abundance with low bias. Therefore, relative abundance is often used instead, as it is generally easier to estimate (Buckland & York, 2009; Henderson, 2002). Relative abundance is an imperfect estimate of the true abundance, where biases, although unknown, are assumed to be either constant or proportional to the estimate, hence allowing comparisons to be made in space and time, and therefore spatial patterns and temporal trends to be detected (Buckland and York, 2009, figure 2.1). This parameter can provide details on where or when a species is more or less abundant (Mac Nally, 2007). In other contexts, the term relative abundance can also refer to a proportional representation of each species within a community (Gotelli et al., 2023) but this understanding is not relevant in this thesis.

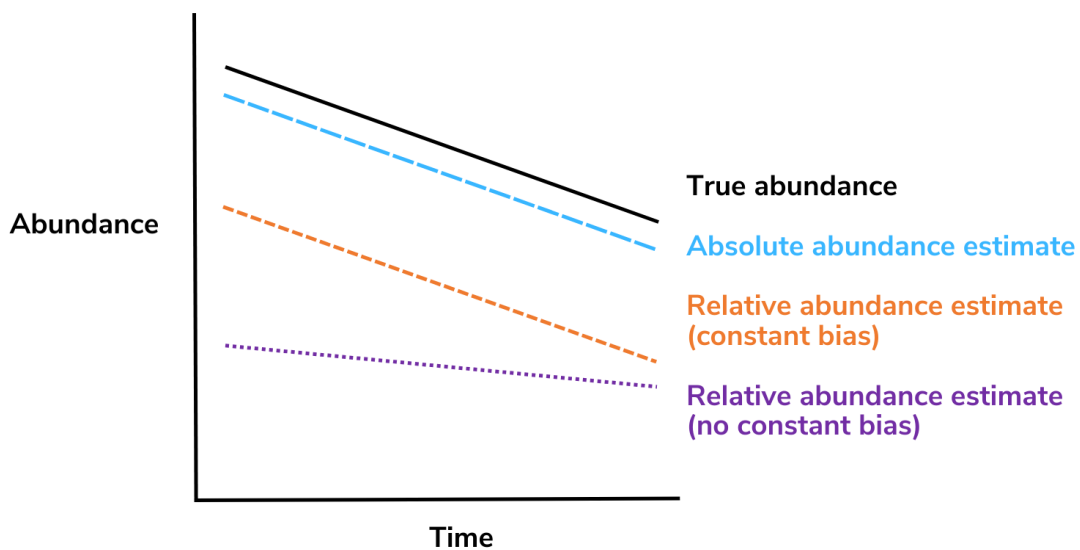


Figure. 2.1: Difference in absolute and relative abundance. An illustration showing the difference in absolute and relative abundance and how they can differ from the true abundance (black) over time. Absolute abundance refers to the total number of individuals within a population present in a given area (blue). Relative abundance is an imperfect estimate of the true abundance where biases, although unknown, are assumed to be either constant or proportional to the estimate (orange). Relative abundance when biases are not constant over time, e.g. when detection probability increases over time (purple). Adapted from Callaghan et al. (2024).

Both relative and absolute abundance estimates require dedicated surveys (Evans & Hammond, 2004). Absolute abundance estimates require a higher level of rigor and

2. Combining passive acoustic and visual methods for cetacean abundance estimates: a review

logistical effort to account for the major sources of detection biases. This can be costly and time consuming (Callaghan et al., 2024). For example, the SCANS surveys are designed to estimate the absolute abundance of small cetaceans in the North Sea and adjacent areas and could only be conducted every decade or so (Hammond et al., 2013; survey interval now reduced to six years). Therefore, the accuracy of the estimates can be particularly limited by the intensity of sampling (Callaghan et al., 2024). Indeed, conservationists and researchers struggling to allocate funding for conservation research often seek to minimize the costs associated with cetacean surveys by sampling large study areas, which can be both time consuming and expensive (Taylor & Gerrodette, 1993). However, reducing the frequency or duration of surveys inevitably reduces sample sizes, resulting in less accurate abundance estimates and more caution in using the estimates. Relative abundance estimation is less time consuming and less expensive to implement because it does not attempt to account for the main detection biases. As a result, surveys can be repeated at shorter time intervals, thus collecting more data and increasing statistical power with larger sample sizes (Callaghan et al., 2024). Relative estimates are useful for predicting extinction risk, but absolute abundance estimates indicate the proximity of a population to extinction and therefore the need for immediate conservation action (IUCN, 2022; Callaghan et al., 2024), as in the case of cetaceans threatened by bycatch.

2.1.4 The importance of obtaining absolute abundances

While most cetacean conservation programs use minimum abundance estimates to take conservation measures (Evans & Hammond, 2004), unbiased absolute abundance is essential to determine acceptable levels of human-caused mortality for cetaceans. Bycatch, particularly of small odontocetes, is a major cause of human-induced cetacean mortality (Reeves et al., 2013), as evidenced by the functional extinction of species such as the Yangtze River dolphin (*Lipotes vexillifer*, Turvey et al., 2007) and the critically endangered vaquita (*Phocoena sinus*, Taylor et al., 2017) due to unsustainable fishing practices. The Potential Biological Removal (PBR) threshold established by the Marine Mammal Protection Act in the US serves as a guideline for estimating sustainable levels of human-caused mortality (Wade, 1998). The calculation of PBR involves an estimate of both absolute abundance and bycatch mortality, and exceeding these thresholds would result in the depletion of the population and trigger management decisions to avoid this path. Although some studies propose alternative frameworks that do not rely on absolute abundance estimates, these methods are generally less robust than the PBR approach (Punt et al., 2021). Updated abundance estimates of harbour porpoise and common dolphins populations with reduced bias suggest that bycatch levels may exceed PBR estimates, highlighting the importance of monitoring abundance to assess potential impacts of fisheries on cetacean species (Zerbini et al., 2022; Parra et al., 2021). Unbiased estimates of absolute abundance are critical for assessing the sustainability of human-induced mortality and facilitating the development of effective conservation and management strategies (Parra et al., 2021).

2.1.5 **Methods for estimating cetacean abundance**

While recognizing the diversity of methods used to estimate cetacean population abundance (Hammond et al., 2021a), two well-known and widely used approaches are mark-recapture and distance sampling (Buckland et al., 2001; Evans & Hammond, 2004). The mark-recapture can be carried out using different techniques such as photo-identification (Genov et al., 2008), DNA (Mills et al., 2000) or acoustic recordings (Longden et al., 2020; Marques et al., 2013). Photo-identification is the most commonly used technique, using natural markings on animals to identify individual cetaceans, and patterns of recaptures in the form of capture histories to estimate the number of undetected animals and hence the population size (Hammond, 2018). The photo-identification-based mark-recapture technique is most effective for studying small coastal populations of well-marked cetaceans living in a limited area. Cetaceans can also be individually identified by genotyping tissue obtained by biopsy, where the initial biopsy sample serves as the "mark". Subsequent samples are compared to this mark: if they match, the animal is considered "recaptured" while a non-match indicates a newly captured individual (Hammond, 2018). This genetic approach has been most common in studies of large whales (Smith et al., 1999). A more recent study has attempted to use fixed acoustic devices. Longden et al. (2020) used bottlenose dolphin signature whistles, which are unique, individually distinctive vocalizations produced by each dolphin, as a proxy for individual abundance in Walvis Bay, Namibia. These signature whistles function as acoustic markers for individual recognition, allowing researchers to track individual dolphins over time (Caldwell & Caldwell, 1965). In this study, each 'captured' whistle was compared to a whistle catalog created for the Walvis Bay population to identify 'recaptured' whistles.

The distance sampling methodology does not require the identification of individuals, but instead focuses on estimating the detection probability of animals at different distances alongside a series of transects (routes) or from multiple fixed points (Buckland et al., 2001). Distances to detected animals are used to model a detection function that allows the overall detection probability and density within the surveyed area to be determined (Buckland et al., 2001). These results can then be extrapolated to estimate density over the entire area. Observers can identify animals from an aircraft (Panigada et al., 2011), a vessel (Barlow, 1995), or by using acoustic devices, whether towed (Lewis et al., 2018) or fixed (Kyhne et al., 2012). The distance sampling methodology is generally used over large study areas and allows the simultaneous monitoring of several species (Buckland et al., 2004; Daura-Jorge & Simões-Lopes, 2017).

2.2 Line-transect distance sampling: a common practice to estimate cetacean abundance

2.2.1 General principles

Line-transect distance sampling has been extensively refined for estimating the density and abundance of cetacean populations using visual data (Buckland et al., 2001; Buckland et al., 2004). A study area is surveyed from an observation platform (usually an aircraft or vessel) following transects that are either randomly spaced and parallel, systematically spaced and parallel with a random starting point or follow a zigzag pattern (Figure 2.2, Buckland et al., 2001). The zigzag pattern optimizes effort since the platform does not have to move from one line to the next without searching for the animals of interest (i.e. "off-effort", Strindberg and Buckland, 2004). Observers search for animals along the transects in a strip of width w (Figure 2.3). They record visual events, i.e., each encounter of an individual or group of individuals, the radial distance r of the event from the observer and the angle θ between the bow of the vessel and the animals. For each event, the radial distance and angle are used to calculate the perpendicular distance d from the transect line as $d = r \times \sin\theta$. With an aerial-based line transect survey, the perpendicular distance is given by equation $d = h \times \tan\theta$ with h the flight elevation and θ the declination angle of the visual event.

The recorded perpendicular distances of all events can then be plotted on a histogram at a given distance x . From the distribution of perpendicular distances, a detection function $g(x)$ can be fitted, which is the probability of detecting an animal given its distance x from the transect with detection probability = 1 on the transect line as assumed in the Conventional Distance Sampling (CDS, figure 2.3). A key underlying concept is that the probability of detecting an animal decreases as its distance from the observer increases. The overall detection probability p over $0 - w$ can then be estimated from the detection function, a crucial parameter for abundance estimates. The density \hat{D} in a given area is thus estimated as:

$$\hat{D} = \frac{nS}{2wLpg(0)} \quad (2.1)$$

where n is the number of detected groups, S is the estimated average group size, p the overall detection probability over $0 - w$, L the total length of the transect surveyed and $g(0)$ the detection probability on the transect line. Abundance \hat{N} is then estimated as:

$$\hat{N} = A.\hat{D} \quad (2.2)$$

where A is the size of the study area. The variance estimate for \hat{N} is determined by the variance of its components: the encounter rate n/L , the detection probability p , the group

2.2. Line-transect distance sampling: a common practice to estimate cetacean abundance

size S and $g(0)$ (Buckland et al., 2001). The coefficient of variation for abundance is calculated using the delta method as described by Buckland et al. (2001):

$$CV(\hat{D})^2 = CV\left(\frac{n}{L}\right)^2 + CV(p)^2 + CV(S)^2 + CV(g(0))^2 \quad (2.3)$$

Finally, the effective strip (half) width, ESW , is the distance from the transect line for which as many animals are detected beyond the ESW as animals are missed within the ESW . This parameter can be estimated by multiplying p by w (Figure 2.3, Buckland et al., 2004).

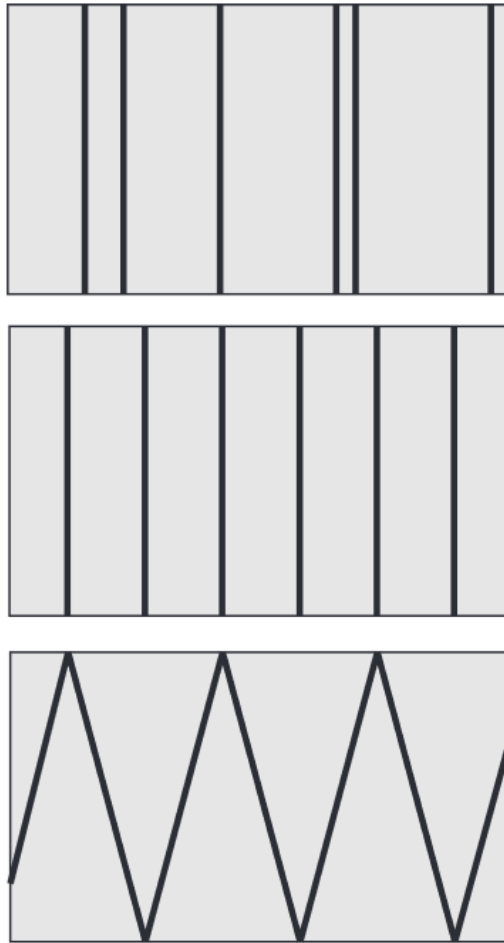


Figure 2.2: Transect designs used in the line-transect distance sampling method. Illustrated here within a simple rectangular survey region are examples of three commonly used designs: (top) randomly spaced parallel lines; (middle) systematically spaced parallel lines with a randomly defined start point; and (bottom) a continuous zigzag sampler with a randomly defined start point. From Strindberg and Buckland (2004).

2.2.2 Application to acoustic data

The line-transect distance sampling approach can be extended to acoustic-based line-transect surveys using towed hydrophone arrays (Marques et al., 2013). This extension involves estimating the perpendicular distances of vocalising animals from the trackline

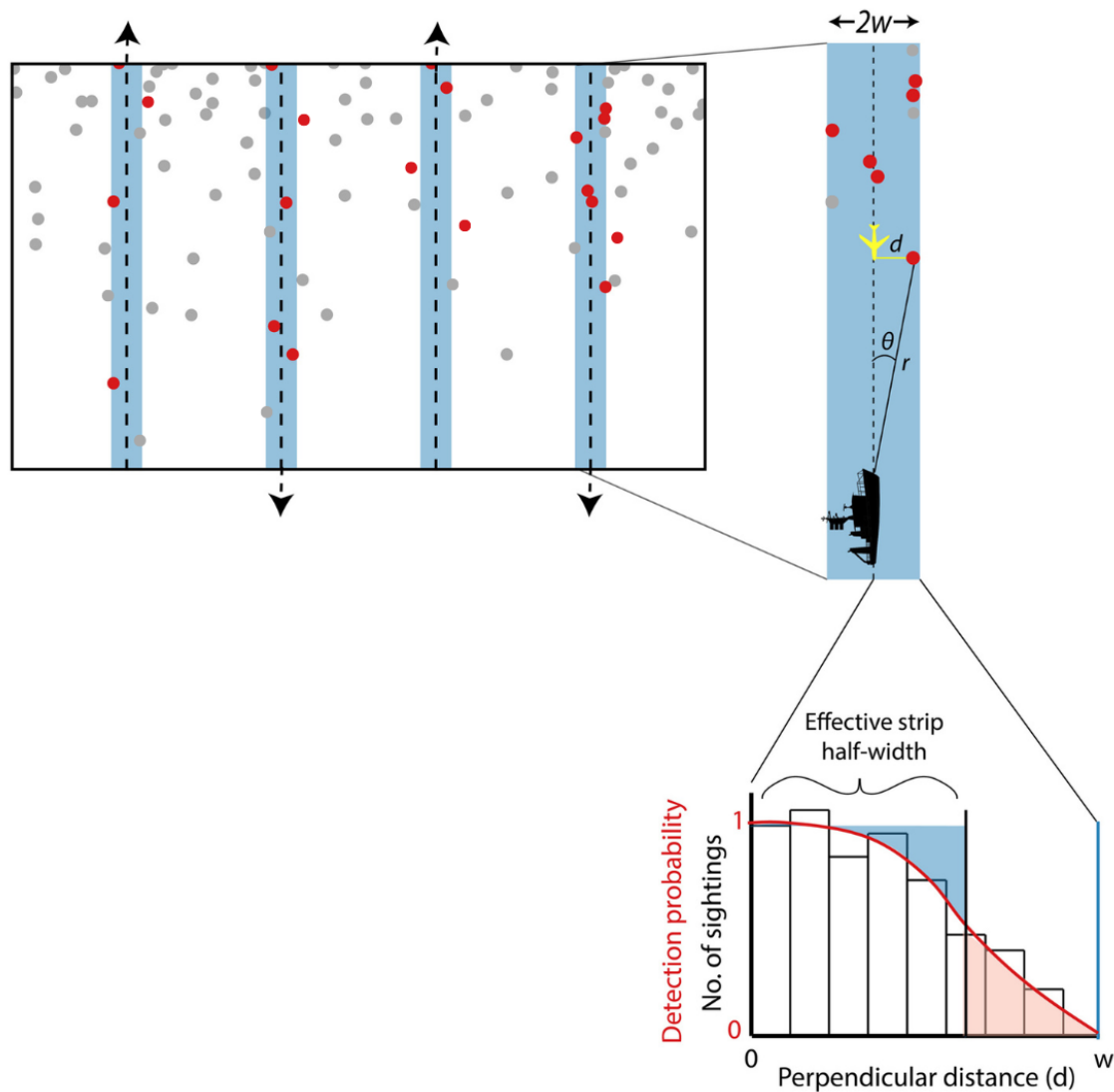


Figure. 2.3: Schematic representation of the elements recorded in a line transect survey. Illustration of a sampling design (top left) in which parallel transects are equidistantly spaced. The shaded areas around the lines represent the strip searched by the observers as they moved in the direction of travel indicated by the arrows at the end of each line. The dots represent animals (or groups of animals); red dots represent detected animals and grey dots represent undetected animals. On the right is an illustration of data collection on one of the transect lines. The width of the strip searched on each side of the line is defined as w . At the end of a survey, the perpendicular distances measured to all the detected animals or groups can be plotted as a frequency histogram. The red curved line represents the detection function fitted to the perpendicular distance data, with detection probability = 1 at perpendicular distance = 0 from the transect. The effective strip half-width, ESW , is the perpendicular distance at which the number of animals detected at longer distances (shown in red) is equal to the number of animals present but not detected at shorter distances (shown in blue). Adapted from Hammond et al. (2021a).

2.2. Line-transect distance sampling: a common practice to estimate cetacean abundance

with multiple hydrophones and using the difference in time of arrival to estimate the position of the vocalising animals (Mellinger et al., 2007; Van Parijs et al., 2009). Another method is to use multipath propagation effects to estimate the distance to the vocal individual (Mellinger et al., 2007); the latter was not used in this study. Knowing the distance of the animals from the transect, a detection function based on the distribution of the perpendicular distances of acoustic events can be fitted to the data, allowing the detection probability p to be estimated. The acoustic group size S needs to be estimated, and this is very complicated because the relationship between vocal behaviour and group size is not well known. Most studies use combined events with visual data to determine the group size of the acoustic events (Barlow & Taylor, 2005; Pirotta et al., 2015) or assume the group size of acoustic events is the same as that of visual events (Gerrodette et al., 2011). Lewis et al. (2007) estimated the abundance of sperm whales in the Mediterranean Sea by estimating acoustic group size because individual sperm whales are easily identified by the regularity of clicks within long click train. When multiple click trains are closely clustered and cannot be distinguished individually, a thorough examination of specific sections within each train helps to determine the number of vocalising animals (Gordon et al., 2020). Another approach to overcome the problem of acoustic group size estimation is to use cue counting to estimate the density of cues produced by animals, such as calls, which can be converted to animal density using the cue production rate of the species (Marques et al., 2009). This method requires detailed behavioural information on the rate of cue production (e.g., vocalisation rate, surfacing rate) and for most species, this information is scarce (Mellinger et al., 2007). Estimates of density or abundance using acoustic data from towed hydrophone arrays have largely focused on sperm whales (Lewis et al., 2018; Gordon et al., 2020; Hastie et al., 2003; Westell et al., 2022) but has also been used for other species such as harbour porpoises (Hammond et al., 2013), vaquitas (Gerrodette et al., 2011), minke whales (*Balaenoptera acutorostrata*, Norris et al., 2017) and beaked whales (Boisseau et al., 2023). Studies have also used towed arrays for delphinids (Rankin et al., 2008). The use of a towed hydrophone may be advantageous in cases involving deep-diving species where visual observation is difficult. However, whether by visual observation or acoustic detection, the line-transect distance sampling approach must meet several assumptions to estimate abundance without bias.

2.2.3 Distance sampling assumptions

CDS usually requires three assumptions to be met:

1. All animals on the transect line are detected, usually referred to as $g(0) = 1$

When this assumption is violated, estimates of abundance are negatively biased. To address this problem, Mark-Recapture Distance Sampling (MRDS) approach was developed to estimate $g(0)$ (Laake & Borchers, 2004),

2. Combining passive acoustic and visual methods for cetacean abundance estimates: a review

2. Animals are detected at their initial location

Animals can either move in response to the survey platform, or independently (random movement). As cetaceans are highly mobile animals, random movement can lead to an overestimation of density because moving animals are more likely to be detected when they are close to the transect line, biasing detection distances downwards (Katsanevakis et al., 2012). This bias can be reduced if the platform moves faster than the animals (Buckland et al., 2001). If animals move in response to the survey platform, their movement can lead to overestimation of density if animals are attracted to the platform and underestimation if they avoid it (Palka & Hammond, 2001). Movement response is difficult to correct at the analysis stage, field protocols should try to avoid such responsive movement, e.g. by using high power binoculars to detect animals before the vessel is close to the animals and triggers their response (Katsanevakis et al., 2012). In acoustic surveys, this assumption has received less attention in the literature likely due to the difficulty of obtaining information about the movements of unobserved animals (Marques et al., 2013),

3. Distance measurements are accurate

Errors in distance measurement have similar effects to those of animal movement. Random errors would generally lead to an overestimation of density. Underestimation of perpendicular distances would lead to overestimation of density, while overestimation of distances would lead to underestimation. This bias can be corrected by modeling measurement error (Borchers et al., 2010).

In addition, there are two less important assumptions: (4) Animals are distributed independently in relation to the transects, and (5) the detection function has a shoulder. Distance sampling is robust to violations of these two assumptions. However, violations of the three first assumptions can lead to significant biases and should be avoided.

2.2.4 Dealing with imperfect detection

In reality, missed events due to detection biases are inevitable. Multi-Covariate Distance Sampling (MCDS) partially addresses these biases by incorporating covariates into the detection function (Marques & Buckland, 2003). MCDS aims to model the effects of additional covariates, in addition to distance, on the probability of detection (Marques & Buckland, 2004). This approach provides insight into the shape of detection across different covariate modes. Several factors can influence visual detectability, including habitat, animal behaviour, species, group size, observer experience and weather (Buckland et al., 2015). In visual surveys, group size and sea state are often the most important factors affecting detectability (Evans & Hammond, 2004; Panigada et al., 2017; Barlow, 1995; Panigada et al., 2011). Barlow and Gerrodette (2001) investigated the factors affecting sighting distance during a vessel-based line transect survey for cetaceans. They used a Generalized

2.2. Line-transect distance sampling: a common practice to estimate cetacean abundance

Additive Model (GAM) to identify the most influential factors, which included species, sighting method (binoculars or not), group size, sighting cue, sea state, swell height, and observer experience. Their results showed that species and sighting method had the largest effects on perpendicular sighting distances. To date, MCDS has rarely been applied to acoustic data because the factors influencing acoustic detectability are not well understood (Boisseau et al., 2023). The acoustic method has been shown to be less affected by sea state than the visual method, although increasing sea state can raise ambient noise levels (Mellinger et al., 2007; Dalpaz et al., 2021). Acoustic detectability can also be negatively affected by group size, as it becomes more difficult to distinguish individual click trains when many animals are vocalizing (Richman et al., 2014). In addition, acoustic detectability can be influenced by ambient noise levels and the directionality of the animals' sound beams; dolphins with narrow beams and high directionality are more likely to be detected when facing the hydrophone (Richman et al., 2014).

The assumption $g(0) = 1$ has been commonly used to estimate cetacean abundance (Barlow, 2006; Øien, 2009; Dick & Hines, 2011; Hildebrand et al., 2015). This hypothesis assumes that all animals present on the transect are detected, which is unlikely because cetaceans spend much of their time at depth, making them visually undetectable, and do not continuously vocalize, making them acoustically undetectable. Consequently, a significant proportion of animals may be missed, leading to negative biases in abundance estimates. To obtain an unbiased abundance estimate, $g(0)$ must be estimated. Several approaches have been used to estimate $g(0)$ in vessel-based and aerial surveys. Barlow et al. (1988) estimated $g(0)$ for harbour porpoises along the U.S. west coast based on their breathing rates observed from shore and helicopter and found that they were near the surface only 23.9% of the time. Laake et al. (1997) estimated $g(0)$ by tracking harbour porpoises from shore during simultaneous aerial surveys in Washington waters. The $g(0)$ was obtained using a detection probability model. They found $g(0)$ to be 0.29 for experienced observers and 0.08 for inexperienced observers. For the same species, Thomsen et al. (2006) used telemetry data from the literature and combined observations from two independent observers to estimate $g(0)$ for harbour porpoises in Dutch coastal waters. They estimated $g(0)$ by multiplying sighting rates from aerial surveys by the average surface time. They estimated $g(0)$ to be equal to 0.24. Hiby and Lovell (1998) used the circle-back method in aerial surveys to estimate $g(0)$. This technique consisted of a single aircraft conducting a line transect survey, leaving the transect 30 seconds after a sighting, circling back, and then resurveying a section of the track line. During the circle-back manoeuvre, observations were off-effort and resumed survey effort when the aircraft returned to the transect. Data from both the first and second passes were used to model detection probability, and $g(0)$ was estimated from the number of detections during the first pass and the number of duplicates during the second pass. They estimated $g(0)$ to be 0.56 for harbour porpoises. This method was

2. Combining passive acoustic and visual methods for cetacean abundance estimates: a review

also used in the SCANS-III survey and they estimated $g(0)$ under good weather conditions to be 0.36 for harbour porpoises and 0.81 for dolphins (Hammond et al., 2021b).

Another approach is the MRDS method, which requires two independent platforms (double platforms) to simultaneously scan the same area and 'mark' animals (Laake & Borchers, 2004). The $g(0)$ and overall detection probability are estimated from the number of animals seen by each platform and by both platforms (duplicate events). The vessel component of the SCANS survey used this double-platform line-transect method with MRDS approach. Two independent visual platforms, the primary and tracker platforms, were used. The tracker platform, which was positioned on a higher platform with high-powered binoculars, searched further towards the horizon. A separate team identified duplicates to ensure that events from both platforms were accurately matched. They estimated different $g(0)$ values for different species, including 0.22 for harbour porpoises, 0.13 for common and striped dolphins, and 0.01 for sperm whales. An interesting approach is to combine acoustic and visual methods within the MRDS framework, which are subject to different detection biases. In the study of Rankin et al. (2020), a double-platform line transect survey was conducted using a towed hydrophone array as the second platform. They estimated $g(0)$ for rough-toothed dolphins to be 0.84 for both platforms combined, with $g(0)$ values of 0.37 for the visual platform and 0.77 for the acoustic platform. Martin et al. (2020) also applied this method to Heaviside's dolphins (*Cephalorhynchus heavisidii*) and dusky dolphins (*Lagenorhynchus obscurus*) in Namibian waters and incorporated this correction into density estimates.

The results of the studies mentioned above indicate that the estimated $g(0)$ values are less than 1, highlighting the importance of estimating $g(0)$. MRDS appears to be a promising approach for estimating $g(0)$ in the context of combined acoustic and visual surveys (Marques et al., 2013). While each method has its own merits and challenges, combining their strengths can lead to more accurate abundance estimates.

2.3 Comprehensive review of efforts to combine visual and acoustic data

2.3.1 Combination of acoustic and visual data: an in-depth examination of the term 'combination'

Visual and acoustic data offer complementary approaches, and an increasing number of research efforts are using the combination of these methods to improve survey efficiency (Verfuss et al., 2018; Duporge et al., 2023). The term "combination" is commonly used in the literature attempting to use acoustic and visual datasets together. A close examination of these studies reveals that they differ in the following broad approaches: (1) comparing

the results of data collected using the visual method alone versus the acoustic method alone, or simply using both methods to increase sample size and spatial and/or temporal coverage (Frouin-Mouy et al., 2022; Duporge et al., 2023), (2) partially combining acoustic and visual data by using one of these methods to support the other (Dalpaz et al., 2021; Oswald et al., 2003), (3) combining acoustic and visual datasets to produce a final combined output (Fleming et al., 2018; Frasier et al., 2021). These examples raise questions about the meaning of combining methods: what does it mean to combine data? At what level? I will review research using both methods and categorise it according to the level of integration, ranging from simple comparison to full integration of both types of data.

2.3.2 Level 1: comparing acoustic and visual data and using both methods to increase sampling

The simplest level is not a combination of acoustic and visual methods, but rather a comparison of the results obtained by each method (e.g. comparison of the number of events or, of the species ecology), or the use of both methods in a survey to increase sample size and spatial and/or temporal coverage. Many studies have compared visual and acoustic results to assess their performance and efficiency in detecting cetaceans (Keen et al., 2018; Liu et al., 2022; Frouin-Mouy et al., 2022; Smith et al., 2020; Clark et al., 2010; Rayment et al., 2018; Gridley et al., 2020). For example, Rayment et al. (2018) compared the performance of acoustic and visual methods to highlight temporal changes in the distribution of southern right whales (*Eubalaena australis*) in New Zealand. Between 2010 and 2012, visual data were collected from shore using a time-lapse camera system, while acoustic data were collected using a recorder deployed near, but not within, the range of the visual point. Despite the different locations, both methods showed similar seasonal occurrence, but during peak seasons the detection rate was higher with the acoustic platform. The authors suggested that this discrepancy was due to the greater range (2 km beyond the visual range) and lower susceptibility to weather conditions.

Other studies have aimed to increase sample size and coverage by using both visual and acoustic methods (Gordon et al., 1999; Burham et al., 2016; Clark et al., 2012; Duporge et al., 2023; Lomac-MacNair et al., 2019; Moore et al., 2010; Ryan et al., 2014; Simard et al., 2015; Swartz et al., 2000; Smultea et al., 2013). For example, Duporge et al. (2023) conducted visual surveys during daylight hours and in shallow waters in the northeastern Red Sea, while acoustic surveys were conducted at night using a towed hydrophone array in deeper waters of the same region and in the Gulf of Aqaba during a similar timeframe to detect whales and dolphins (Figure 2.4). They built a GAM model to understand how cetaceans were spatially distributed in relation to bathymetry and distance from shore with acoustic events. They found an encounter rate of 3.6 per 100 km using the acoustic method, with higher encounter rates in offshore areas and at intermediate depths (500

2. Combining passive acoustic and visual methods for cetacean abundance estimates: a review

-1,000 m). In addition, they identified 35 visual events of five different species: bottlenose dolphin, Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), pantropical spotted dolphin (*Stenella attenuata*), Risso's dolphin (*Grampus griseus*), and spinner dolphin (*Stenella longirostris*). These surveys were conducted in two different areas to fill data gaps on cetacean occurrence in the Red Sea and the Gulf of Aqaba.

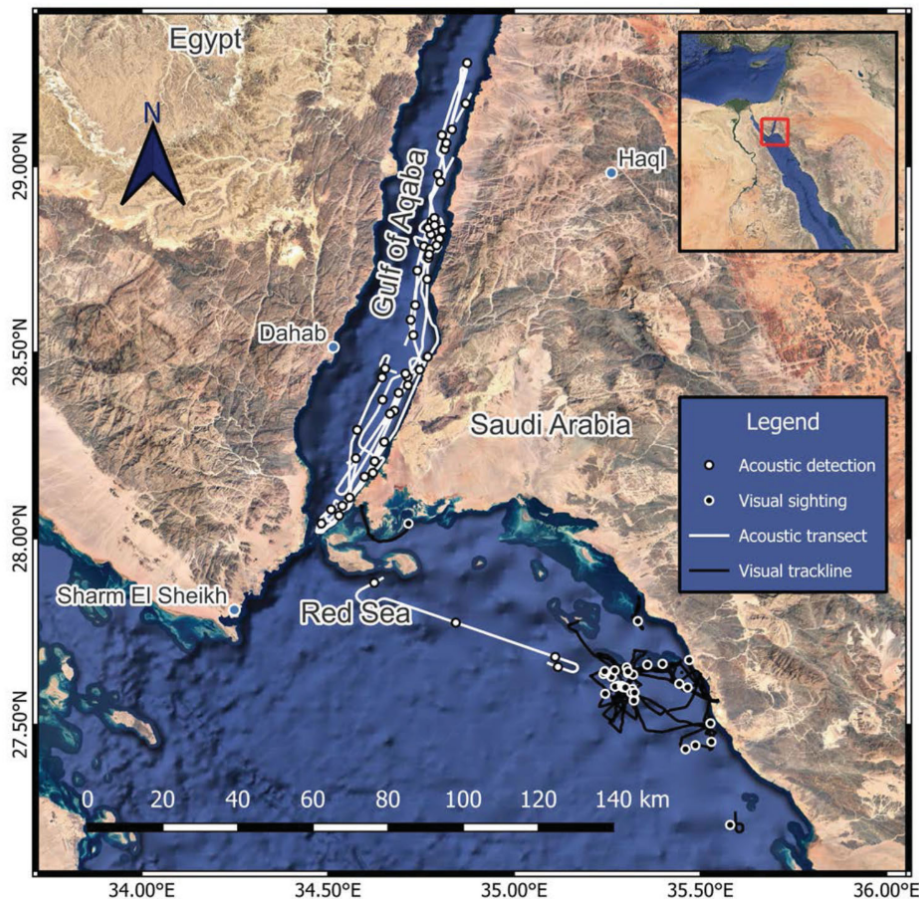


Figure. 2.4: Transect line for acoustic and visual survey with sighting locations in the Gulf of Aqaba and northeastern Red Sea, Saudi Arabia. Visual surveys (black line) were conducted during daylight hours and in shallow waters in the northeastern Red Sea, while acoustic surveys (white line) were conducted at night in deeper waters in the same region and in the Gulf of Aqaba during a similar period. From Duporge et al. (2023)

In a more concerted effort of comparison, some studies compare the results of each method obtained independently (Barlow & Taylor, 2005; Williamson et al., 2016; Booth et al., 2013; Brookes et al., 2013). A good example is the study of Booth et al. (2013), which aimed to determine the habitat preferences of harbour porpoises west of Scotland. Visual and acoustic line transects were conducted, mostly simultaneously, from the same platform between 2003 and 2010. GAMs were used from each type of data to investigate relationships between density and oceanographic covariates and to predict species distribution. Although each method was subject to different biases, the results showed a consistent distribution

pattern: harbour porpoises tend to inhabit coastal regions and show a preference for water depths between 50 and 150 meters in slope areas (Figure 2.5).

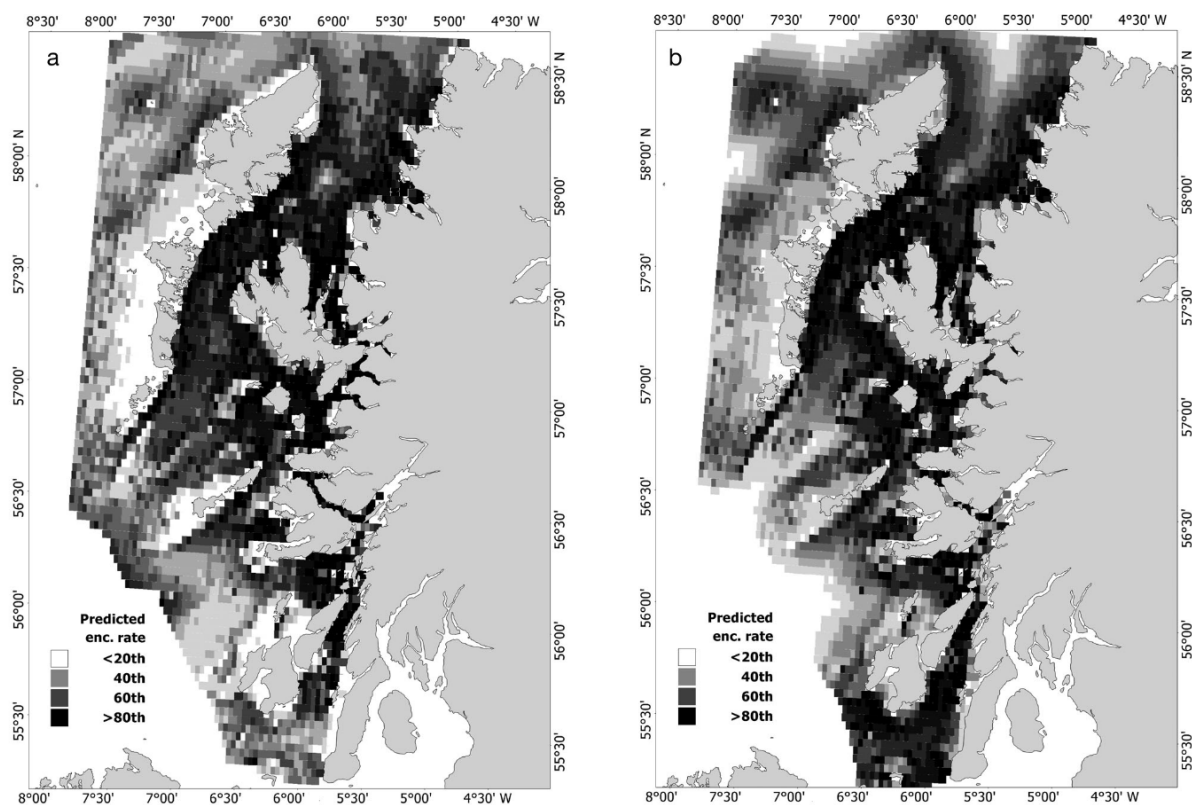


Figure 2.5: Relative distribution patterns of harbour porpoises on the west coast of Scotland. Predictions modeled using (A) visual and (B) acoustic data (displayed in percentiles). Enc.: encounter. From Booth et al. (2013).

2.3.3 Level 2: partially combining acoustic and visual data by using one method to support the other

This section refers to studies that go beyond simple comparisons by using one method to complement the analysis of data from the other method without fully integrating visual and acoustic data into the same analysis. For example, as distinguishing dolphin species by their vocalisations can be challenging (Azzolin et al., 2014), acoustic experts may attempt to identify species vocalisations by using visual data in combination with acoustic data to improve sound libraries with confirmed visual events (Oswald et al., 2003).

Another approach is to estimate a parameter (such as detection probability or group size) of either the acoustic or visual method by using the other (Gerrodette et al., 2011; Craig et al., 2004; Kyhn et al., 2012; Akamatsu et al., 2001; Jacobson et al., 2017). When estimating abundance using the acoustic method, some parameters need to be estimated. For example, Jacobson et al. (2017) aimed to estimate the effective detection area (EDA) of passive

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acoustic sensors in order to convert them into density estimates for harbour porpoises in Monterey Bay, California. The EDA represents the area around a logger in which as many vocalisations are missed as are detected outside it, and it can serve as a measure of the area monitored by an acoustic sensor (Nuuttila et al., 2018). Harbour porpoise densities were estimated from aerial line transect surveys and interpolated across the study area to obtain densities at C-PODS locations from aerial surveys. The proportion of porpoise-positive seconds (PPS) was estimated from acoustic data. With these two pieces of information, they used a Bayesian model to combine visual and acoustic data with previously published information to estimate EDA. Another example is the estimation of acoustic detection probability of vaquita in the Gulf of California (Gerrodette et al., 2011). Deeper areas were surveyed using only visual methods, while shallow waters were surveyed using only acoustic methods because they were too shallow for large vessels (Figure 2.6). The $g(0)$ for the visual platform was 0.57, based on the literature using two independent observer teams on the same vessel. However, the acoustic detection probability was unknown and was estimated within a calibration area where both acoustic and visual line-transect surveys were conducted (on separate vessels and different transects). By using the line transect abundance estimator and setting the visual and acoustic estimators as equal, they were able to estimate $g(0)$ for the acoustic platform, which was 0.41.

2.3.4 Level 3: combining acoustic and visual datasets to produce a final combined output

The third level represents the highest level of combination, characterised by balanced use of each method with a concerted effort to develop statistical methods beyond simple summation (Sigourney et al., 2023). This approach integrates data from both methods to estimate parameters of interest such as occurrence, detection probability, or abundance. Distribution models are developed using both acoustic and visual data and are often compared to models developed using only one method (Frasier et al., 2021; Thompson et al., 2014; Fleming et al., 2018). For example, Thompson et al. (2014) aimed to combine acoustic data from fixed stations with visual events from a variety of surveys (mostly aerial and vessel-based surveys) to model spatial patterns of bottlenose dolphin occurrence in waters adjacent to the Moray Firth Special Area of Conservation in north-east Scotland. PAM arrays were used to detect echolocation clicks, which provide information on dolphin occurrence. A Generalized Estimating Equation (GEE) was used to predict spatial variation in the probability of detecting all species combined. However, PAM alone does not allow species identification. Visual data were used to determine the likely species identity of dolphins sighted in each grid cell based on local habitat. Classification tree analyses were used to predict the probability that a dolphin encountered in each cell was likely to be a bottlenose dolphin. The results of both models were integrated in each cell to predict the probability of encountering bottlenose dolphins (Figure 2.7). In contrast, Fleming et al.

2.3. Comprehensive review of efforts to combine visual and acoustic data

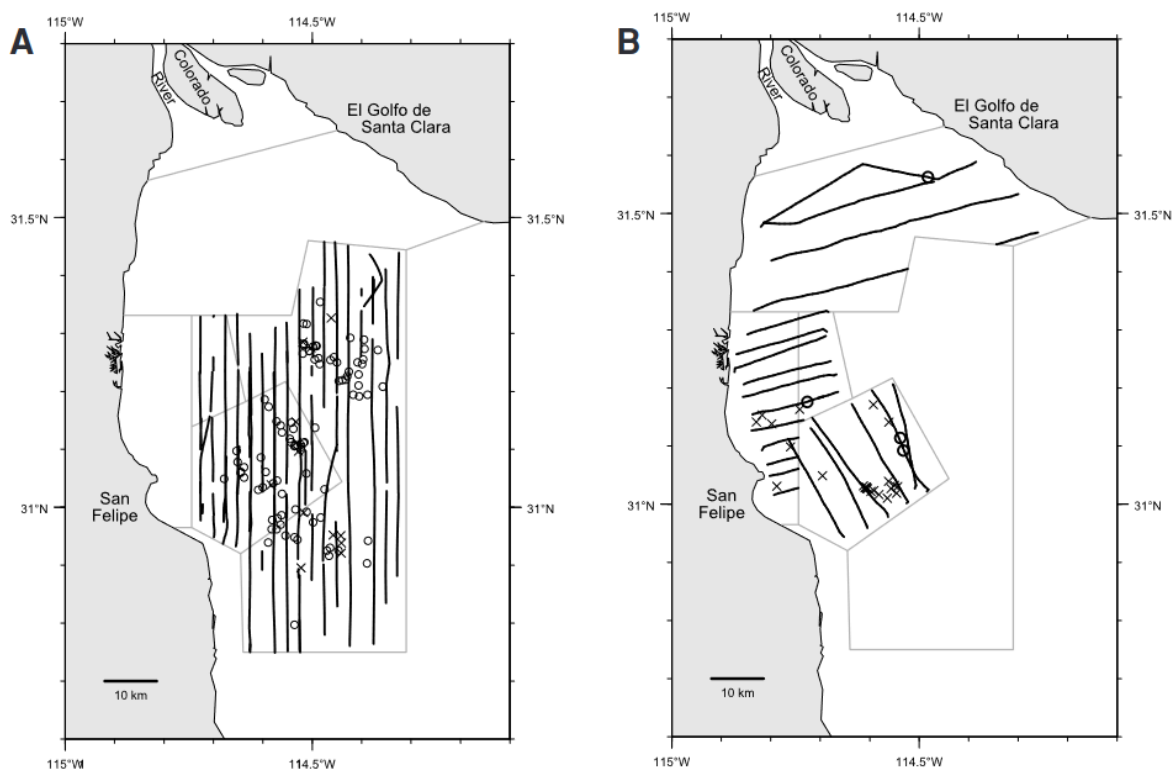


Figure. 2.6: Transects and vaquita detections in the Gulf of California. (A) Visual-based line transect surveys were conducted in deep waters, while (B) acoustic-based line transect surveys were conducted in shallow waters. Strata are shown as grey lines. On-effort vaquita detections are indicated by circles, and off-effort detections are indicated by crosses (x). From Gerrodette et al. (2011).

(2018), compared distributions predicted by species distribution models using visual and acoustic data collected simultaneously from the same platform during a transect survey in the California Current. They developed a combined model using both acoustic and visual events and showed that the data were complementary rather than directly additive, as the predictions obtained from acoustic data differed from those obtained from visual data.

Some studies have attempted to combine data to estimate detection probability for each detection method and for both (Martin et al., 2020; Akamatsu et al., 2008; Rankin et al., 2020; Richman et al., 2014). These studies require both acoustic and visual data to be collected simultaneously and from a single vessel. For example, Martin et al. (2020) estimated the $g(0)$ of each platform for Heaviside's and dusky dolphins in Namibian waters. They used the MRDS approach as described in section 2.2.4, but relied solely on acoustic data to estimate abundance with correction for missed events. They estimated $g(0)$ to be 0.84 for Heaviside's dolphins and 0.93 for dusky dolphins. Other studies have integrated visual and acoustic estimates to produce a conclusive abundance estimate (Sigourney et al., 2023; Gerrodette et al., 2011).

2. Combining passive acoustic and visual methods for cetacean abundance estimates: a review

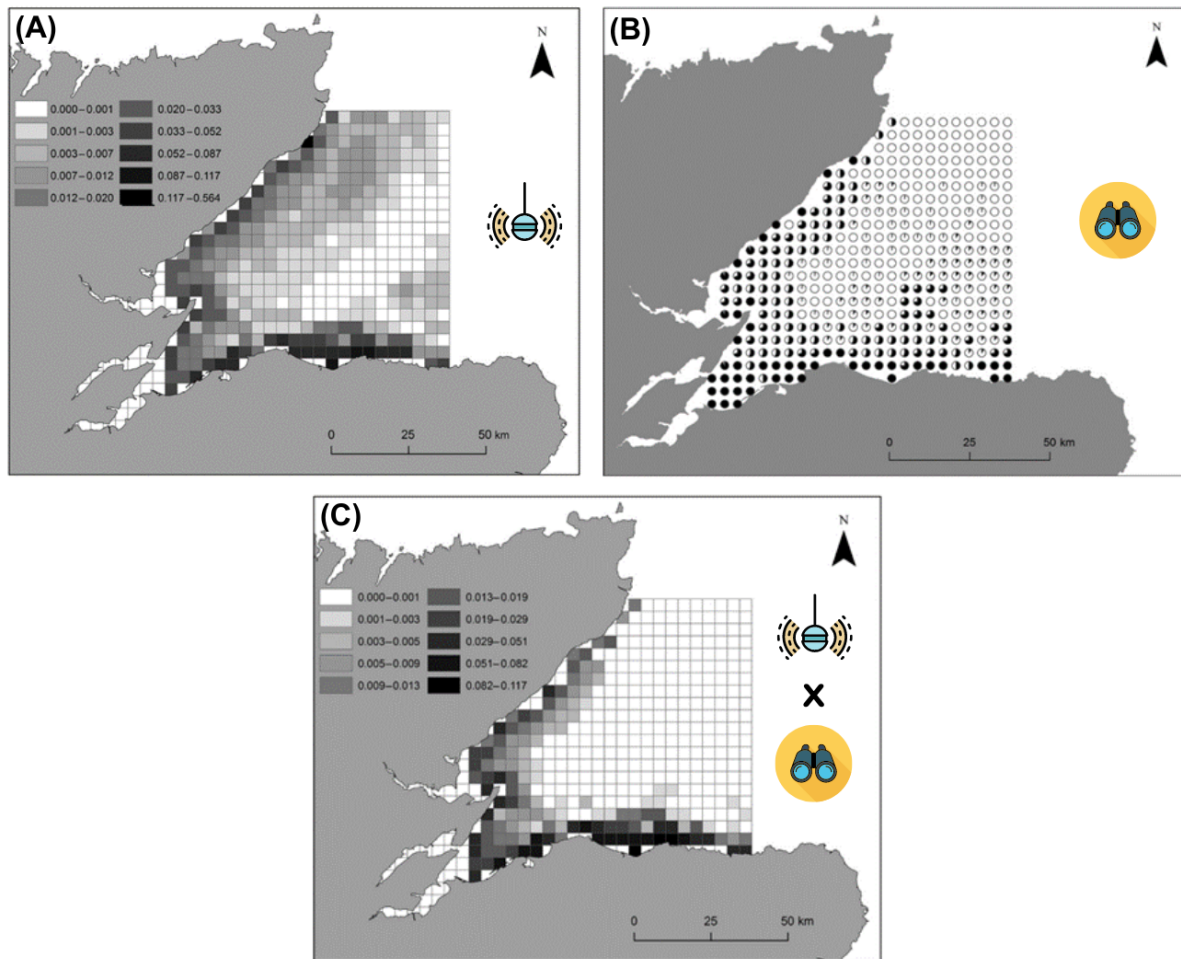


Figure. 2.7: Predicted spatial variation in the probability of detecting bottlenose dolphins in the Moray Firth Special Area of Conservation in north-east Scotland. (A) Predicted spatial variation in the probability of detecting dolphins (of all species) based on the Generalized Estimating Equation (GEE) analysis of passive acoustic data. (B) Classification tree-based predictions of the probability (black portion of the pie chart) that dolphins encountered in each 4 × 4 km grid cell were likely to be bottlenose dolphins. (C) Spatial variation in the predicted probability of bottlenose dolphin occurrence across the Moray Firth. Predictions for each cell are based on the outputs of both the GEE and the classification tree analyses and represent the probability of bottlenose dolphins occurring in that cell at any given hour. Adapted from Thompson et al. (2014).

2.3.5 Conclusion

By categorising the studies into three levels of combination, it becomes clear that there are different ways of using acoustic and visual approaches together, from simple comparison to the integration of both types of data into species distribution models. The term "combination" can have multiple meanings, and it is challenging to define this term when combining visual and acoustic data.

Several perspectives emerge from this review. Some studies use simultaneously collected-data, such as in vessel-based line transect surveys, where data are collected simultaneously

2.3. Comprehensive review of efforts to combine visual and acoustic data

from the same platform, facilitating the temporal and spatial matching of the data due to the common transect travelled (Gridley et al., 2020; Richman et al., 2014). Conversely, there are situations of simultaneous but spatially misaligned collection, where visual data are collected from a moving platform and acoustic data from fixed points or another platform, making event matching almost impossible (Craig et al., 2004; Jacobson et al., 2017). There are also studies with different temporal extents where one method is used more extensively than the other and all data are included in the analysis (Frasier et al., 2021; Thompson et al., 2014; Moore et al., 2010). To make the best use of both methods, some studies use only data with temporal overlap between the two methods (Jacobson et al., 2017; Williamson et al., 2016). Alternatively, others collect data without spatial overlap in separate zones (Gerrodette et al., 2011).

Finally, "**combined data**" typically refers to data collected simultaneously from the same platform, ensuring temporal and spatial alignment. But can data collected simultaneously on different platforms be combined? Should they be in the same zone? And if collected in different zones, can they still be combined? In this thesis, I propose to define the combination of acoustic and visual data as exploiting the strengths of both methods to estimate a parameter of interest within a study area.

3

General methodology

This chapter aims to provide a comprehensive overview of the oceanographic features and biodiversity of the study area, as well as the ecology of the species studied. Furthermore, this chapter aims to describe the origin of the data, the collection process, and the subsequent data analysis procedures which are common to chapters 4, 5 and 6.

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3.1 The Mediterranean Sea: a study area

3.1.1 The origin of the Mediterranean Sea

The name 'Mediterranean Sea' is derived from the Latin '*Mare Mediterraneum*', which means 'sea in the middle of the land'. This ancient Roman term was used to describe the body of water enclosed by the land masses of Europe, Africa and Asia. Many millions of years ago, the movement of the African tectonic plate towards the Eurasian plate caused the Mediterranean Sea to close. Theories suggested that this process created a narrow passage between the Atlantic Ocean and the western Mediterranean Sea, giving rise to the Strait of Gibraltar (Blanc, 2002). This closure caused the water level in the Mediterranean to drop significantly due to increased evaporation, effectively turning it into a vast, almost dry salt lake (Krijgsman et al., 1999). Subsequently, erosion and tectonic tilting caused the Strait of Gibraltar to widen and deepen, resulting in a sudden influx of water from the Atlantic Ocean. This event formed the Mediterranean Sea as we know it today (Garcia-Castellanos et al., 2009).

3.1.2 Diverse topography and geography

The Mediterranean is an intercontinental sea bordered by southern Europe, northern Africa and western Asia. It extends over 4,000 km from west to east and up to 800 km from north to south. This sea is partially enclosed and is connected to the Atlantic Ocean by a narrow 22-kilometer passage known as the Strait of Gibraltar. It is also connected to the Black Sea by the Bosphorus Strait. The connection to the Red Sea through the Suez Canal was artificially created in the 19th century for commercial purposes.

The Mediterranean Sea can be divided into two distinct basins: the western basin and the eastern basin (Figure 3.1). These are connected by the Straits of Messina and Sicily, located between mainland Italy, Sicily and Tunisia. The western basin can be further subdivided into three areas: the Alborán Sea, the Algerian-Provençal Sea, and the Tyrrhenian Sea. The eastern basin, meanwhile, includes the Ionian, Levantine, Adriatic and Aegean seas.

Covering a vast area of 2,967,000 km^2 , the Mediterranean Sea has an average depth of 1,500 m and reaches its maximum depth of 5,139 m in the Ionian sea (Eakins & Sharman, 2010). Characterised by its diverse topography, including submarine canyons, seamounts, steep slopes, and narrow continental shelves, the Mediterranean Sea is known for its complex geological features (Sardà et al., 2004).

3. General methodology

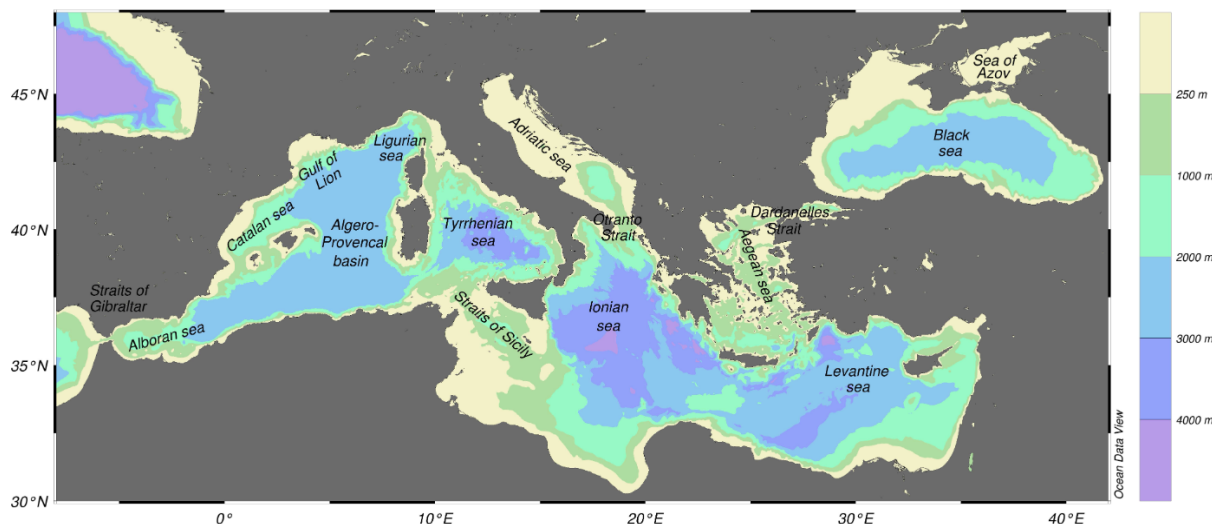


Figure. 3.1: Major seas, connecting straits and bottom topography of the Mediterranean Sea. From Siokou-Frangou et al. (2010).

3.1.3 Navigating the complex currents

The water circulation in the Mediterranean Sea is conditioned by its semi-enclosed configuration (Millot & Taupier-Letage, 2005). The Mediterranean Sea acts as a natural reservoir, but its water sources, which include river inflow, precipitation, and runoff, are insufficient to offset the substantial evaporation, estimated at about $3,500 \text{ km}^3$ per year (La Violette, 1994; Boudouresque, 2004). As a consequence, water levels decrease and salinity levels rise progressively from west to east. To counteract this water loss, there is an inflow of cool, low-salinity Atlantic Ocean waters into the surface layer of the Mediterranean Sea, occurring between depths of 30 to 200 m through the Strait of Gibraltar (Bethoux, 1979; Dubois-Dauphin, 2016). As it travels east along the Algerian coast, seasonal eddies disrupt the current and export surface water toward the Balearic Islands (Benzohra & Millot, 1995; Millot et al., 1997). Upon reaching the Strait of Sicily, the water mass bifurcates: one portion warms up and becomes saltier, descending into the Levantine Sea at depths between 200 and 600 m (Dubois-Dauphin, 2016), where it eventually retraces its path westward, returning to the western basin through the Strait of Sicily before exiting via the Strait of Gibraltar (Bas, 2009; Pinardi et al., 2006; Coll et al., 2010; Millot & Taupier-Letage, 2005; Tsimplis et al., 2006). The other part enters the Tyrrhenian Sea and follows a clockwise circulation pattern along the western coast of Italy, ultimately reaching the Ligurian Sea and then the Gulf of Lion. Here, the influence of strong coastal winds, such as the Mistral and the Tramontane, pushes warm surface waters away from the coastline, facilitating the upwelling of cold, nutrient-rich water towards the surface in the Gulf of Lion (Figure 3.2). Except for specific regions like the Gulf of Lion and areas of freshwater inflow such as the Nile Delta and the Northern Adriatic Sea, the Mediterranean Sea exhibits a pronounced nutrient gradient from west to east.

As a consequence, primary production decreases as one moves eastward, marked by a seasonal pattern featuring winter and spring blooms of phytoplankton, followed by reduced productivity during the summer months (López García, 2021).

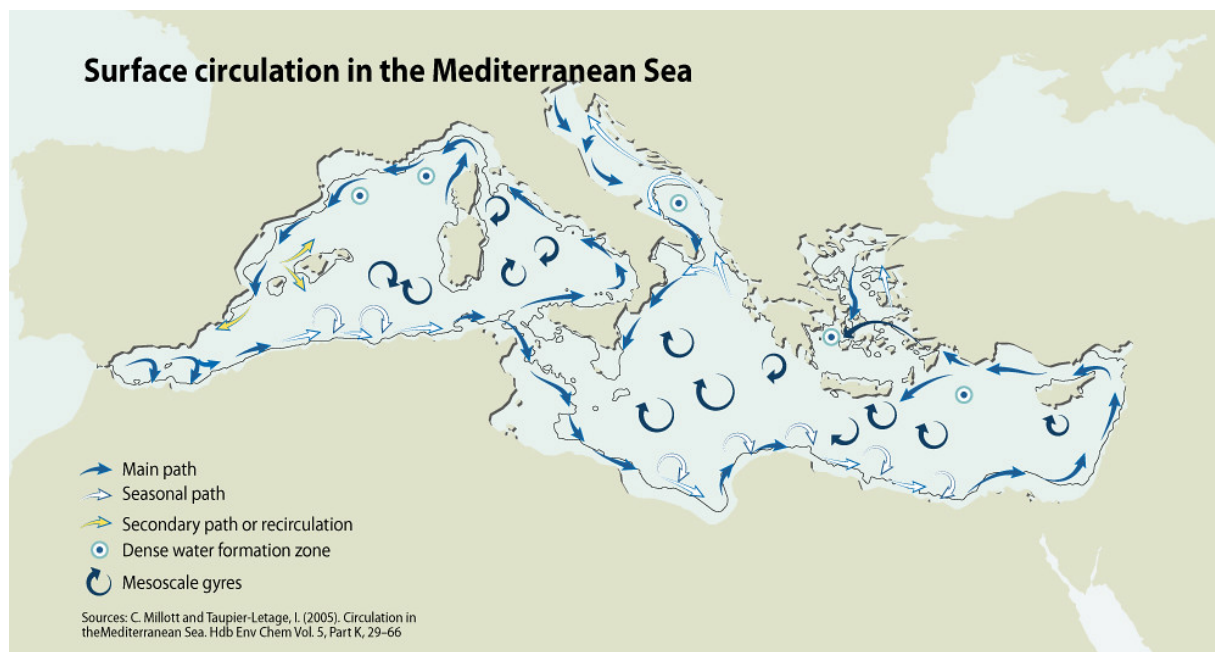


Figure. 3.2: Map of the surface circulation patterns in the Mediterranean Sea. General circulation in the Mediterranean originates from the differences in density between the different water masses. It is structured in three layers (surface, intermediate, and deep) and shows a cyclonic pattern around the western and eastern sub-basins (according to Millot and Taupier-Letage, 2005). From López García (2021).

3.1.4 Diving into the rich biodiversity

Although classified as an oligotrophic basin, the Mediterranean Sea remarkably hosts over 7.5% of the world's global biodiversity, comprising approximately 17,000 marine species (Costello et al., 2010), and has a notably high endemism rate of 20.2%. This sea is home to several emblematic species, including cetaceans, sea turtles, and the critically endangered Mediterranean monk seal (*Monachus monachus*), which has disappeared from certain regions of the Mediterranean due to insufficient population monitoring and conservation programs (SPA/RAC-UNEP/MAP, 2020; Notarbartolo Di Sciara et al., 2009). All these species require significant conservation efforts (Bearzi et al., 2004; Casale et al., 2018; Mo et al., 2011; Notarbartolo Di Sciara et al., 2009). Furthermore, the Mediterranean Sea serves as the primary spawning area for the Atlantic bluefin tuna (*Thunnus thynnus*; MacKenzie et al., 2009). In addition to its charismatic fauna, the Mediterranean Sea hosts several endangered biogenic habitats that give rise to rich and unique ecosystems. These include the endemic seagrass *Posidonia oceanica*, a key ecosystem engineer that provides essential ecosystem services such as protecting coastlines from erosion,

3. General methodology

providing spawning grounds and nurseries for marine species, and sequestering carbon (Boudouresque et al., 2015). Additionally, the vermetid reefs, a carbonate bioconstruction formed through the close association of the red alga *Neogoniolithon*, are recognised as vital biodiversity hotspots (Hüseyinoğlu et al., 2020; Boudouresque, 2004). Furthermore, Mediterranean wetlands and other habitats serve as vital stopovers or breeding grounds for millions of migratory birds from distant regions. Despite its relatively modest size, the Mediterranean Sea is a major reservoir of marine and coastal biodiversity and plays a key role in maintaining ecological balance.

3.1.5 Anthropogenic treats

The Mediterranean Sea is widely recognised as one of the world's biodiversity hotspots due to its specific richness (Lejeusne et al., 2010) but is also one of the most threatened regions (Coll et al., 2012; Coll et al., 2010; Cuttelod et al., 2008). The escalating urbanization of its coastal areas has led to unprecedented anthropogenic pressures on this marine ecosystem. Approximately 512 million people inhabit the countries bordering the Mediterranean Sea, with more than a third of them concentrated along its coastlines (UNEP/MAP Plan Bleu, 2020). Coastal development, driven by industrialization and tourism, poses substantial threats to biodiversity and disrupts critical habitats that numerous species rely upon, such as seagrass meadows, oyster reefs, and bioconstructions (Beck et al., 2011; Holon et al., 2015; Ingrosso et al., 2018). Coll et al. (2010) identified the main threats impacting a diverse range of Mediterranean biodiversity, spanning from microorganisms to top predators across both deep-sea and coastal environments. Threats to marine biodiversity based on published data and expert opinion were ranked from 0 to 5 for 13 taxonomic groups from this time (2010) and predicted for ten years later (Figure 3.3). Habitat degradation was the most important threat to marine biodiversity in the Mediterranean Sea followed by fishing impacts, pollution, climate change, eutrophication and the introduction of alien species. These ongoing disturbances, which are accumulating and being intensified by climate change (Micheli et al., 2013), have resulted in significant and potentially irreversible damage to marine ecosystems (Brierley & Kingsford, 2009). They have led to fluctuations in sea temperature (Pisano et al., 2020), changes in chemical composition of the water column (Kress et al., 2014), and shifts in the distribution and abundance of various species (Azzellino et al., 2017; Givan et al., 2018; Tsikliras, 2008). These climatic changes may lead to long-term disruptions in the food web structure, with major consequences for ecosystem functioning (Albouy et al., 2020; Hattab et al., 2016). As a result of the cumulative impacts of these human-induced pressures, an increasing number of species are facing threats (Lascelles et al., 2014).

Among these threatened species, many cetaceans are listed on the IUCN Red List of Threatened Species due to human-induced factors. Research studies have highlighted

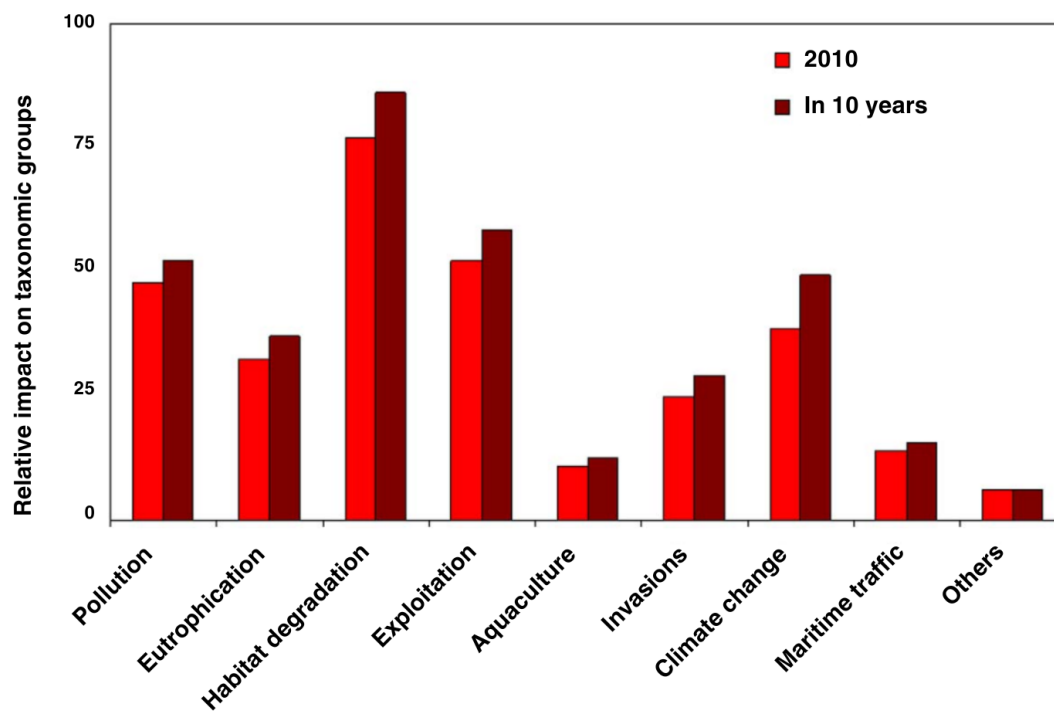


Figure. 3.3: Threats to biodiversity in the Mediterranean Sea. Data published on specific taxa and expert opinion. Threats to diversity were ranked from 0 to 5 for 13 taxonomic groups and results are shown as the percentage of the ranking to the maximum values. From Coll et al. (2010).

significant declines in the population sizes of certain cetaceans, mainly due to human pressures in the Mediterranean Sea (Bearzi et al., 2003; Gonzalvo et al., 2008). The Mediterranean fin whale population (*Balaenoptera physalus*) has experienced a significant decline in the number of mature individuals, from less than 10,000 to less than 2,500 since 2010 (Notarbartolo Di Sciara & Tonay, 2021). Ship strikes have been identified as the main cause of their mortality (Panigada et al., 2006). Cetaceans are at the top of the trophic food web and are widely distributed in a variety of habitats. As a result, they face a variety of anthropogenic threats that have increased dramatically in the last decade, including entanglement in fishing gear, chemical contamination, and disruptions caused by maritime traffic (Pace et al., 2015; Micheli et al., 2013). For example, Campana et al. (2015) showed that cetaceans were more frequently observed in areas with fewer vessels, suggesting a relationship between maritime activity and disturbances faced by these cetaceans. Indeed, vessel presence can cause direct disturbance to cetaceans, such as physical harm due to collision, as well as entanglement in fishing gear and exposure to elevated noise (Geijer & Jones, 2015; Cuvertoret-Sanz et al., 2020; Simonis et al., 2020). This can lead to long- and short-term changes in distribution patterns (Arcangeli et al., 2015; Castellote et al., 2012). The Mediterranean is one of the world's busiest waterways, and increasing maritime traffic, along with explosions, seismic activity, military sonar, fishing and recreational vessels, contribute significantly to noise pollution (Notarbartolo Di Sciara & Tonay, 2021).

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Because cetaceans rely on their acoustic senses for vital functions such as communication and echolocation, they are highly sensitive to noise. Elevated noise levels can disrupt their hearing, force them to abandon habitats, alter their behaviour or mask acoustic signals essential for communication and prey detection (Cuttelod et al., 2008; Hildebrand, 2005; Aguilar Soto et al., 2006; Richardson et al., 1995). In extreme cases, it can cause temporary or permanent hearing loss (Southall et al., 2008). Interaction with fisheries has also been assessed as a potential concern due to depleted fish stocks (Gómez-Campos et al., 2011), bycatch incidents (Bearzi et al., 2003), and entanglement in fishing gear. Cetaceans naturally follow boats to take advantage of discarded fish from the net, which increases the risk of bycatch and entanglement accidents. This type of accident has been documented in many areas in the Mediterranean Sea, where areas frequented by fisheries overlap with habitats especially used by bottlenose dolphins and common dolphins (Milani et al., 2019; Diaz López, 2006; Tudela et al., 2005). These threats, particularly when cumulative, may significantly disrupt the stability of cetacean populations, especially in regions where high biodiversity intersects with these cumulative threats (Coll et al., 2012; Micheli et al., 2013). These potential outcomes highlight the importance of conducting further studies to better understand these issues and inform cetacean conservation efforts.

3.2 Studied cetaceans

To date, 25 cetacean species have been regularly or occasionally observed in the Mediterranean Sea (Notarbartolo Di Sciara & Tonay, 2021). Of these, nine species are considered as resident, as they are regularly found in the region. Among them are striped dolphin, bottlenose dolphin, common dolphin, long-finned pilot whale (*Globicephala melas melas*), Risso's dolphin, rough-toothed dolphin (*Steno bredanensis*) as well as Cuvier's beaked whale (*Ziphius cavirostris*), sperm whale and fin whale. Four species are categorised as visitors, including killer whale (*Orcinus orca*), false killer whale (*Pseudorca crassidens*), common minke whale, and humpback whale (*Megaptera novaengliae*). Additionally, 12 species are identified as vagrants (extremely rare, found outside their native distributional range) in the Mediterranean Sea, comprising Atlantic harbour porpoise (*Phocoena phocoena phocoena*), Black Sea harbour porpoise (*Phocoena phocoena relicta*), dwarf sperm whale (*Kogia sima*), northern bottlenose whale (*Hyperoodon ampullatus*), Blainville's beaked whale (*Mesoplodon densirostris*), Gervais' beaked whale (*Mesoplodon europaeus*), Sowerby's beaked whale (*Mesoplodon bidens*), short-finned pilot whale (*Globicephala macrorhynchus*), sei whale (*Balaenoptera borealis*), North Atlantic right whale (*Eubalaena glacialis*), grey whale and Indian Ocean humpback dolphin (*Sousa plumbea*).

This thesis focused exclusively on small cetaceans considered resident species in the Mediterranean Sea, specifically the striped dolphin, the bottlenose dolphin, the common dolphin, the long-finned pilot whale, the Risso's dolphin and the rough-toothed dolphin, with an emphasis on the first three species.

3.2.1 Striped dolphin (*Stenella coeruleoalba*)

The striped dolphin takes its name from the distinctive blue and white stripes that appear when submerged, which is reflected in its Latin name '*coeruleoalba*' where '*caeruleus*' means sky-blue and '*albus*' means white (Figure 3.4). It is characterized by a prominent black stripe extending from the eye to the anal region and a white 'flame' pattern running along its body to the falciform dorsal fin (Archer, 2018). Striped dolphins typically exhibit adult body lengths ranging from 1.80 m to 2.50 m (Archer, 2018).

On a global scale

Striped dolphins have a wide distribution that includes the Pacific, Indian and Atlantic Oceans and their adjacent waters (Figure 3.5, Archer, 2018). Typically, they are found in deep tropical to warm waters, inhabiting regions between latitudes 50°N and 40°S, although occasional sightings further north have been reported (Isaksen & Syvertsen, 2002). They are often observed in offshore waters and frequently associated with upwelling regions, where cold, nutrient-rich waters rise to the surface (Ballance et al., 2006).



Figure. 3.4: The Striped dolphin (*Stenella coeruleoalba*). Illustration from NOAA Fisheries.

These sociable and demonstrative animals typically form groups of between 15 and 500 individuals (Archer, 2018). They are opportunistic feeders, whose distribution is closely

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linked to the movements of their prey, which includes fish, cephalopods, and crustaceans. The dietary preferences of striped dolphins seem to vary across different geographical areas. For example, in Japan and South Africa waters, they prey primarily on lanternfish (family Myctophidae), which have diurnal migratory patterns (Ringelstein et al., 2006; Spitz et al., 2006). In contrast, Mediterranean striped dolphins tend to prefer squids (family Ommastrephidae, Histioteuthidae and Onychoteuthidae), while those in the Northeast Atlantic Ocean commonly consume a variety of mesopelagic fish (family Myctophidae), squids (family Onychoteuthidae, Histioteuthidae and Cranchiidae) and crustaceans (family Pasiphaeidae and Sergestidae, Ringelstein et al., 2006; Spitz et al., 2006).

Globally, the IUCN Red List of Threatened Species has listed the striped dolphin in 2018 as a species of ‘Least concern’ (Braulik, 2019).

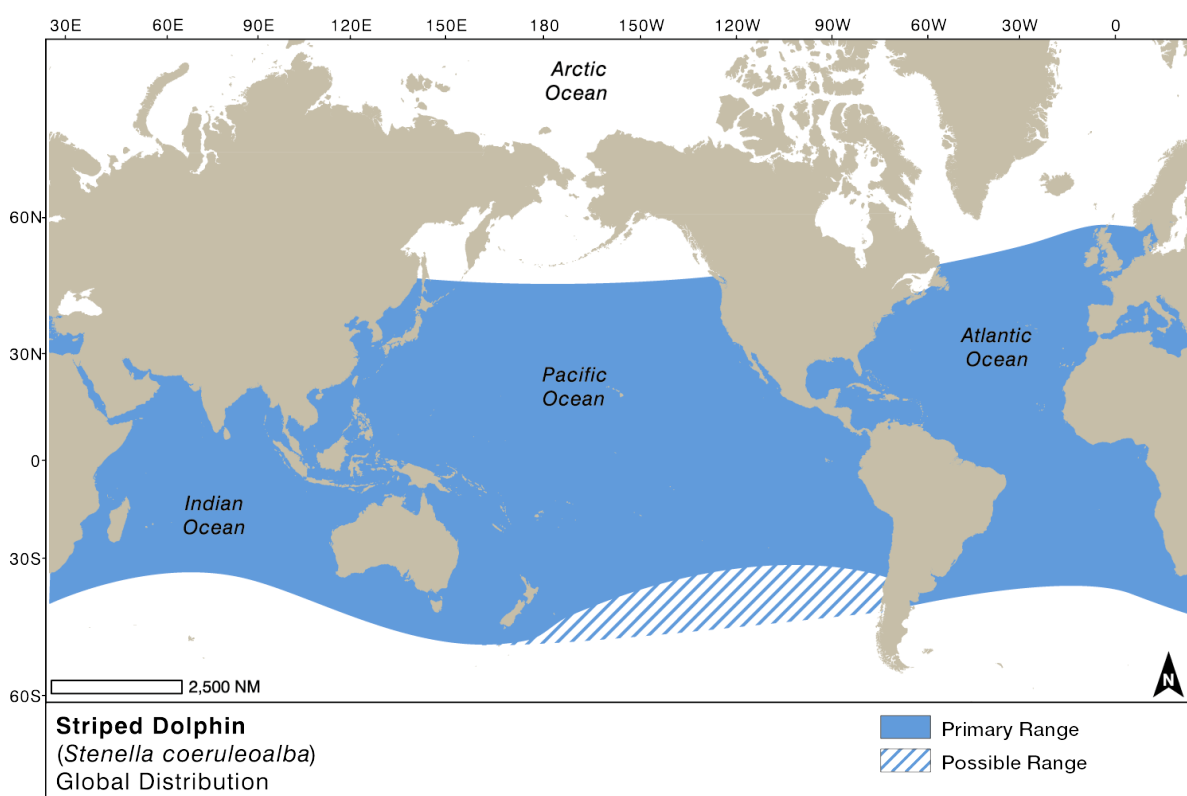


Figure. 3.5: Distribution range of the striped dolphin. From Archer (2018).

In the Mediterranean Sea

Striped dolphins are recognised as the most abundant cetacean species in the Mediterranean Sea, with a decreasing abundance gradient from west to east (Aguilar, 2000; Cañadas et al., 2023; Forcada et al., 1994; Kinzelbach, 1997; Notarbartolo Di Sciara & Tonay, 2021). They are particularly abundant in certain regions such as the Alborán Sea, the Balearic Islands, the Gulf of Lion and the Ligurian Sea (Cañadas et al., 2023). While less frequently observed in the eastern Mediterranean Sea, the striped dolphin is considered a regular

resident in the Levantine basin (Kerem, 2012). As an oceanic species, striped dolphins have a wide distribution spanning from the continental shelf to the open ocean, with a preference for slope and deep waters (Azzellino et al., 2008; Cañadas et al., 2023). These dolphins often form groups that vary in size, ranging from 1 to 60 individuals (Forcada et al., 2004). They are also known to frequently associate with mixed groups that include common dolphins and Risso's dolphins (Notarbartolo Di Sciara & Tonay, 2021).

The ASI aerial survey conducted in the Mediterranean Sea in 2018 resulted in an estimate of 418,589 striped dolphins ($CV = 0.14$) in the entire basin (Panigada et al., 2024). The striped dolphin has been listed by the IUCN Red List of Threatened Species as 'Least concern' in the Mediterranean Sea in 2022 (Lauriano, 2022).

3.2.2 Bottlenose dolphin (*Tursiops truncatus*)



Figure. 3.6: The Bottlenose dolphin (*Tursiops truncatus*). Illustration from NOAA Fisheries.

The bottlenose dolphin, has been recognised since ancient Greek and Roman times for its frequent presence along the Mediterranean coast. The term '*Tursiops*' is derived from the Latin words '*Tursio*' (meaning 'marine animal') and '*ops*' (meaning 'appearance'), while '*truncatus*' comes from '*trunco*' (meaning 'truncated'), referring to the worn teeth that Montagu (1821) used as an identifying feature (Wells & Scott, 2018). This species can be distinguished by its variable colouration on the dorsal side, ranging from light to dark, depending on the population (Figure 3.6). There is a clear separation between the melon and the short rostrum. Their body length ranges from 2.5 to 3.8 m (Wells & Scott, 2018).

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There are currently four recognised subspecies of bottlenose dolphin: the Black Sea bottlenose dolphin (*Tursiops truncatus ponticus*), Lahille's bottlenose dolphin (*Tursiops truncatus gephyreus*), which inhabits Brazilian to Argentinian waters, the eastern tropical Pacific bottlenose dolphin (*Tursiops truncatus nuuanu*), and the common bottlenose dolphin (*Tursiops truncatus truncatus*), found widely across various regions (Committee on Taxonomy, 2023).

In this manuscript and the subsequent chapters, we will specifically employ the term "bottlenose dolphin" (together with its Latin name, *Tursiops truncatus*) to refer exclusively to the common bottlenose dolphin subspecies.

On a global scale

The bottlenose dolphin is a widely distributed species that inhabits both temperate and tropical waters (Figure 3.7) and is one of the most well-known cetacean species (Leatherwood & Reeves, 1989; Reynolds III et al., 2013; Wells & Scott, 2018; Bearzi et al., 2009). It can be found in a variety of environments, including coastal areas such as lagoons, semi-enclosed bays, and estuaries, as well as offshore waters (Wells & Scott, 2018). The size of dolphin groups can vary between populations, ranging from small groups of 2-15 individuals to large aggregations of up to 1,000 individuals (Wells & Scott, 2018). Coastal populations tend to form smaller groups than offshore populations (Wells & Scott, 2018). Their diet consists mainly of fish, squids and crustaceans, and can vary depending on the specific habitats they inhabit (Wells & Scott, 2018). However, they have a consistent preference for fish, especially from the Scianidae, Scombridae, and Mugilidae families (Wells & Scott, 2018).

According to the IUCN Red List of Threatened Species, the global population of common bottlenose dolphins has been listed as 'Least concern' in 2018 (Wells et al., 2019).

In the Mediterranean Sea

In the Mediterranean waters, the bottlenose dolphin is one of the most frequently sighted dolphin species (Bearzi et al., 2009; Notarbartolo Di Sciara & Demma, 1994; Reeves & Notarbartolo di Sciara, 2006). Bottlenose dolphins have been reported from different areas of the Mediterranean Sea, including the Alborán Sea, the Algero-Provencal basin, the Tyrrhenian Sea, the Adriatic Sea, the Aegean Sea, the Ionian Sea, and the Levantine Sea (Bearzi et al., 2009; Cañadas et al., 2023), highlighting the widespread distribution of the species throughout the basin. The Mediterranean subpopulation of bottlenose dolphin mainly occupies coastal regions (Bearzi et al., 2009), although it shows adaptability by inhabiting a wide range of habitats, including continental shelf waters and offshore waters as well (Cañadas et al., 2023; Laran et al., 2017). These dolphins are often observed in

relatively small groups, typically consisting of around 10 individuals, and can occasionally be seen with short-beaked common dolphins and long-finned pilot whales (Cañadas et al., 2023; Bearzi et al., 2009).

The estimated population of this species in the Mediterranean basin is 75,762 (CV = 0.21, Panigada et al., 2024). The Mediterranean population of bottlenose dolphins was assessed for the ICUN Red List of Threatened Species in 2021 and is listed as ‘Least concern’ (Natoli et al., 2021).

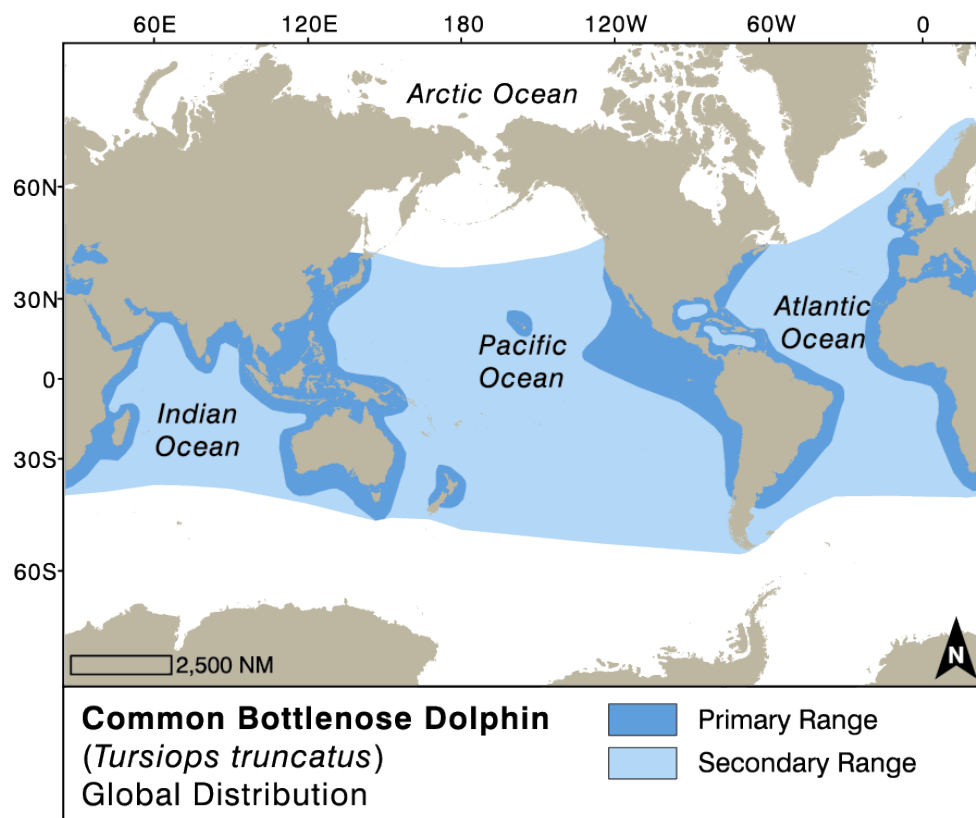


Figure. 3.7: Distribution range of the bottlenose dolphin. From Wells and Scott (2018).

3.2.3 Common dolphin (*Delphinus delphis*)

The name ‘common dolphin’ is derived from its worldwide presence. The scientific name ‘*Delphinus delphis*’ is derived from Greek and Latin. ‘*Delphis*’ comes from the Greek word ‘*delphis*’, meaning dolphin, while ‘*Delphinus*’ is the Latin term for dolphin, which in turn is derived from the Greek. The common dolphin is easily recognisable by the distinctive ‘hourglass’ pattern on its flanks (Figure 3.8). Just below the dorsal fin, a ‘V-shaped pattern’ can be seen on both sides of the body, with a yellow/tan coloration towards the front of the dorsal fin and a light grey shading behind it. A dark grey cape covers the dolphin’s back, and a dark stripe runs from the lower jaw to the flipper.



Figure. 3.8: The Common dolphin (*Delphinus delphis*). Illustration from NOAA Fisheries.

These dolphins are of medium size, typically between 1.5 and 2.3 m in length (Perrin, 2018).

The common dolphin includes four distinct subspecies: the common common dolphin (*Delphinus delphis delphis*), the eastern North Pacific long-beaked common dolphin (*Delphinus delphis bairdii*), the Black Sea common dolphin (*Delphinus delphis ponticus*), and the Indo-Pacific common dolphin (*Delphinus delphis tropicalis*, Committee on Taxonomy, 2023; Cunha et al., 2015).

In this manuscript, we will refer specifically to the subspecies common common dolphin when using the term ‘common dolphin’.

On a global scale

As its name suggests, the common dolphin has a wide distribution (Figure 3.9), favoring tropical and temperate waters (Perrin, 2018). This species occupies both neritic (coastal) and oceanic (open sea) habitats, with its dietary preferences varying according to the environment. In coastal waters, common dolphins tend to feed on epipelagic shoaling fish (Perrin, 2018), while in oceanic waters, particularly in highly productive areas, they mainly consume cephalopods and fish from deep waters that migrate to shallower depths at night (Ballance et al., 2006; Au & Perryman, 1985; Palacios, 2003). Regarding their social structure, common dolphins can form groups of between 50 and 100 individuals,

sometimes more (Notarbartolo Di Sciara & Tonay, 2021). They also have been observed interacting in mixed groups with other dolphin species, such as striped and spinner dolphins.

In terms of conservation status, the common dolphin was listed in 2020 as ‘Least concern’ on the Red List of Threatened Species (Braulik et al., 2021).

In the Mediterranean Sea

In the Mediterranean Sea, the population of common dolphins is more abundant in the Alborán Sea, the westernmost part of the basin (Bearzi et al., 2003; Cañadas et al., 2023). These dolphins have also been documented in several areas, including the Maltese Islands, the Aegean Sea, the south-eastern Tyrrhenian Sea, the Adriatic and the eastern Ionian Sea, with occasional sightings off the coasts of Algeria and Tunisia (Bearzi et al., 2003). They can be found in both offshore and coastal waters, even in areas where the water depths do not exceed 70 m (Brand et al., 2019; Milani et al., 2021). Coastal common dolphins are typically observed in groups ranging from 4 to 10 individuals, occasionally forming larger groups of up to 35 individuals (Milani et al., 2021). The Mediterranean population of common dolphins tends to form smaller groups compared to populations in other regions (Notarbartolo Di Sciara & Tonay, 2021).

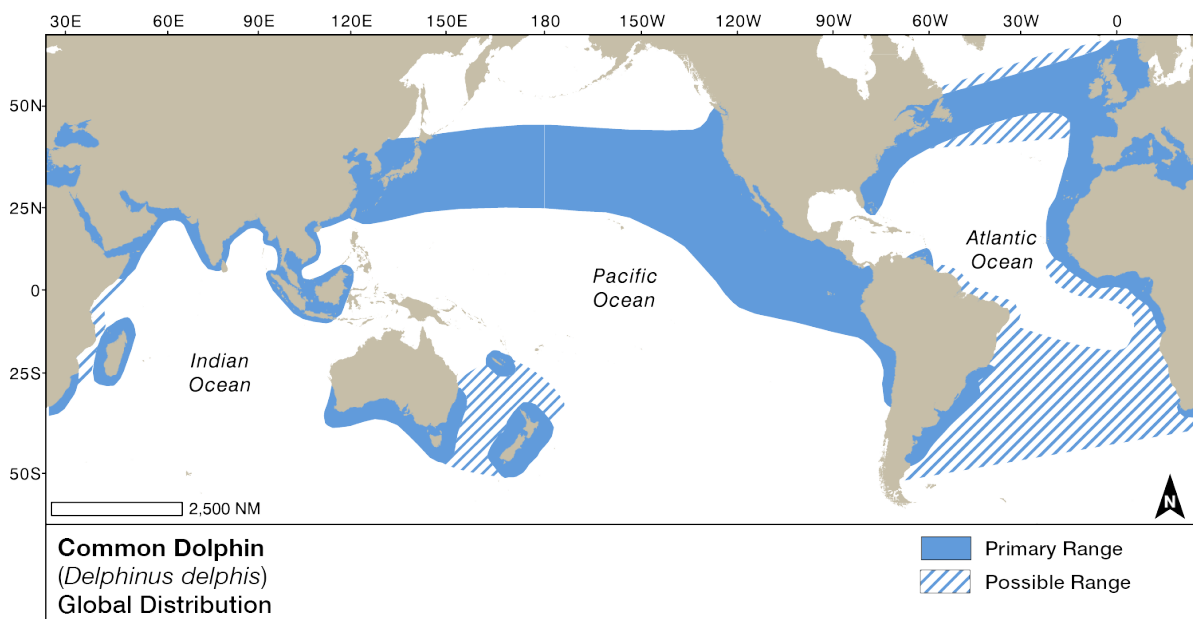


Figure. 3.9: Distribution range of the common dolphin. From Perrin (2018).

Despite the challenges associated with studying common dolphins due to the rarity of sightings, the current estimated abundance of these dolphins in the Mediterranean basin is 64,925 individuals (CV = 0.40, Panigada et al., 2024). However, their status in the Mediterranean was assessed in 2022 as ‘Endangered’ on the IUCN Red List of Threatened Species, indicating a concerning decline in their population (Bearzi et al., 2022).

3.2.4 Long-finned pilot whale (*Globicephala melas melas*)

The long-finned pilot whale, one of the largest toothed cetaceans, can be distinguished by its deep black colour and unique cup-shaped melon (Figure 3.10). This distinctive melon shape is the basis for its scientific name, ‘*Globicephala*’ which is derived from the Greek words ‘globe’ (*Globei*) and ‘head’ (*kephalos*), as well as the Greek term ‘*melas*’ meaning ‘black’. It also has a long, rounded dorsal fin and scythe-like fins. Long-finned pilot whales are classified as medium-sized, with an average length of 6 m (Olson, 2018).

The species comprises two subspecies: the southern long-finned pilot whale (*Globicephala melas edwardii*) and the northern Atlantic long-finned pilot whale (*Globicephala melas melas*).

Throughout the manuscript, we will use the term ‘long-finned pilot whale’ (*Globicephala melas*) exclusively to refer specifically to the subspecies known as the northern Atlantic long-finned pilot whale.



Figure 3.10: The Long-finned pilot whale (*Globicephala melas melas*). Illustration from NOAA Fisheries.

On a global scale

The long-finned pilot whale’s range encompasses the Southern Ocean and the North Atlantic Ocean, including regions such as the east coast of the United States, the Gulf of St. Lawrence, North Africa, the western Mediterranean Sea, the North Sea, Greenland, and the Barents Sea (Figure 3.11, Abend and Smith, 1999; McComb-Turbitt et al., 2021). They are

primarily found in offshore waters and along the continental slope (Abend & Smith, 1999). Their habitat shows a seasonal shift in areas such as the Strait of Gibraltar, where they are more dispersed in deeper waters in the fall than in the summer (De Stephanis et al., 2008a). They make deep dives, often exceeding 500 m, primarily for foraging purposes (Baird et al., 2002). Squids, especially *Loligo pealeii*, dominate their diet (Gannon et al., 1997). Long-finned pilot whales live in groups comprised of 6 to 20 individuals, each with its own social structure (Ottensmeyer & Whitehead, 2003).

According to the most recent assessment of the IUCN Red List of Threatened Species in 2018, the long-finned pilot whale is listed as ‘Least Concern’ (Minton et al., 2018).

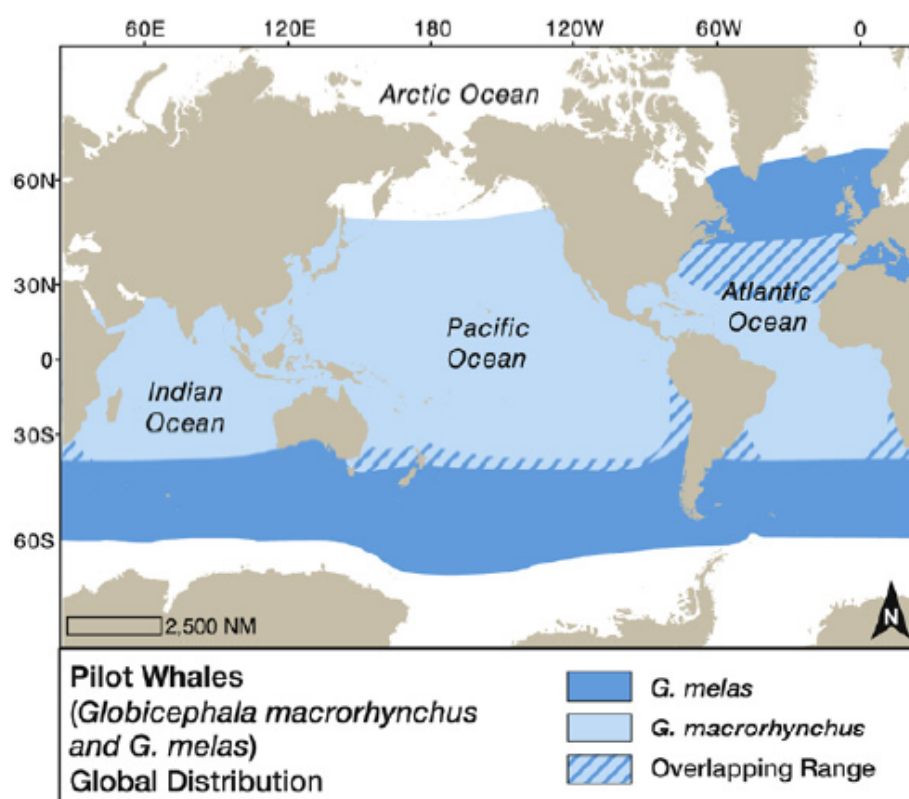


Figure. 3.11: Distribution range of the long-finned pilot whale. From Olson (2018).

In the Mediterranean Sea

The long-finned pilot whale is mainly found in the western basin (Cañadas et al., 2023; Kerem, 2012). It is known to occur annually in the Alborán Sea (De Stephanis et al., 2008a), and less frequently in the Balearic Islands, the Provençal Basin, the Ligurian Sea, and the Tyrrhenian Sea (Notarbartolo Di Sciara & Tonay, 2021). These pilot whales generally have a preference for deep pelagic waters (Azzellino et al., 2008; Cañadas et al., 2023). Pods of long-finned pilot whales consist of relatively small groups, usually comprising a few dozen individuals (Cañadas et al., 2023; Notarbartolo Di Sciara & Tonay, 2021; De Stephanis et al., 2008b).

3. General methodology

Based on the results of the ASI aerial survey, the abundance of Mediterranean long-finned pilot whales was estimated to be around 5,866 individuals (CV = 0.41, (Panigada et al., 2024)). The population size of long-finned pilot whales is declining, and they were listed as ‘Endangered’ on the IUCN Red List of Threatened species in 2021 (Gauffier & Verborgh, 2021), reflecting their precarious conservation status.

3.2.5 Risso’s dolphin (*Grampus griseus*)



Figure. 3.12: The Risso’s dolphin (*Grampus griseus*). Illustration from NOAA Fisheries.

The Risso’s dolphin, scientifically known as *Grampus griseus*, derives its name from the Latin and Greek words, ‘*Grampus*’ meaning ‘large’ and ‘*griseus*’ meaning ‘grey’. This species is easily recognised by the absence of a rostrum and its distinctive grey colouring adorned with white scars (Figure 3.12). These scars result from social interactions between individuals. These white markings do not regain their pigmentation over time, making them a useful indicator of the approximate dolphin’s age (Hartman et al., 2016). The more extensive the white markings, the older the individual. Risso’s dolphins are characterised by their large size, typically between 3.6 and 4 meters (Hartman, 2018).

On a global scale

Risso’s dolphins are found in temperate and tropical waters worldwide, inhabiting regions between 64°N and 46°S latitude (Figure 3.13, Jefferson et al., 2013). While they can be encountered in both coastal and deep-sea environments, they exhibit a distinct preference for mid-temperate waters within the 30° to 45° latitude range (Jefferson et al., 2013). They

are found in continental shelf and slope habitats and have been observed in depths ranging from 400 to 1,000 m (Baird, 2009; Jefferson et al., 2013). Their primary diet consists mainly of cephalopods, with the most abundant ones belonging to the Histioteuthidae family (Luna et al., 2022). Risso's dolphins often travel in groups of 10 to 50 individuals (Baird, 2009). In some exceptional cases, observed groups have been notably larger, with estimates exceeding 4,000 individuals (Baird, 2009).

This species has received limited attention in terms of scientific research, resulting in a relatively small number of regional population estimates. According to the IUCN Red List of Threatened Species, Risso's dolphins were listed under the 'Least concern' conservation status in 2018 (Kiszka & Braulik, 2018).

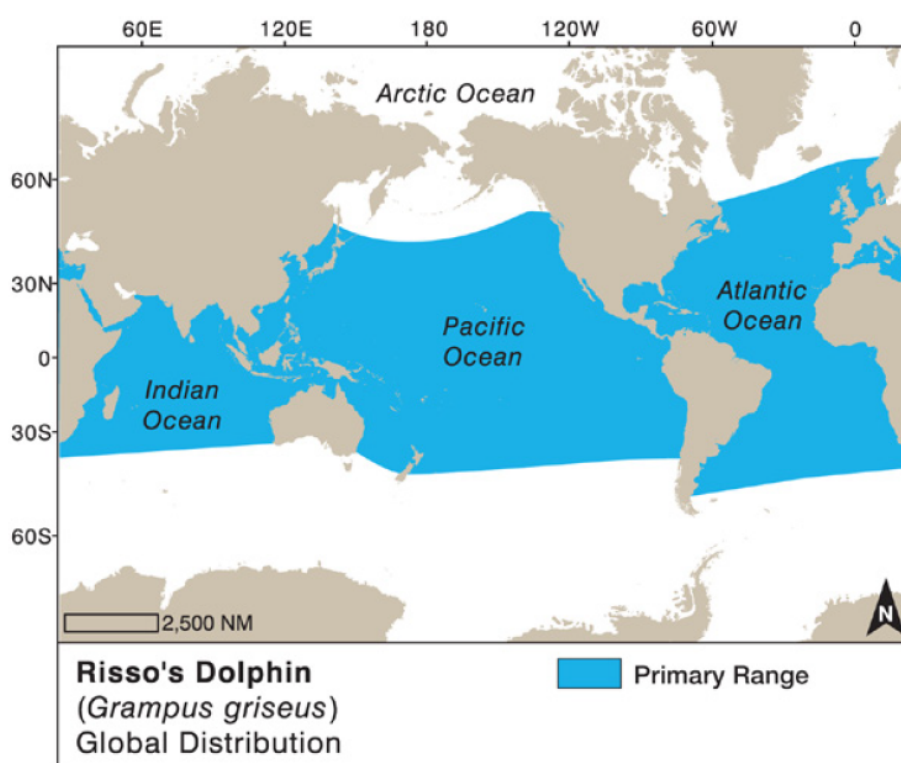


Figure. 3.13: Distribution range of the Risso's dolphin. From (Hartman, 2018).

In the Mediterranean Sea

The Risso's dolphin is one of the least known cetacean species in the Mediterranean Sea (Bearzi et al., 2011). The presence of Risso's dolphins has been documented mainly along the northern coast of the western Mediterranean Sea, specifically in the Alborán Sea (Cañadas et al., 2002; Gannier, 2005; García-Polo et al., 2014), the Ligurian Sea (Azzellino et al., 2008; Gannier, 2005; Di Méglio et al., 1999; Notarbartolo Di Sciara & Tonay, 2021), the Tyrrhenian Sea (Campana et al., 2015; Marini et al., 1996), the Ionian Sea (Dimatteo et al., 2011; Frantzis et al., 2003), the Adriatic Sea (Azzellino et al., 2016) and the

3. General methodology

Aegean Sea (Frantzis et al., 2003). They mainly concentrate in deep-sea regions, primarily in the western basin (ACCOBAMS, 2021). They mainly feed on cephalopods (Bearzi et al., 2011; Luna et al., 2022). Risso's dolphins form relatively small groups of 4 to 8 individuals. However, these group sizes can occasionally expand to include as many as 55 individuals (Notarbartolo Di Sciara & Tonay, 2021). They often share their habitat with other cetacean species such as striped dolphins, common dolphins, short-finned pilot whales and rough-toothed dolphins.

The estimated population of Risso's dolphins throughout the entire Mediterranean basin stands is around 26,659 (CV = 0.29) individuals (Panigada et al., 2024). Their status in the Mediterranean was recently assessed in 2022 as 'Endangered' on the IUCN Red List of Threatened Species (Lanfredi et al., 2022).

3.2.6 Rough-toothed dolphin (*Steno bredanensis*)



Figure. 3.14: The Rough-toothed dolphin (*Steno bredanensis*). Illustration from NOAA Fisheries.

The nomenclature '*stenos*' derives from the Greek term '*stenos*' meaning "narrow," and is directly related to the distinctly narrow morphology of the rostrum of the species (West et al., 2011). The rough-toothed dolphin is characterised by a melon and a rostrum with no clear boundary, resulting in a melon that appears leaden and uniform (Figure 3.14). Other distinctive physical characteristics include prominent dorsal and pectoral fins, a dark back and pale sides with occasional white patches. This species is characterised by its

comparatively small size compared to other dolphin species, typically in the range of 2.1 to 2.7 m (Miyazaki & Perrin, 1994).

On a global scale

There is little information on distribution patterns or preferred habitats in most areas where rough-toothed dolphins have been documented. It is known to occur in tropical and temperate waters in the Atlantic, Indian, and Pacific Oceans (Figure 3.15, West et al., 2011). Its distribution extends from 40°N to 35°S latitude (Kiszka et al., 2019). Rough-toothed dolphins primarily inhabit offshore regions but it is not uncommon to encounter them in continental shelf or shallow waters (West et al., 2011). While studies of their diet are limited, rough-toothed dolphins exhibit dietary preferences for fish and cephalopods (West et al., 2011). For example, in Hawaii, they consume fish from the families Atherinidae, Scomberesocidae and Coryphaenidae and in the Northeast Pacific, they also feed fish from the Atherinidae family (West et al., 2011). They are usually observed in relatively small groups, typically between 10 and 20 individuals (West et al., 2011).

In terms of conservation status, the rough-toothed dolphin was listed as ‘Least Concern’ on the IUCN Red List of Threatened Species in 2018 (Kiszka et al., 2019).

In the Mediterranean Sea

Mediterranean rough-toothed dolphins are understudied (Kerem et al., 2016). Over time, as more evidence of their presence within the basin has been documented, their status has evolved. They were initially categorized as visitors to the Mediterranean Sea, but due to increasing documentation of their occurrence (Boisseau et al., 2010), they have since been reclassified as a regular species in the region. This species is primarily found in the eastern basin and does not extend its range westwards beyond the Strait of Sicily (Boisseau et al., 2010). Two distinct clusters of rough-toothed dolphins have been documented in the eastern basin, with one inhabiting the Levantine Sea and the other the Ionian Sea (Foskolos et al., 2023; Kerem et al., 2016; Kerem, 2020). While their primary habitat is mid-pelagic waters, they have also been occasionally observed in shallow coastal waters (Kerem, 2012). They form small groups of about 10 individuals, but larger groups of 40 to 160 individuals have been documented (Kerem, 2012; Watkins et al., 1987).

Sightings of rough-toothed dolphins occur in the eastern Mediterranean but encounters remain low (ACCOBAMS, 2021; Boisseau et al., 2010), making it difficult to estimate their abundance. There is no information on density estimates, a rough estimate suggests around 1,200 individuals (ACCOBAMS, 2021; Kerem et al., 2021). The conservation status of the rough-toothed dolphin was assessed in 2020 by the IUCN Red List of Threatened Species and it is listed as ‘Near threatened’ in the region (Kerem et al., 2021).

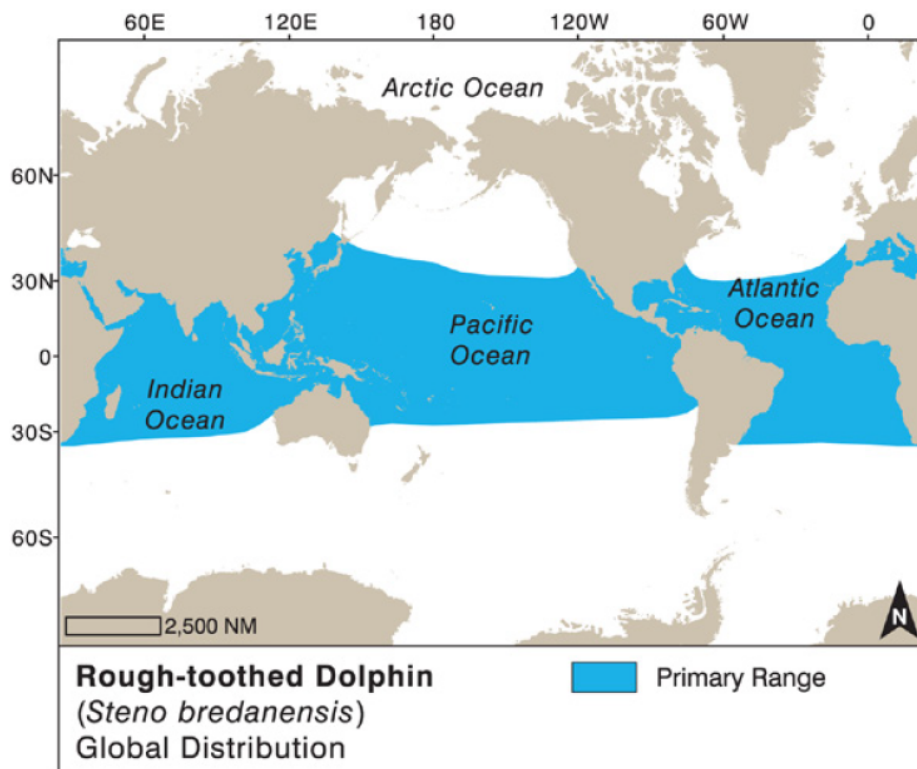


Figure. 3.15: Distribution range of the Rough-toothed dolphin. From Jefferson (2018).

3.3 Previous visual and acoustic surveys in the Mediterranean Sea

Numerous surveys have been conducted in the Mediterranean Sea to assess the abundance of small cetaceans (Table 3.1; Mannocci et al., 2018). Aerial-based line transect surveys mainly covered various sub-regions of the western Mediterranean Sea, including the Alborán Sea, the Balearic Sea, the Ligurian Sea, the Tyrrhenian Sea, the Provençal basin and the Ionian Sea (Forcada et al., 2004; Gómez De Segura et al., 2006; Laran et al., 2017; Lauriano et al., 2014; Panigada et al., 2011; Panigada et al., 2017). Vessel-based line-transect surveys were more scattered in the Mediterranean basin, mainly carried out in the Algero-Provençal Basin and the Alborán, Balearic and Ligurian Seas (Boisseau et al., 2010; Cañadas et al., 2002; Cañadas & Hammond, 2006; Forcada et al., 1994; Forcada & Hammond, 1998; Lauriano et al., 2010; Chicote et al., 2012). A few vessel-based surveys were conducted in the Ionian, Aegean and Levantine Seas (Boisseau et al., 2010; Carlucci et al., 2018; Kerem, 2012; Ryan et al., 2014). Most estimates of small cetacean abundance are derived from these visual surveys, either vessel-based (Ben Naceur et al., 2004; Cañadas & Hammond, 2006; Carlucci et al., 2018; Chicote et al., 2012; Forcada et al., 1994; Forcada & Hammond, 1998; Lauriano et al., 2010) or aerial-based (Forcada et al., 2004; Gómez De Segura et al., 2006; Laran et al., 2017; Lauriano et al., 2014; Panigada et al., 2011; Panigada et al., 2017). Although some studies have recorded

the presence of small cetaceans acoustically (Boisseau et al., 2010; Ryan et al., 2014), abundance estimates based on acoustic surveys have never been carried out for small cetaceans in the Mediterranean Sea, but only for sperm whales (Lewis et al., 2007; Gannier et al., 2002; Lewis et al., 2018). Regional line-transect surveys, for the most part, have mostly targeted the north-western and central Mediterranean Sea, leading to a recognised heterogeneity in survey coverage throughout the basin (Mannocci et al., 2018). Some species, such as Risso’s dolphin or rough-toothed dolphin have received less attention than others (Boisseau et al., 2010; Kerem, 2012; Luna et al., 2022).

3.4 Presentation of the ASI survey

3.4.1 Comprehensive overview of the ASI survey

In response to the growing threats to marine biodiversity, particularly cetaceans, the international Agreement on the Conservation of Cetaceans in the Black Sea, Mediterranean Sea and contiguous Atlantic area (ACCOBAMS) was established in 1996, involving the countries bordering the regions. Its main objective is to improve the conservation efforts of cetaceans and their habitats. The ACCOBAMS Survey Initiative (ASI) is a large-scale program that is part of the ACCOBAMS effort to collect data and information on cetaceans. This program is crucial to understanding the status of cetacean populations at the macro-regional scale, thereby optimizing and strengthening the effectiveness of transboundary approaches to the conservation of these species and their habitats. The survey adopted a multi-species approach including the assessment of other threatened species like sea turtles and seabirds, and also marine litters. The ASI was conducted in the summer of 2018, using a combination of aerial and vessel-based visual methods and PAM. This approach followed a protocol based on line-transect distance sampling throughout the Mediterranean region. The ASI aerial component involved eight aircrafts, while the vessel component involved four vessels. One of these vessels, the *R/V Song of the Whale*, surveyed most of the western Mediterranean basin and parts of the Central Basin, while other vessels surveyed waters under national jurisdiction in Syria and Egypt (ACCOBAMS, 2021).

This thesis focused on the ASI vessel component conducted with the *R/V Song of the Whale*, in the western and central Mediterranean Sea, representing a unique survey using a double acoustic-visual platform between May and September 2018 (ACCOBAMS, 2021).

3.4.2 Survey design

The study area covered by the ASI vessel component encompassed the Alborán Sea/Strait of Gibraltar, the Algero-Provencal basin, the Tyrrhenian Sea/eastern Ligurian Sea, the Strait of Sicily/Tunisian Plateau/Gulf of Sirte, and the Ionian Sea/Central Mediterranean

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Table 3.1: Details of the line transect surveys of the studied species in the Mediterranean Sea. This table was adapted and updated from Mannocci et al. (2018).

| References | Platform | Method | Areas | Year | Studied species | Abundance estimates |
|-------------------------------|----------|--------------------|---|-------------|--|---------------------|
| Ben Naceur et al. (2004) | Vessel | Visual | Gulf of Tunis Gulf of Gabes | 2001, 2003 | Bottlenose dolphin | Yes |
| Boisseau et al. (2010) | Vessel | Acoustic Visual | Mediterranean basin | 2003-2007 | Bottlenose dolphin Common dolphin Long-finned pilot whale Risso's dolphin Rough-toothed dolphin Striped dolphin | No |
| Cañadas et al. (2002) | Vessel | Visual | Alborán Sea | 1992-2001 | Bottlenose dolphin Common dolphin Long-finned pilot whale Striped dolphin Risso's dolphin | No |
| Cañadas and Hammond (2006) | Vessel | Visual | Alborán Sea | 200-2003 | Bottlenose dolphin | Yes |
| Carlucci et al. (2018) | Vessel | Visual | Ionian sea | 2009-2016 | Striped dolphin | Yes |
| Chicote et al. (2012) | Vessel | Visual | Balearic sea | 2011 | Bottlenose dolphin Common dolphin Long-finned pilot whale Striped dolphin Risso's dolphin | Yes |
| Forcada et al. (1994) | Vessel | Visual | Alborán sea Algero-Provençal basin Balearic sea Ligurian sea | 1991 | Bottlenose dolphin Common dolphin Long-finned pilot whale Risso's dolphin Striped dolphin | Yes |
| Forcada et al. (1995) | Vessel | Visual | Ligurian sea | 1992 | Striped dolphin | Yes |
| Forcada and Hammond (1998) | Vessel | Visual | Alborán sea Algero-Provençal basin Balearic sea Ligurian sea | 1991-1992 | Common dolphin Striped dolphin | Yes |
| Forcada et al. (2004) | Aircraft | Visual | Balearic sea | 2002 | Bottlenose dolphin Striped dolphin | Yes |
| Fortuna et al. (2018) | Aircraft | Visual | Adriatic sea | 2010, 2013 | Bottlenose dolphin | Yes |
| Gómez De Segura et al. (2006) | Aircraft | Visual | Alborán sea Balearic sea | 2001-2003 | Bottlenose dolphin Risso's dolphin Striped dolphin | Yes |
| Kerem (2012) | Vessel | Visual | Levantine sea | 2005 | Bottlenose dolphin Common dolphin Long-finned pilot whale Risso's dolphin Rough-toothed dolphin Striped dolphin | No |
| Laran et al. (2017) | Aircraft | Visual | Ligurian sea Provençal basin Tyrrhenian sea | 2011-2012 | Bottlenose dolphin Striped dolphin | Yes |
| Lauriano et al. (2010) | Vessel | Visual | Ligurian – Provençal sea | 2008 | Striped dolphin | Yes |
| Lauriano et al. (2014) | Aircraft | Visual | Tyrrhenian sea Ligurian sea | 2010 - 2011 | Bottlenose dolphin | Yes |
| Panigada et al. (2011) | Aircraft | Visual | Ligurian sea | 2011 | Striped dolphin | Yes |
| Panigada et al. (2017) | Aircraft | Visual | Ligurian sea Tyrrhenian sea Provençal basin Ionian sea | 2009-2014 | Bottlenose dolphin Long-finned pilot whale Risso's dolphin Striped dolphin | Yes |
| Ryan et al. (2014) | Vessel | Acoustic Visual | Aegean sea Levantine sea | 2013 | Bottlenose dolphin Common dolphin Risso's dolphin Rough-toothed dolphin Striped dolphin | No |

(from 6°W to 36°E and from 30°N to 46°N; figure 3.16). The surveyed area was divided into 21 blocks with a total surface area of 1,312,625 km². Transects were surveyed with the *R/V Song of the Whale*, a 21-m quiet vessel, owned by the Marine Conservation Research (www.marineconservationresearch.co.uk), operated with minimal disturbance to marine life by using noise-reduction devices, including vibration-damping mounts for the main engine and a five-bladed propeller. The study required the vessel to move continuously, day and night. Therefore, some transects were surveyed using either a visual platform (during daylight hours and whenever the observation conditions were suitable, i.e. Beaufort sea state ≤ 4) or an acoustic platform (when Beaufort sea state was below 5 and local water depths greater than 50 m, submitted to bordering states' authorizations). The transects were surveyed using both platforms whenever it was possible. Transects were designed using the Distance software (Thomas et al., 2010) as equal-spaced zig-zag transects to provide a uniform coverage probability.

In the manuscript, transects will be labelled based on the type of platform used. If only the visual platform was used, the corresponding transects are labeled "Visual transects" (VT). If only the acoustic platform was used, the corresponding transects are labeled "Acoustic transects" (AT). If both platforms were used, the transects are labelled as "Acoustic-visual transects" (AVT). Acoustic effort may correspond to acoustic or acoustic-visual transects or both, and visual effort may correspond to visual or acoustic-visual transects or both.

3.4.3 Data collection

For a total covered area of 42,918 km², the vessel sailed a distance of 14,304 km in Beaufort Sea State 6 or less (Figure 3.16). This included 499 km of visual transects (3%), 7,127 km of acoustic transects (50%) and 6,678 km of acoustic-visual transects (47%).

3.4.3.1 Visual data collection

During the visual effort, two observers were positioned on a 5 m elevated platform to search for cetaceans. Each observer was positioned on either side of the platform. The first observer scanned the starboard side from 340° to 90° and the second observer scanned the port side from 270° to 20°, with 0° representing the bow (Figure 3.17). They scanned their respective areas with the naked eye and used binoculars to confirm species identity when necessary. For each visual event, observers provided information to a dedicated data logger using the Logger software package (www.marineconservationresearch.org). Information on species, group size, bearing angle and distance from the boat (between the observer and the centre of the group) were recorded for each visual event, typically at the point where the group was first sighted. Bearings and distances were estimated by eye and group sizes were reported as best, high and low estimates of the number of animals for each visual event. To improve efficiency and consistency between the observers,

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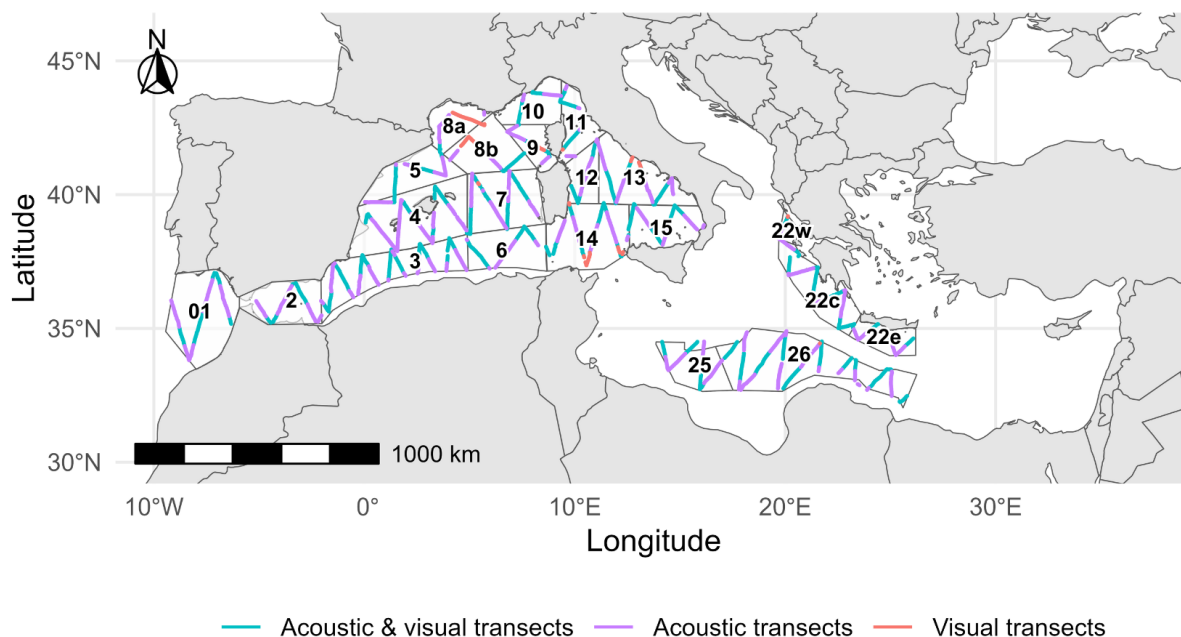


Figure. 3.16: Study area covered by the ASI survey in 2018. The area was divided into 21 blocks: 1) Gulf of Cadiz, 2) Alboran, 3) Algeria West, 4) Balears, 5) North East Spain, 6) Algeria East, 7) West Sardinia, 8a) Gulf of Lion shelf, 8b) Gulf of Lion deep, 9) Pelagos South West, 10) Pelagos North West, 11) Pelagos East, 12) Tyrrhenian Central West, 13) Tyrrhenian Central East, 14) Tunisia North, 15) Tyrrhenian South East, 22w) Hellenic Trench West, 22c) Hellenic Trench Central, 22e) Hellenic Trench East, 25) Libya East and 26) Libya East. The purple and orange lines represent acoustic transects and visual transects, respectively. The blue lines represent the acoustic-visual transects (double platform).

distance trials and training on the survey protocol were carried out prior to the survey. Additional information on cue type and animal behaviour was recorded. When necessary, the vessel interrupted the transect line to approach animals for species identification or photo-identification before returning to the transect line at the point where it was left. Information on environmental conditions i.e., Beaufort sea state (out of 9), wave and swell heights (m), cloud cover (out of 10), glare, visibility (from 1, low visibility, to 3, good visibility), wind direction ($^{\circ}$) and speed (m/s) and boat speed (m/s) were recorded hourly or whenever conditions changed by the data logger member. The Logger software automatically recorded the GPS position, heading and boat speed every 10 s. The visual survey team, consisting of at least five members, rotated between different roles lasting a maximum of one hour for the port and starboard observers and three hours for the data logger, followed by a minimum of two hours of rest to avoid fatigue. Any duplicate visual events made by both observers in the overlap area were removed.

3.4.3.2 Acoustic data collection

The acoustic effort was conducted 24 h a day using a towed hydrophone array capable of detecting all cetacean species. A 400 m tow cable was used to avoid any boat self-noise;

at this distance, any vessel noise, such as propeller cavitation, was inaudible to both the human ear and the detection algorithms described below. The hydrophone array was housed in an oil-filled tube and consisted of a pair of hydrophones in a linear configuration. The two hydrophone elements (Magrec HP03), separated by 0.25 m apart, had a sensitivity of -204 dB re 1V/ μ Pa with a flat frequency response (± 3 dB) from 1 to 100 kHz in the frequency band of most odontocete vocalisations. Pre-amplifiers with a gain of 29 dB were used to prevent voltage drop between the array and the research vessel. The outputs of the pair of hydrophones were digitised at a sampling rate of 192 kHz and were monitored in real-time using a click detector in PAMGuard, a passive acoustic monitoring software package (Gillespie et al., 2008). Audio recordings were stored as 16-bit WAV files. The click detector outputs were compressed into binary storage files in PAMGuard and these files were manually analyzed post-hoc with a focus on small odontocetes.

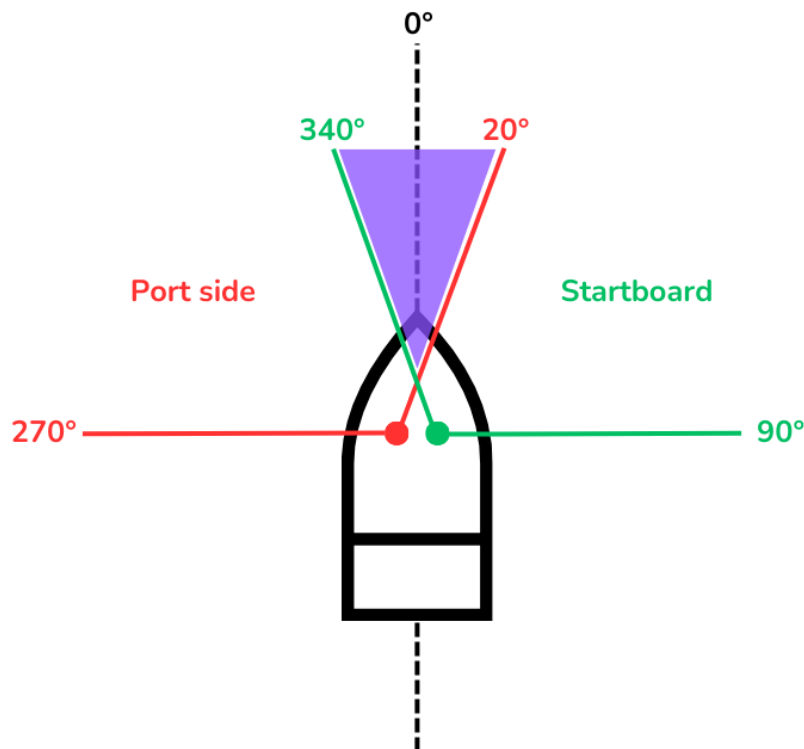


Figure 3.17: Areas scanned by the observers during the visual effort on the *R/V Song of the Whale*. The port side observer (red dot) scanned the area between 270° and 20°. The starboard observer (green dot) scanned the area between 340° and 90°. The purple zone is where both observers scanned between 340° and 20°. The 0° represents the bow.

3.5 Data processing

3.5.1 Acoustic data analysis

3.5.1.1 PAMGuard: click detector module

Acoustic analyses were conducted using the open-source software PAMGuard, developed by the Sea Mammal Research Unit (SMRU) at the University of St-Andrews in Scotland (Gillespie et al., 2008). This software is designed for the acoustic detection, localisation and classification of marine mammals. It operates independently as a detector and classifier for a wide range of cetacean vocalisations, including baleen whale calls, dolphin whistles and odontocete clicks. Echolocation clicks were detected on recordings using a Click detector module. The differences in signal arrival times on the two hydrophones were used to calculate a bearing angle for each detected click in relation to the hydrophone array. These bearing measurements were then visualised in the click detector's bearing-time display figure 3.18). The vertical axis represents the bearing angle, where 0° corresponds to the bow and 180° to the stern of the vessel (or more specifically, the hydrophone's position). The horizontal axis shows the recording time. The data was scrolled through manually to search for click series. A threshold of 130 dB was applied for separating clicks from background noise. Characteristics of a signal can be obtained by analysing the waveform window, the spectrum window, and the associated Wigner-Ville transformation plot. Each individual click was manually categorised and assigned a specific colour for identification purposes.

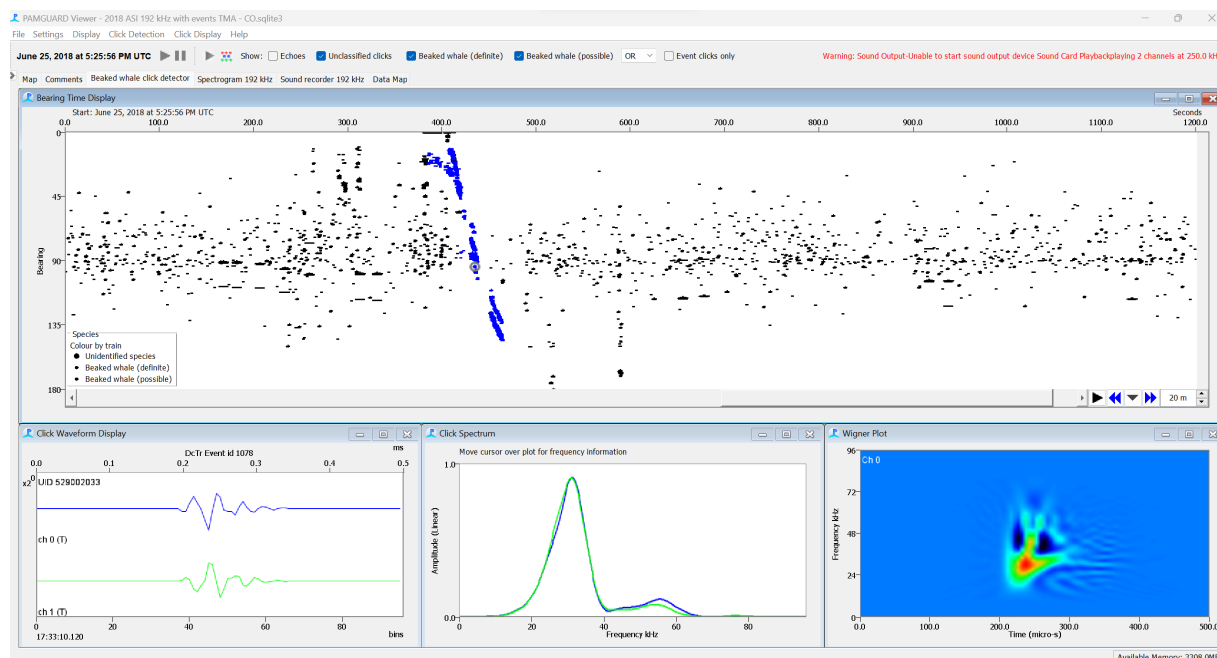


Figure 3.18: Click detector module display in PAMGuard showing an example of 20 min period of acoustic effort. The top window shows the bearing time display with the bearing angle on the y-axis ($0-180^\circ$) and time on the x-axis. The click track is marked with a blue colour, which represents an acoustic event. The lower windows show the characteristics of a click: waveform (left), power spectrum (middle) and Wigner plot (right).

3.5.1.2 Acoustic events: identification process

In this thesis, an acoustic event was defined as a sequence of clicks that was produced by the same animal or group of animals and that showed a consistent change in bearing (e.g., when a vocalising cetacean passed from in front of to behind the hydrophone array; figure 3.19). Sequences of clicks that did not show a consistent trajectory of bearings (e.g., clouds of clicks) or did not cross the 90° line (e.g., detections that did not pass the array) were not considered as acoustic events. Clouds of clicks with a consistent bearing angle at either the beginning or end of the acoustic event were excluded from the analysis. This decision was made because they were perceived to originate at a considerable distance from the boat and could introduce potential biases in distance estimations. These sequences of clicks may suggest the presence of a group of dolphins but were missed in the analysis. The missed events could be accounted for when estimating $g(0)$ for the acoustic platform (see chapter 4).

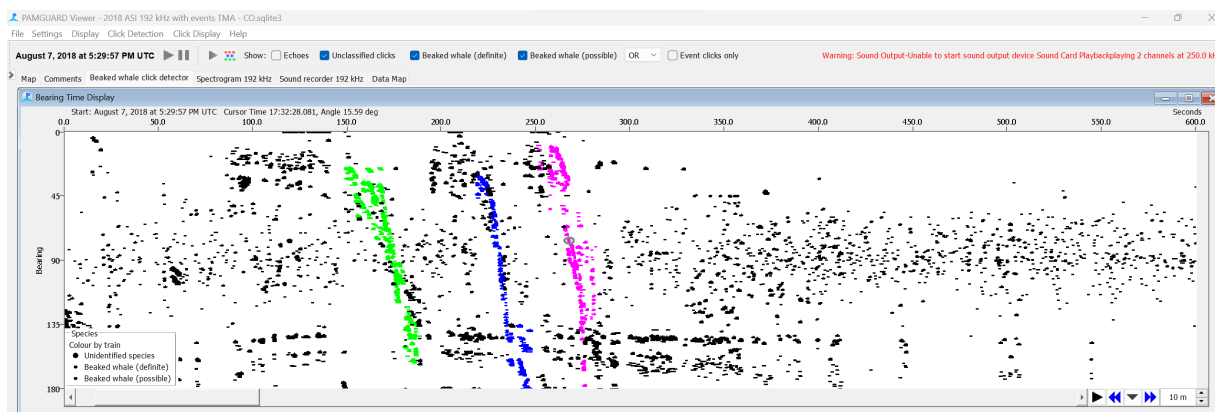


Figure 3.19: Click detector module display in PAMguard showing an example of 10 min period of acoustic effort. The top window shows the bearing time display with the bearing angle on the y-axis (0-180°) and time on the x-axis. Sequences of clicks that show a consistent change in bearing angle were marked with different colours. Each colour represents an acoustic event.

To confirm that an acoustic event was likely produced by a small cetacean, we relied on information from the waveform, spectrum and associated Wigner-Ville transformation plots. The ‘Click Waveform Display’ window (figure 3.18) showed the waveform of a signal, which needed to be clear and cross the horizontal axis several times (known as ‘zero crossing’). The spectrum, which was the most decisive parameter, was presented in the ‘Click Spectrum’ window, allowing the frequency to be studied as a function of amplitude (figure 3.18). We hypothesised that signals between 10 and 80 kHz were most likely produced by a cetacean. Echolocation clicks are short, broadband pulses that range from 10 to 150 kHz in many species (Au, 1993). Odontocetes emit echolocation clicks in a narrow beam projected forward from the melon and the signal energy is more focused in the forward direction (“on-axis”) than to the sides (“off-axis”; Au et al., 1978). Most studies

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focus on understanding clicks produced “on-axis” (Table 3.2), i.e., when the animals are facing the hydrophone where the signal transmission loss is minimal, which is not typically applicable to the recording of free-ranging cetaceans in the field (Baumann-Pickering et al., 2010; Soldevilla et al., 2008). Signal waveforms can vary greatly between “off-axis” and “on-axis” clicks. Because higher frequencies attenuate more quickly than lower frequencies, the higher frequency peaks in clicks recorded “off-axis” (or clicks recorded from distant animals) may not be evident. Although acoustic events, in this thesis, can be recorded either “off-axis” or “on-axis” depending on the swimming direction of the animals relative to the hydrophones, most free-ranging animals are unlikely to produce many clicks “on-axis” of the hydrophone (Miller, 2002). Therefore, we expected to record echolocation clicks with lower bandwidths than those reported in table 3.2 (marked with*), which only included "on-axis" clicks. The frequency range expected for small cetaceans corresponded to those of the ASI hydrophones which recorded sounds up to 92 kHz. If a frequency peak occurred below 10 kHz, it could have indicated a sound signal emitted by a vessel. Conversely, if observed over 50 kHz, the source of the signal could have been a beaked whale. The Wigner transformation plot was used as a visual representation of the signal, primarily to determine whether the signal is characteristic of a beaked whale’s upswept signal (figure 3.18) . If the signal did not match this characteristic, it could have been a click from a delphinid. If the characteristics of the signal closely resembled those of small cetaceans, the sequence was classified as a series of clicks and was therefore considered an acoustic event. For each acoustic event, the confidence in the identification was categorized as either a certain event or a likely event.

To estimate the number of acoustic events n and the acoustic group size S in the line-transect distance sampling formula, I established a standardized protocol for identifying acoustic events (figure 3.20). Occasionally, multiple tracks may occur in close proximity and may be perceived as a single acoustic event. In such cases, an imaginary 90° reference line was introduced at the location of the first track and a perpendicular line was drawn from the intersection of the reference line and the first track. If the subsequent track started before the perpendicular line of the first track, it was categorised as part of the same event (resulting in two tracks within that event). Conversely, if the subsequent track started after the perpendicular line, it was treated as a separate event and this allowed the estimation of n . Within a single acoustic event, it is possible to have multiple tracks. To identify this, I used a vertical line and counted how many tracks intersected this line. The vertical line could be repositioned at different points throughout the duration of the acoustic event to calculate the minimum, maximum, and optimum number of tracks. The number of acoustically active individuals per acoustic event was determined as the number of tracks that occurred at the same time. This method allowed the number of vocalising animals S to be counted instead of the number of vocalisations (Richman et al., 2014; Akamatsu et al., 2008).

Table 3.2: Frequencies of peaks energy characteristics (kHz) for each studied species. Studies that included only “on-axis” signals were marked with *.

| Species | Energy range of the peaks (Hz) | References |
|---|--|---------------------------------|
| Bottlenose dolphin | 120 - 130 | Au et al. (1974)* |
| | 60 - 140 | Akamatsu et al. (1998) |
| | 35 - 60 | Diercks et al. (1971) |
| | 33 - 109 | Wahlberg et al. (2011)* |
| | 40 - 80 | Soldevilla et al. (2008) |
| | 24 - 30 | Baumann-Pickering et al. (2010) |
| | 40 - 120 | Finneran et al. (2014)* |
| Long-finned pilot whale | 50 | Eskesen et al. (2011)* |
| Short-finned pilot whale (behaviourally similar sp.) | 40 | Pedersen et al. (2021)* |
| Risso’s dolphin | 22 - 39 | Soldevilla et al. (2008) |
| | 50 | Madsen et al. (2004) |
| Rough-toothed dolphin | 18 - 30 | Rankin et al. (2015) |
| Common dolphin | 40 - 80 | Soldevilla et al. (2008) |
| | 23 - 67 | Evans (1973) |
| Striped dolphin | Striped dolphin clicks have not been described but we assumed they are produced in the same frequency range as bottlenose and common dolphin | |

3.5.1.3 Estimation of the perpendicular distance for acoustic events

Once acoustic events are identified, they can be used to derive an estimation of the perpendicular distance from the transect using the Target Motion Analysis (TMA) module’s 2D simplex method implemented in PAMGuard (Figure 3.21). The bearing angle of each detected click was determined from the time delay of arrival of a signal detected by the pair of hydrophones. The convergence of successive bearing lines was used to locate the sound source and allow the estimation of the perpendicular distance from the crossing point. When possible, the TMA algorithm used changes in the vessel’s heading to resolve the left/right ambiguity and to identify on which side of the vessel the animal was located. A distance estimate was proposed for each side and the distance of the acoustic event with the lowest AIC was selected for analysis.

The ‘Target motion analysis’ method is commonly employed to locate marine mammals from acoustic signals. The bearing angle of each detected click is determined using the time delay of arrival of a signal detected by the pair of hydrophones. The convergence of successive bearing lines is used to locate the sound source and allows the distance perpendicular to the crossing point to be estimated.

Since the vessel was navigating in a linear transect, the heading remained constant and therefore the left/right ambiguity may not be resolved. However, distance sampling

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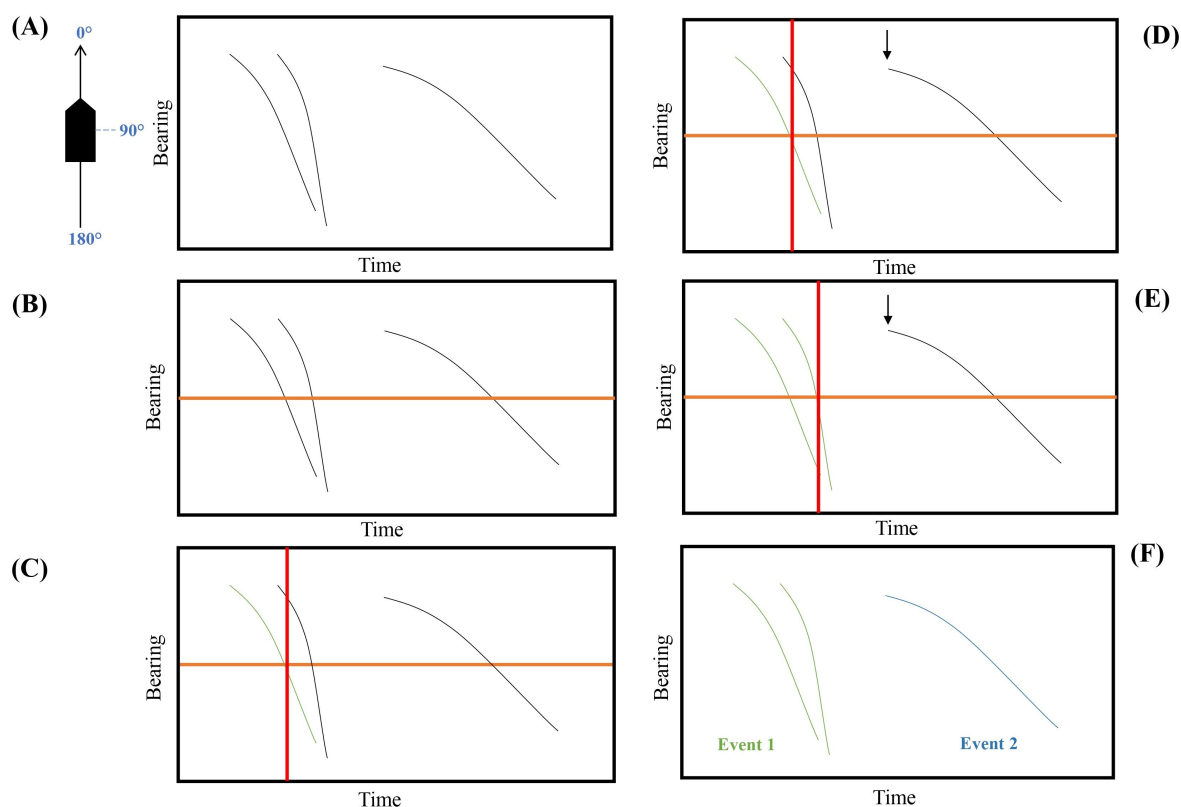


Figure. 3.20: Protocol for determining acoustic events using PAMGuard Click detector module. (A) Determination of the number of events. (B) Set a 90° reference line representing the bearing of 90° of the boat. (C) Set a perpendicular line where the first track is crossing the 90° reference line. (D) If the following track starts before the perpendicular line of the 1st track, it will be considered as the same event. (E) If we set a perpendicular line on the 2nd track, the 3rd track starts after the perpendicular line, this would be considered as a distinct event. (F) In conclusion, the first two tracks are the same event but probably from two different animals and the 3rd one is another acoustic event.

methodology requires a perpendicular distance from the trackline (Buckland et al., 1993) and it is not necessary to know which side of the track line an animal is on.

3.5.2 Overview of the final database

This section illustrates the process of transforming raw data into the final database. Data was processed using R (version 4.1.0; R Core Team, 2021).

3.5.2.1 Acoustic database

To obtain a summary of events from the PAMGuard database, the software SQLite Studio was employed (<https://sqlitestudio.pl>). This software serves as a free and open-source SQLite database manager, providing capabilities for editing and visualising database structures. The SQLite database module was integrated into PAMGuard, and all analyses were documented in the SQL file. After completing the analyses, which included identifying acoustic events and estimating perpendicular distance with TMA, the dataset

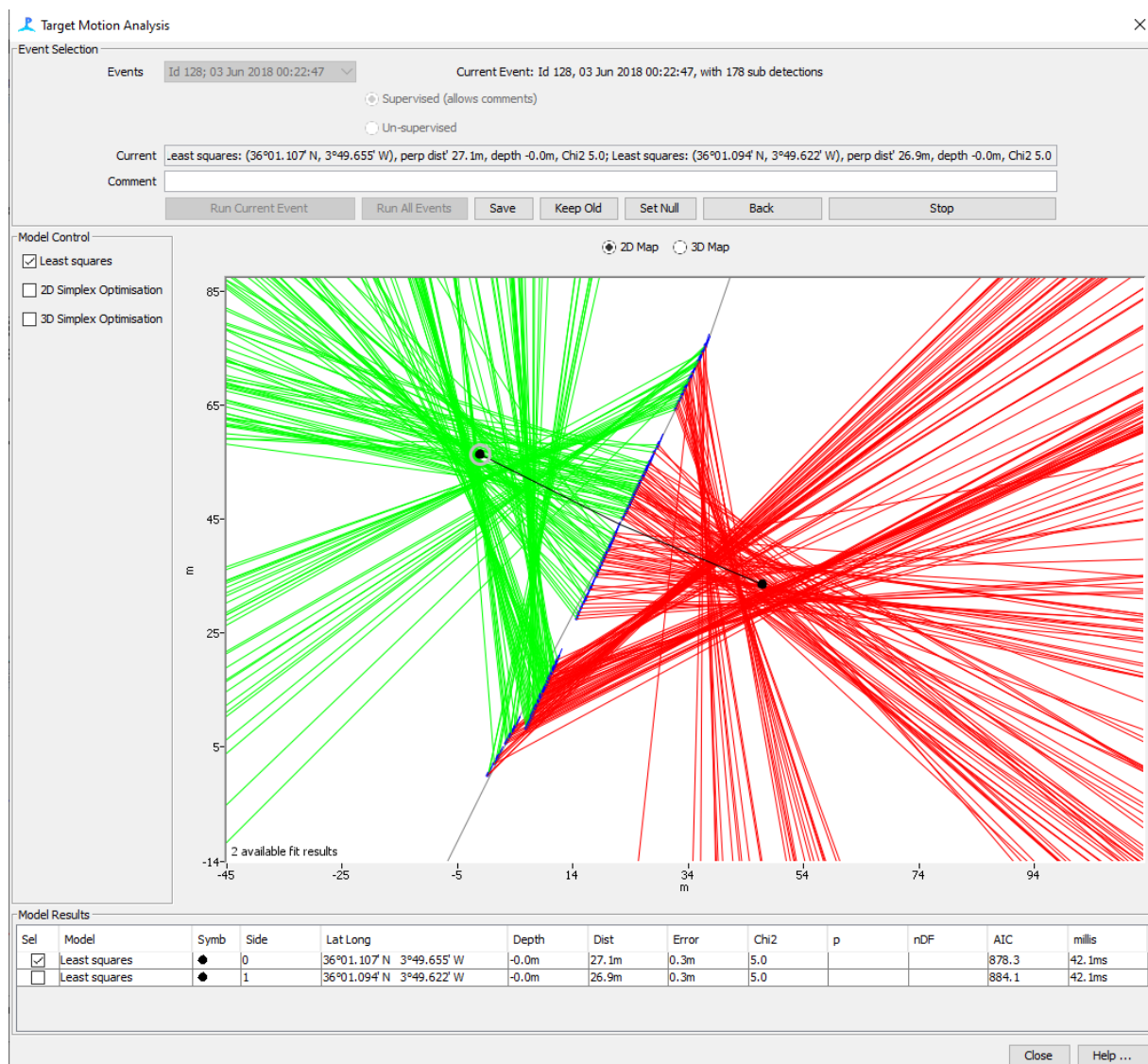


Figure. 3.21: Estimating perpendicular distances in PAMguard using the target motion analysis. The grey line is the vessel’s track and the red and green lines are bearing lines for consecutive clicks projected to either side of the vessel. In this example, the left/right ambiguity could not be resolved and the 2D position of the animal was located either 27.1 meters to the port (green bearing lines) or 26.9 meters to the starboard (red bearing lines). Based on the lowest AIC, the model with a distance of 27.1 meters was selected.

was converted into CSV files and I kept only the essential columns. This resulting table comprises 9 columns, and the corresponding variables are outlined below (Table 3.3).

Any events where TMA failed were subsequently removed from the database. The acoustic database was temporally associated with GPS points based on the closest date. This linkage was established using the 'which.closest' function from the 'birk' package (Birk, 2016), ensuring that each acoustic event was associated with the corresponding coordinates. For this study, only acoustic events produced by delphinids that were classified as certain were included in the acoustic database.

3. General methodology

Table 3.3: Variables in the acoustic database. Database was extracted from PAMGuard and only essential variables were kept in this database.

| Variable | Meaning |
|-------------------------------|---|
| Id | Identification number of the acoustic event |
| UTC | Date of the acoustic event (format: dd/mm/yyyy hh:mm:ss) |
| nClicks | Number of clicks identified |
| minNumber | Minimum estimation of the group size |
| bestNumber | Best estimation of the group size |
| maxNumber | Maximum estimation of the group size |
| comment | Any comment related to the acoustic event |
| TMPerpendicularDistance1 | Estimated distance from TMA |
| TMPerpendicularDistanceError1 | Estimated distance error from TMA |

3.5.2.2 Visual database

The visual database was extracted from Microsoft Access database management software, generated by PAMGuard’s real-time mode. For the analyses, I specifically filtered visual events occurring during the visual transects and acoustic-visual transects, focusing on the following study species: bottlenose dolphin, common dolphin, long-finned pilot whale, Risso’s dolphin, rough-toothed dolphin, striped dolphin, and unidentified dolphins (belonging to one of the above species). The coordinates of each visual event have already been assigned in the field using PAMGuard. During fieldwork, only angle measurements θ (in radians) and radial distances between observers and detections were estimated (Figure 3.22). Subsequently, the perpendicular distance was calculated as:

$$\text{Perpendicular distance} = \text{radial distance} \times \sin(\theta) \quad (3.1)$$

Some visual events were detected outside the visual field, beyond the range of 270° to 90°. To follow the distance sampling protocol, these events were removed from the database. This resulting table comprises 16 essential columns, and the corresponding variables are outlined below (Table 3.4).

3.5.2.3 Final databases: integration with environmental variables and field survey information

The detection of the animals may be impacted by environmental variables. To account for this, environmental variables collected in the field were linked to each transect (Table 3.5)

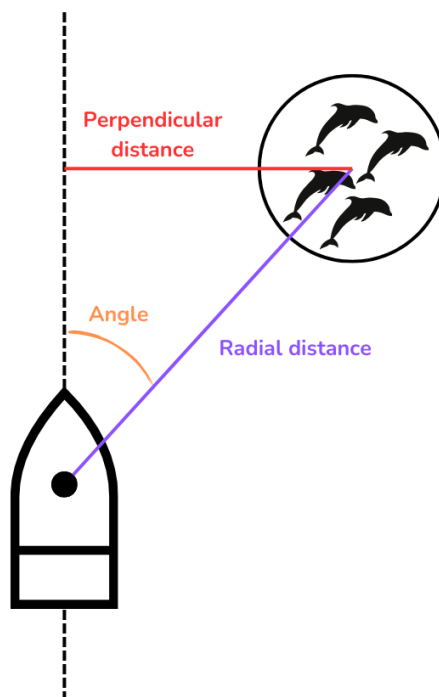


Figure. 3.22: Estimating the perpendicular distance of a visual event. A visual event was identified by an observer (black dot) on the vessel that followed the transect (dotted line). The observer then recorded the radial distance (purple line) between the observer and the center of the animal group, as well as the angle formed between the transect and the group (orange line). These two measures can be used to calculate the perpendicular distance to the transect (red line).

in the effort database. Transects were then divided into legs with constant environmental conditions, and each leg was finally divided into 5 km segments for analysis. Each event, whether visual or acoustic, was then associated with the nearest coordinates from the effort database. Environmental variables and field survey details (Table 3.5) were associated with these events using the 'st_nearest_feature' function from the 'sf' package (Pebesma & Bivand, 2023).

In conclusion, three databases were generated: the visual database, the acoustic database, and the effort database.

3.5.3 Grouping species

This study focused on small cetaceans in the Mediterranean Sea, including bottlenose dolphins, long-finned pilot whales, Risso's dolphins, rough-toothed dolphins, common dolphins and striped dolphins. The echolocation clicks of these species have similar frequency ranges (Table 3.2), making species identification difficult (Soldevilla et al., 2008), hence all species studied were pooled for all analyses in this thesis. Striped dolphins were the most abundant small odontocetes in the Mediterranean basin, accounting for 52% of visual events during the vessel-based survey (ACCOBAMS, 2021) and 85% during the

3. General methodology

Table 3.4: Variables in the visual database. Only essential variables were kept in this database.

| Variable | Meaning |
|--------------|---|
| Date | Date of the visual event (format: dd/mm/yyyy hh:mm:ss) |
| Sighting No | Identification number of the visual event |
| Observers | Name of the observers |
| Angle | Angle between the transects and the animals |
| Est.Distance | Radial distance between the observer and the animals |
| Species1 | Observed species |
| Species 2 | Second observed species in the case of mixed group |
| Cue | Indicator that assists in the identification of animals |
| Meangroup | Best estimation of the group size |
| minNo | Minimum estimation of the group size |
| maxNo | Maximum estimation of the group size |
| Heading | Heading of the vessel |
| Latitude | Latitude coordinate of the visual event |
| Longitude | Longitude coordinate of the visual event |
| Distance | Perpendicular distance of the visual event |
| Effort | Designed transects (VT or AVT) |

aerial-based survey (Panigada et al., 2024). These species do not share the same behaviours (i.e. group size, habitat preference, dive duration, responses to the boat) and by grouping all small odontocetes in the same analysis, we assumed that all species behave in the same way in terms of visual and acoustic events; this simplification will be discussed later on.

In summary, the purpose of this chapter was to outline the overall methodology, including the presentation of the study area and its characteristics, the ecology of the species studied, the ASI survey, and the raw data. In addition, it provided an insight into the data processing steps that were undertaken to facilitate the subsequent analyses in the following chapters.

Table 3.5: Environment variables and field information in the effort database

| Variable | Unit |
|----------------|---|
| Sea state | Date of the visual event Beaufort scale [0, 1, 2, 3, 4, 5,6] |
| Wave Height | Wave height in m [0 to 0.5m, 0.6 to 1m, 1.1 to 1.5m, 1.6 to 2m] |
| Swell Height | Swell height in m [0 to 0.5m, 0.6 to 1m, 1.1 to 1.5m, 1.6 to 2m] |
| Weather | Weather condition FA = Fair HZ = Haze MS = Mist DR = Drizzle RN = Rain FO = Fog |
| Cloud cover | Octave [0 - 8] |
| Visibility | 0 = Fog (<1000m) 1 = Poor (1000 - 2nm) 2 = Moderate (2 - 5nm) 3 = Good (>5nm) |
| Pressure | Pressure of the atmosphere in bar |
| Heading | Heading direction of the vessel |
| Speed | Speed of the vessel in Knots |
| Wind speed | Speed of the wind in Knots |
| Wind direction | Direction of the wind |
| SST | Sea Surface Temperature in degrees |
| Block | Block number |
| LegID | Identification number of the leg |
| LegLengthKm | Length of the leg in km |
| SegID | Identification number of the seg |
| SegLengthKm | Identification of the seg in km |

4

Estimation of the detection probability using visual and acoustic data

The objective of this chapter is to estimate the detection probability, especially $g(0)$, of small cetaceans using a double acoustic and visual platform and to highlight the importance of accounting detection biases. Duplicate events between these platforms were identified and the $g(0)$ was estimated using the MRDS approach. An article based on this chapter has been published in *Frontiers in Marine Science* (Ollier et al., 2023) and is available in appendix A.

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4.1 Introduction

Abundance estimation is indeed closely linked to the detectability of individuals during surveys (Mccarthy et al., 2013). Detectability can be affected by both an availability bias and a perception bias (Laake & Borchers, 2004), constituting together the detection biases. Availability bias corresponds to the unavailability of animals for detection, either because they are below the sea surface, which depends on the time spent at depth by the species and the platform speed, or because they are not acoustically active, which depends on the vocalisation rate of the species. Perception bias accounts for the non-detection of available animals by observers or recorders due to imperfect observer vigilance or unfavourable conditions for detection (e.g. high sea states). Detection biases are major concerns in abundance estimation and failure to account for these biases will lead to overestimates of detection probability and hence underestimates of abundance (Saavedra et al., 2018). The assumption that all individuals on the transect line are detected, i.e. $g(0) = 1$, has been commonly used to estimate cetacean abundance (Barlow, 2006; Øien, 2009; Dick & Hines, 2011). However, to obtain an unbiased abundance estimate of small cetaceans, $g(0)$ must be estimated.

One approach to estimating the $g(0)$ is to use Mark-Recapture Distance Sampling (MRDS) model with a double platform (Laake & Borchers, 2004). This method requires two independent platforms scanning the same area simultaneously, which are used to ‘mark’ animals (Laake & Borchers, 2004). The $g(0)$ and overall detection probability are estimated by using the number of animals seen by each platform and by both platforms (duplicate events). Most double-platform line-transect surveys use two visual platforms, either with a single survey platform or with two separate survey platforms (Cañadas et al., 2004; Hammond et al., 2013; Laran et al., 2017; Lambert et al., 2019). The number of surveys using an acoustic platform with a towed hydrophone array in parallel with a visual platform has increased in recent years (Barlow & Taylor, 2005; Boisseau et al., 2010; Richman et al., 2014; Martin et al., 2020; Rankin et al., 2020; Dalpaz et al., 2021). The acoustic platform has the advantage of detecting cetaceans even when they are not visible at the surface, and therefore not available to the visual platform. The visual platform may detect cetaceans when they are not vocalizing, and therefore not available to the acoustic platform. These two methods are complementary and can improve the overall detection efficiency (Verfuss et al., 2018). However, this kind of analysis can be challenging due to the complexity of identifying duplicate events; acoustic events are typically validated during post-field analysis, while visual events are recorded directly during the survey. The MRDS method appears to be a promising solution for assessing detection biases in combined acoustic and visual surveys (Marques et al., 2013).

4. Estimation of the detection probability using visual and acoustic data

The ACCOBAMS Survey Initiative (ASI) vessel component, conducted in the summer of 2018 with the *R/V Song of the Whale* in the western and central Mediterranean Sea, was a unique survey using a visual-acoustic double platform (ACCOBAMS, 2021). This region is exposed to increasing levels of anthropogenic impacts (Coll et al., 2012) and is home to cetacean populations that are often distinct from their nearby Atlantic counterparts. Numerous studies have been conducted in the Mediterranean Sea to estimate the abundance of cetaceans (Laran et al., 2017; Panigada et al., 2017; Lewis et al., 2018) but survey efforts have been recognised as heterogeneous across the basin (Mannocci et al., 2018). Some species, like the Risso’s dolphin (*Grampus griseus*) or the rough-toothed dolphin (*Steno bredanensis*), have received less attention than others (Boisseau et al., 2010; Kerem, 2012; Luna et al., 2022) and some areas have been studied more extensively, especially within the western basin (Mannocci et al., 2018). Therefore, the ASI project aimed at filling these data gaps.

This chapter aimed to estimate the detection probability of small cetaceans in the Mediterranean Sea using acoustic and visual data collected simultaneously during the ASI survey. To this end, a decision tree (rule-based classification) was developed to identify duplicate events. An MRDS with environmental covariates affecting detectability was then implemented based on the prior identification of visual/acoustic event duplicates. The MRDS analysis allowed the detection probability and ESW of the visual, acoustic, and combined platforms to be estimated, taking into account detection biases. It is expected that $g(0)$ will be less than 1, as detection cannot be considered perfect for either platform, and some animals will inevitably be missed on the transect line.

4.2 Methodology

Acoustic and visual data used here come from the formatting process described in chapter 3.

4.2.1 Identification of duplicate events

For this study, acoustic-visual transects were retained to identify duplicate events collected by the visual and acoustic platforms. The MRDS analysis is based on the reliable identification of duplicate events between the two platforms. Two events are considered duplicates when the same group of individuals is detected both visually and acoustically. For this purpose, a two-stage decision tree (i.e. a rule-based classification system) was constructed based on a set of temporal and spatial criteria that determine how close in time and space a visual and an acoustic event were recorded. A putative duplicate was a pair of events consisting of a visual and an acoustic event to be tested with the decision tree. A putative duplicate became a potential duplicate and then a confirmed duplicate when the first and the second step of the decision tree were respectively passed successfully.

1st step of the decision tree: time threshold

The time window in which a pair of visual and acoustic events could originate from the same group of individuals was defined by considering that the two platforms, visual and acoustic, that were 400 m apart, had a specific detection radius and were moving at the vessel speed (Figure 4.1). The visual buffer was defined as the 270°-90° sector scanned by the observers in front of the vessel with a radius calculated as 95% of the distribution of the visual perpendicular distances recorded during the survey (here 2,107 m). The acoustic buffer was a disk centred on the hydrophone array with a radius calculated as 95% of the distribution of the acoustic perpendicular distances recorded during the survey (here 1,266 m). When a first event was identified from either platform, we calculated the minimum and maximum time lags (Δt_1 and Δt_2) for an event from the second platform to be identified in the corresponding buffer, assuming that the detected animal was stationary. The time lag (in s) was determined by:

$$\Delta t = \frac{L}{v} \quad (4.1)$$

where L is the maximum distance (in m) travelled by the vessel between an acoustic event (vs visual event) and a subsequent visual event (vs acoustic event) forming a putative duplicate and v is the average speed of the boat. It was estimated to be 866 m (1,266 m – 400 m) when the acoustic event came first and 3,773 m (1,266 m + 400 m + 2,107 m) when the visual event came first. Based on an average boat speed of 3.2 m/s (6.2 knots), $\Delta t_1 = -271$ s and $\Delta t_2 = 1,179$ s. Hence any pair of records where the acoustic event occurred within 271 s before and 1,179 s after the visual event was considered as a potential duplicate.

2nd step of the decision tree: distance threshold

Once potential duplicates were identified using the temporal criteria related to the platform structure and movement, another threshold was applied to account for the potential movement of the target animal(s) between the two events of the potential duplicate. Thus, a mobility buffer was estimated based on published values of the routine swimming speeds of small cetaceans. This mobility buffer represented the area centred on the first record of the potential duplicate in which the target animal(s) could be at the time of the second record if they were moving at a routine swimming speed, assuming no responsive movement relative to the vessel. If the location of the second record of a potential duplicate was felt to be within the mobility buffer, the potential duplicate became a confirmed duplicate (Figure 4.2).

The radius of the mobility buffer (in m) was calculated as:

$$r = \Delta t \times v_r \quad (4.2)$$

4. Estimation of the detection probability using visual and acoustic data

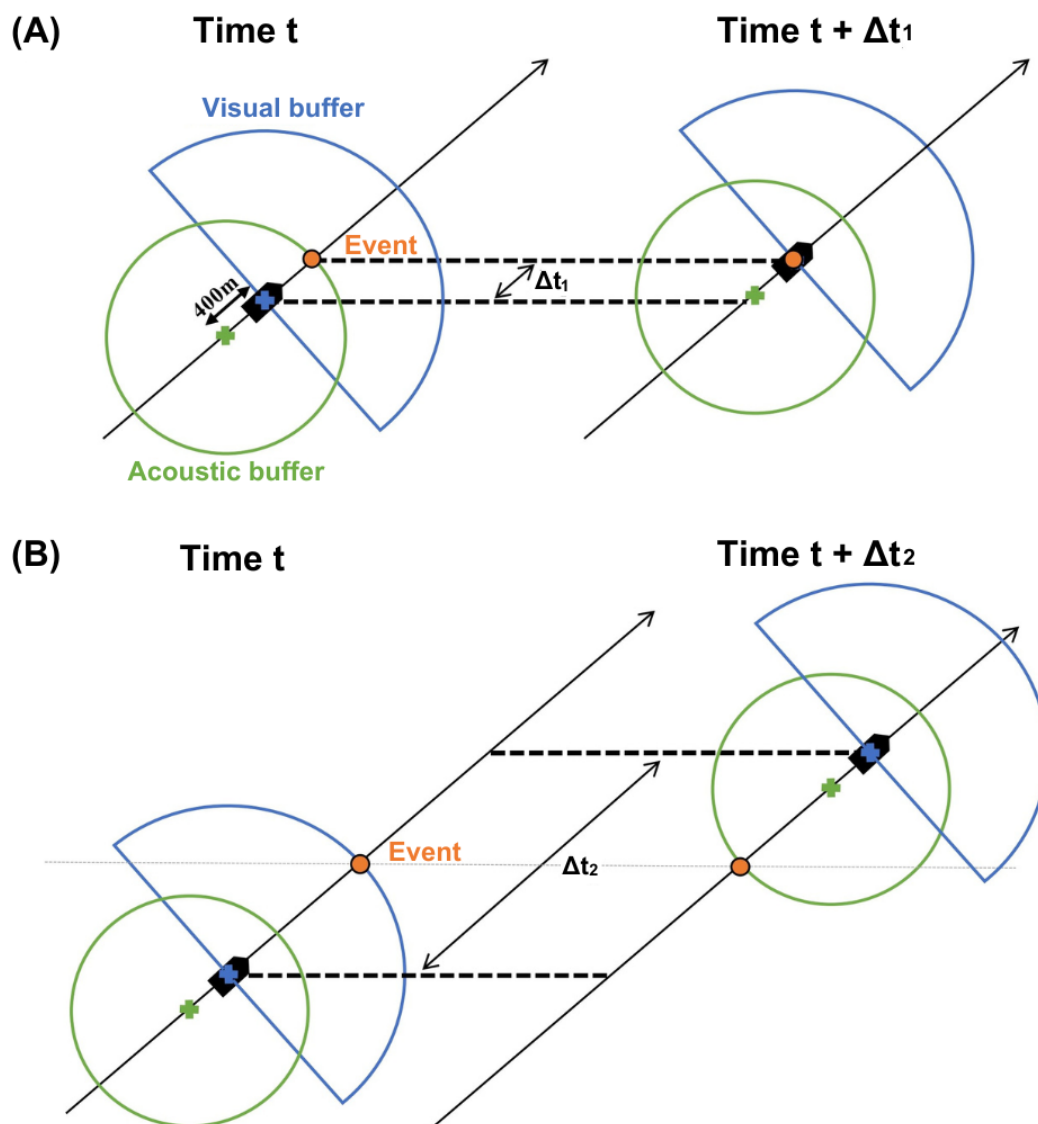


Figure. 4.1: First step of the decision tree: the platform-related time lag. The visual semi-buffer (blue) was centred on the vessel (blue cross) and the acoustic buffer (green) was centred on the hydrophone (green cross). A potential duplicate event was considered if a visual and an acoustic event were close in time (between Δt_1 and Δt_2). **(A)** The minimum time lag Δt_1 would correspond to the same group of small cetaceans being acoustically detected as early as possible by the hydrophone array and visually sighted as late as possible by the onboard observers. **(B)** The maximum time lag Δt_2 would correspond to the same group of small cetaceans being visually sighted as early as possible by the onboard observers and acoustically detected as late as possible by the hydrophone array. All intermediate situations between A and B would be accepted as potential duplicates.

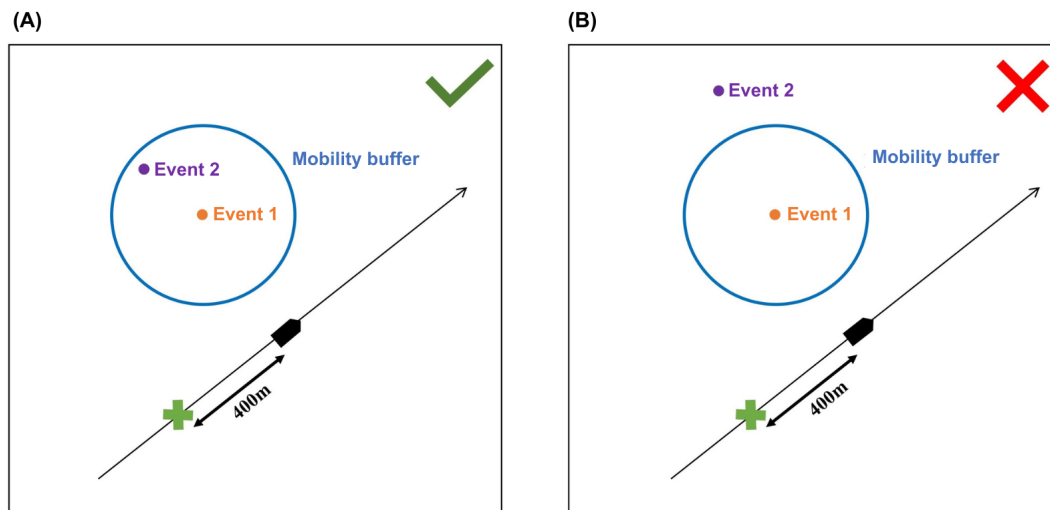


Figure. 4.2: Second step of the decision tree: the animal-movement-related spatial lag or mobility buffer. The black line is the surveyed transect. The hydrophone array (green cross) was located 400 m behind the vessel (black pentagon). The mobility buffer is centred on the first event by either platform (blue circle). **(A)** The status of confirmed duplicate was accepted when the 2nd event was within the mobility buffer. **(B)** The status of confirmed duplicate was rejected when the 2nd event was outside of the mobility buffer.

where Δt was the time lag (in s) between a visual and an acoustic event and v_r was the routine swimming speed of the animal (in m/s). The routine speed was determined from the literature. Values from the literature were plotted as a distribution, and the value corresponding to the 95% quantile was chosen, i.e. 3.6 m/s (7 knots; table 4.1). Given the potential left/right ambiguity of the localised acoustic event, we assumed that the acoustic event of a potential duplicate was on the same side as the corresponding visual event.

After passing the two steps of the decision tree, multiple replicate events could be confirmed (e.g. one visual event could correspond to up to three different acoustic events). Among these replicate events, the one with the shortest distance difference was selected to limit biases arising from possible responsive movement of the animal(s) (e.g. if the distance of the visual event was 200 m, and the distances for the three acoustic events were 10 m, 100 m and 1000 m, the acoustic event with a distance of 100 m was chosen). The rest of the replicate events were deleted. In the end, a confirmed duplicate event was finally composed of one visual and one acoustic event. For each duplicate event, we selected the highest “best” group size estimate and the larger distance value between the visual and acoustic events.

4.2.2 Detection function and $g(0)$

The detection function and $g(0)$ were calculated using data from both visual and acoustic platforms using the MRDS method (Laake & Borchers, 2004). Events from each platform were set as trials for the other. If events from the same group of animals were detected

4. Estimation of the detection probability using visual and acoustic data

Table 4.1: Routine speeds recorded for each studied species. Routine swimming speed values from the literature for each species, given in m/s and knots in parentheses.

| Species | Routine speed in m/s (knots) | References |
|-----------------------------|------------------------------|----------------------------|
| Bottlenose dolphin | 2.7 (5.2) | Saayman et al. (1972) |
| | 1.7 (3.3) | Würsig and Würsig (1979) |
| | 4.2 (8.2) | Fish and Rohr (1999) |
| | 2.1 (4.1) | Tanaka (1987) |
| | 2.2 (4.3) | Ridoux et al. (1997) |
| | 2.2 (4.3) | Wood (1998) |
| | 2.1 (4.1) | Williams et al. (1992) |
| | 2.5 (4.9) | Yazdi et al. (1999) |
| Long-finned pilot whale | 2.6 - 3.6 (5.1 - 7.0) | Pilleri and Knuckey (1969) |
| Risso's dolphin | 1.7 - 3.6 (3.3 - 7.0) | Fish and Rohr (1999) |
| Rough-toothed dolphin | - | - |
| Short-beaked common dolphin | 1.6 (3.1) | Hui (1987) |
| | 2.8 (5.4) | Fish and Rohr (1999) |
| Striped dolphin | - | - |

by both platforms (confirmed duplicate, see above), they were considered successful, if not, they were considered failed. There are two possible assumptions in MRDS (Burt et al., 2014): full independence (FI) or point independence (PI). The FI assumption considers the two platforms to be independent at any distance and thus a mark recapture (MR) model is applied at all distances (including distance zero) to estimate the overall detection probability p . It appears that this assumption generates negative biases in abundance estimates in the case of failure of the independence assumption (Laake et al., 2011; Burt et al., 2014). The failure can be identified if the abundance estimate is lower than the abundance estimates from the CDS, resulting in the presence of heterogeneity in detection probabilities which generates biases in abundance estimates (Buckland et al., 2010). Attempts have been made to minimize the unmodelled heterogeneity for example by including the effect of covariates in the detection function (Borchers et al., 1998; Laake & Borchers, 2004). To provide a solution to the problem of unmodelled heterogeneity, the concept of PI assumption was introduced by Laake (1999). The PI assumption considers the two platforms to be independent only at distance zero and reduces the impact of unmodeled heterogeneity on detection probability estimates (Buckland et al., 2010). The PI assumption uses a combination of MR and DS submodels. The MR submodel is used to estimate $g(0)$, while the DS submodel is used to estimate the decrease in detectability

with distance, and these two are combined to get the overall detection probability p (Burt et al., 2014).

In this study, the visual and acoustic platforms were beforehand assumed to be independent, but it was uncertain whether this independence was valid for all distances or only at distance zero, so MRDS models were tested with both FI and PI assumptions. Factors affecting the detectability for both platforms were investigated and included in the model to improve precision (Marques & Buckland, 2003; Buckland et al., 2004). To assess the effect of the platform on detectability, the platform was included as a covariate in all models tested. Additionally, the effects of the sea state (0, 1, 2, 3, 4 Beaufort scale), as well as wave and swell height (values in m grouped into classes: 0 to 0.5 m, 0.6 to 1 m, 1.1 to 1.5 m and 1.6 to 2 m), were tested. Single covariates and combinations of two covariates were tested. For the DS model, models with hazard-rate (HR) and half-normal (HN) key functions and with or without covariates were tested. The right truncation distance was set at 1,500 m, based on the inspection of the histogram of detection frequencies plotted against distance from the transect line (Buckland et al., 2001). Only segments conducted with good conditions (i.e. Beaufort sea state ≤ 4) were considered in the analysis. The decision was made to focus exclusively on Beaufort sea state because visibility, swell and wave height are highly subjective metrics. All models were tested with FI and PI assumptions, with HR and HN key functions for the DS submodel, and combinations of covariates. The Akaike Information Criterion (AIC, Akaike, 1998) and the goodness of fit were used to select the best model fit for each key function. The MRDS analyses were performed in R 4.0.3 using the 'mrds' package (Laake et al., 2013). Finally, to estimate the ESW, the overall detection probability was multiplied by the truncation distance (Buckland et al., 2004).

4.2.3 Sensitivity analysis of the decision tree

Correctly classifying events as unique or duplicate is a critical step in MRDS analysis (Hamilton et al., 2018). The effect of the thresholds was investigated in the two-step decision tree on the number of duplicates and the detection probability. Different values of the distance distribution used to set the visual and acoustic buffers in the first step of the decision tree were tested: 70%, 80%, 90%, and 100% based on a fixed value of the routine swimming speed, which was 3.6 m/s (7 knots). For the second step of the decision tree, different routine speeds were found in the literature, ranging from 1.6 to 4.2 m/s (3.1 and 8.2 knots). The effect of routine speed was investigated by testing different values: 1.60, 2.25, 2.90, 3.55 and 4.20 m/s (3.11, 4.37, 5.64, 6.90, 7.00, 8.16 knots) with a fixed value of the distance distribution of 95%. For each value of the distance distribution and the routine speed, the number of duplicate events and $g(0)$ were estimated, as well as the overall detection probability using half-normal and hazard-rate key functions. This sensitivity analysis allowed a comparison of the number of duplicate events and detection probability estimates obtained to assess the effect of using the values in the decision tree.

4.3 Results

4.3.1 Summary of survey data

Acoustic-visual transects in good conditions (when Beaufort sea state ≤ 4) totalled 6,679 km of effort (Figure 4.3). The lengths and average speed of surveyed transects for each survey block are given in appendix B. A total of 108 visual and 122 acoustic events of small cetaceans were identified. Species identification based on the visual survey component is shown in figure 4.4. The striped dolphin was the most frequently observed species and represented 52.8% of the total visual events. The second most observed species was the short-beaked common dolphin (11.1%) followed by the bottlenose dolphin (4.6%). The Risso’s dolphin (2.8%), the long-finned pilot whale (0.9%), and the rough-toothed dolphin (0.9%) were occasionally observed during the survey. About a quarter of the visual events could not be identified at the species level (26.9%). The estimated “best” group size was higher in visual events at 9.9 ± 14.0 individuals than in acoustic events at 3.8 ± 1.5 individuals.

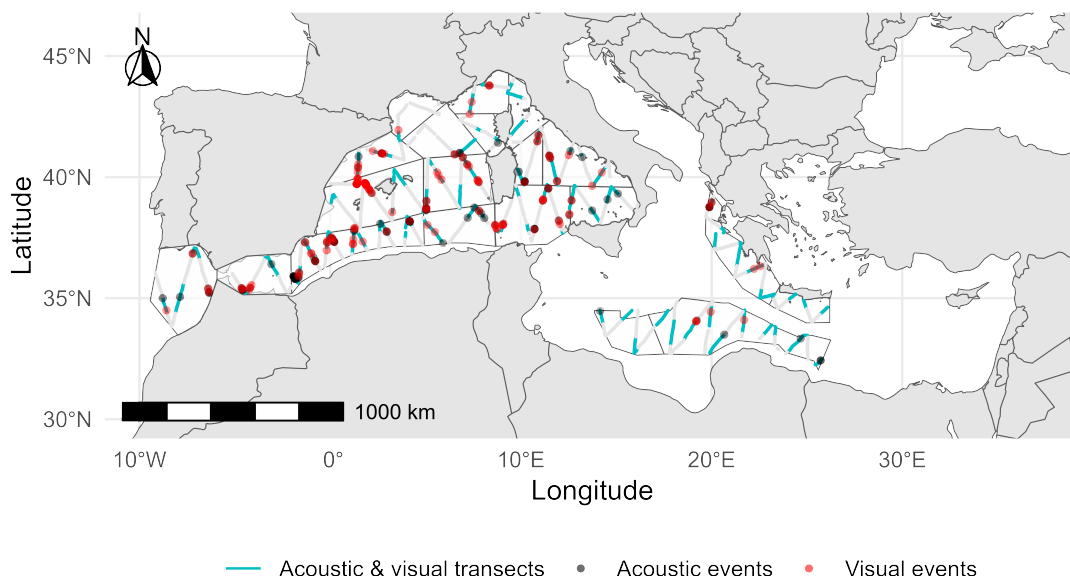


Figure. 4.3: Vessel-based line transect based on acoustic and visual effort. The map shows the linear transects sampled by the *R/V Song of the Whale*, with recorded acoustic (black dots) and visual (red dots) events. Polygons represent sampled blocks. The blue lines represent the acoustic and visual transects. Grey lines represent the remaining transects not used in this chapter.

4.3.2 Matching visual and acoustic events

A total of 87 potential duplicates were identified after the first temporal threshold was applied, reducing to 44 confirmed duplicates after applying the second spatial threshold. By selecting a single visual and acoustic event for each match, we finally obtained 30 unique duplicate events, which represent 16% of the total events. The visual platform recorded

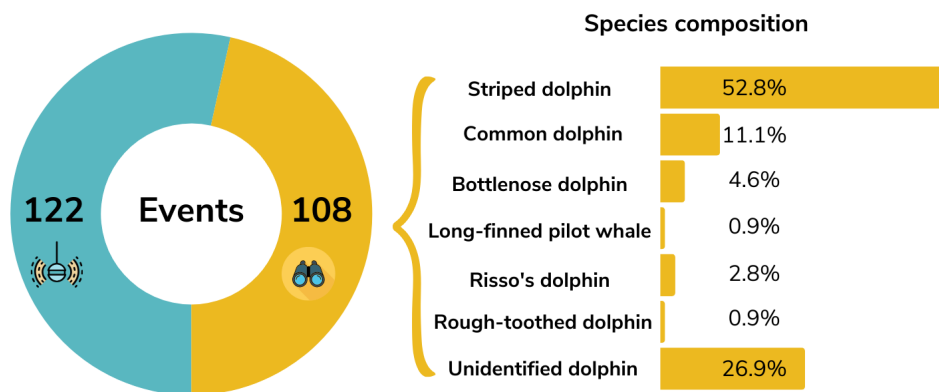


Figure. 4.4: Number of acoustic and visual events identified. Species composition of visual events displayed in percentage.

77 events that the acoustic platform did not. Conversely, 79 events were identified by the acoustic platform only. Among the duplicate events, the species most observed by the visual platform was the striped dolphin (56.7%) followed by the common dolphin (16.7%) and unidentified dolphins (13.3%). Not surprisingly, bottlenose (6.7%), Risso's (3.3%) and rough-toothed (3.3%) dolphins were rarely seen in the duplicate events. Under the assumption that unidentified dolphins have the same species composition as the identified dolphins, about 63% of the duplicate events would be striped dolphins. This estimate includes 56.7% from the directly identified striped dolphins and at least half of the unidentified dolphins assumed to be striped dolphins ($13.3\% / 2 = 6.7\%$; total $56.7\% + 6.7\% = 63.4\%$).

4.3.3 Estimation of the detection probability

A truncation distance was set at 1,500 m, which removed 10 unique visual, 2 unique acoustic and 2 duplicate events, representing 7.5% of the total events (Figure 4.5). Thus, in total, 67 unique visual, 77 unique acoustic and 28 duplicate events were used to fit the detection function in the MRDS method.

Based on the AIC and the goodness of fit, the PI model with a HR key function was the best model (Figure 4.6 and table 4.2). The MR submodel included perpendicular distance, swell height and platform as covariates. The DS submodel with the HR key function included sea state only. However, the model did not appear to fit the data well and overestimated detectability close to the transect line (Figure 4.7). Although the PI model with a HN key function was not optimal, it had a better fit to the data (Figure 4.7) and could therefore be considered as a more conservative model for estimating detection probabilities.

For both key functions, all parameters of the detection function were negative (Table 4.3), such that the detection probability decreased with increasing perpendicular distance from

4. Estimation of the detection probability using visual and acoustic data

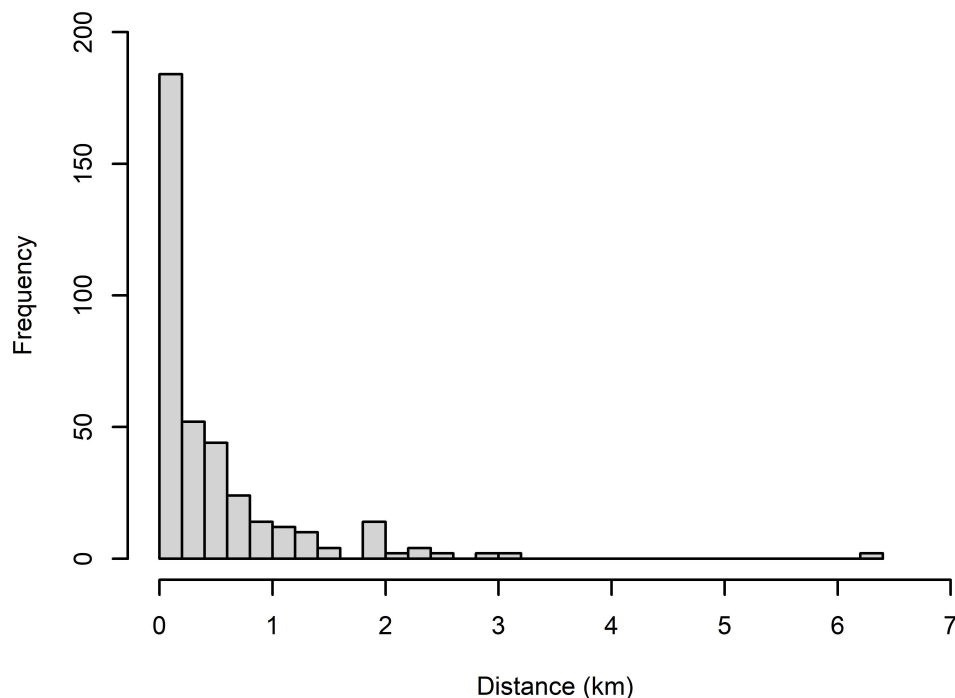


Figure. 4.5: Perpendicular distance frequency distributions. Bars plots represent the frequency of events from either acoustic or visual platforms. The distance is in km.

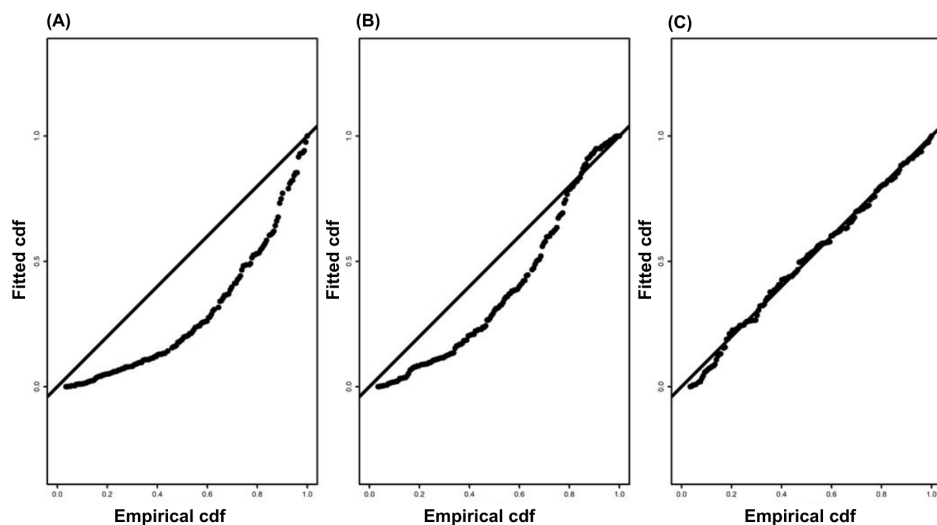


Figure. 4.6: Goodness of fit of the fitted models. (A) Full independence assumption and Point Independence assumption with (B) a half-normal key function and (C) a hazard-rate key function.

the transect, swell height and sea state (the further away from the vessel and the worse the conditions, the more difficult it is to detect the animals). However, $g(0)$ was fixed in all conditions. The detection probability in the MR submodel was slightly higher with the acoustic platform than with the visual platform (parameter estimate for the visual platform equal to -0.14), but the SE was high relative to the parameter estimate, so the effect of the platform was marginal (Table 4.3) which means their effect on the detectability

Table 4.2: AIC of the best models fitted. With full independence and point independence assumptions (with a half-normal and a hazard-rate key function).

| Assumption | Covariates | AIC |
|--|---|-----|
| Full independence | Distance + Wave height | 398 |
| Point independence (half-normal key function) | MR submodel: Perpendicular distance + Swell Height + Platform DS submodel: Sea state | 352 |
| Point independence (hazard-rate key function) | MR submodel: Perpendicular distance + Swell Height + Platform DS submodel: Sea state | 292 |

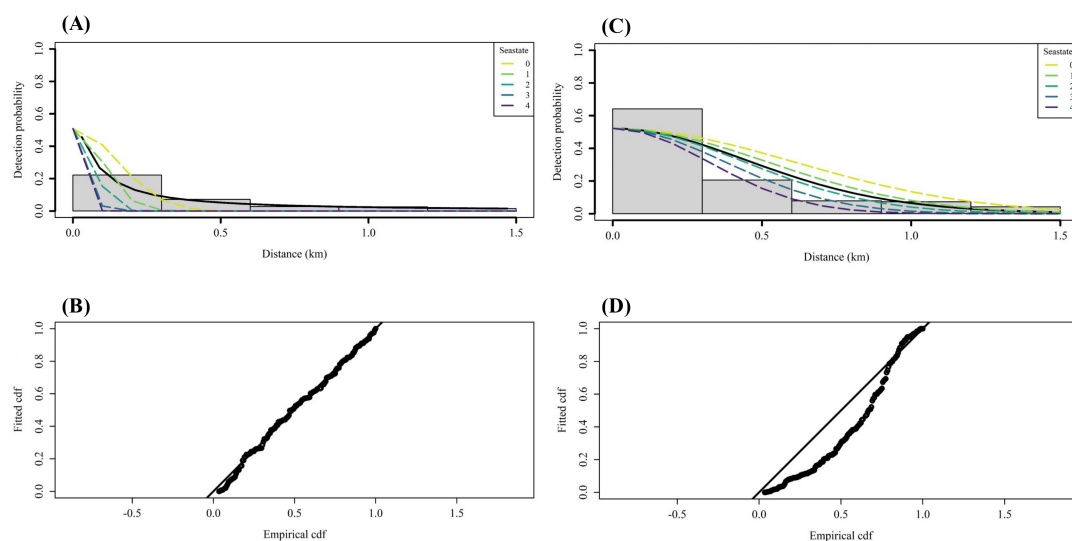


Figure. 4.7: Fitted detection function of the best models with their performance. (A) Model with a hazard-rate key function with (B) the associated goodness of fit and (C) with a half-normal key function with (D) the associated goodness of fit. The selected model is a point-independence model with an MR submodel including the covariate platform and a DS submodel including the covariate sea state. Each line represents the fitted detection function for each class of the sea state covariate.

of small cetaceans was negligible. In contrast, the SE was low for the distance and swell height covariate in the MR submodel and for the sea state in the DS submodel (Table 4.3). These results highlighted the strong effect these covariates have on the detectability of small cetaceans on the transect line.

The number of events identified by the visual and acoustic platforms did not differ greatly and duplicate events occurred mainly within 500 m of the transect line. However, the acoustic platform detected more events on the transect line and at a greater distance (Figure 4.8). Indeed, the $g(0)$ was slightly higher for the acoustic platform from 0.32 (CV = 25.1%) to 0.33 (CV = 23.2%) depending on the key function (Table 4). The $g(0)$ of the visual platform was estimated between 0.29 (CV = 25.6%) and 0.30 (CV = 23.8%). Finally,

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Table 4.3: Coefficients of the best models. Coefficients are associated with standard errors estimated in the PI model with a hazard-rate key function (HR) and a half-normal key function (HN).

| | Coefficients (HR) | SE (HR) | Coefficients (HN) | SE (HN) |
|------------------------|-------------------|---------|-------------------|---------|
| MR submodel | | | | |
| Intercept | - 0.34 | 0.32 | - 0.34 | 0.32 |
| Perpendicular distance | - 1.11 | 0.72 | - 1.11 | 0.72 |
| Swell Height | - 0.49 | 0.30 | - 0.45 | 0.30 |
| Visual platform | - 0.14 | 0.17 | - 0.14 | 0.17 |
| DS submodel | | | | |
| Intercept | - 1.47 | 0.44 | - 0.34 | 0.12 |
| Sea state | - 0.42 | 0.16 | - 0.16 | 0.04 |

by using combined platforms, we obtained a $g(0)$ of 0.51 (CV = 21.7%) with the HR key function and 0.52 (CV = 19.8%) with the HN key function. The use of the key function had a large effect on the overall detection probability estimations and therefore on the ESW. It was estimated to be 0.07 (CV = 28.9%) and 105 m for the HR key function and 0.21 (CV = 20.3%) and 315 m for the HN key function respectively. If detection biases were not accounted for, i.e. assuming $g(0) = 1$, the estimated overall detection probability and ESW would be 0.14 and 210 m respectively for the HR key function and 0.40 and 600 m for the HN key function.

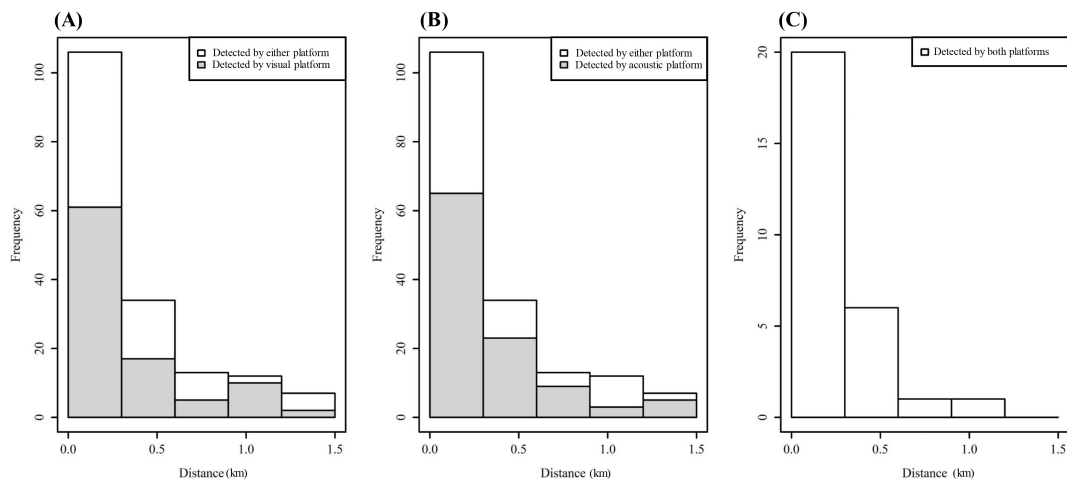


Figure. 4.8: Histogram of event distances according to the platform in use. The shaded regions show the number for (A) visual platform and for (B) acoustic platform. Events recorded by both platforms are shown in (C).

The sensitivity analysis explored the effect of using different values of the distance distribution and routine swimming speed on the number of duplicate events and the

Table 4.4: Detection probabilities obtained from the MRDS model with a hazard-rate key function (HR) and a half-normal key function (HN).

| Probability | Model used | Estimate (HR) | SE (HR) | CV (HR) | Estimate (HN) | SE (HN) | CV (HN) |
|--|-------------|---------------|---------|---------|---------------|---------|---------|
| Probability of detection assuming $g(0) = 1$ | DS submodel | 0.14 | 0.03 | 18.2% | 0.40 | 0.02 | 4.2% |
| $g(0)$ of the visual platform | MR submodel | 0.29 | 0.07 | 25.6% | 0.30 | 0.07 | 23.8% |
| $g(0)$ of the acoustic platform | MR submodel | 0.32 | 0.08 | 25.1% | 0.33 | 0.08 | 23.2% |
| $g(0)$ of combined platform | MR submodel | 0.51 | 0.11 | 21.7% | 0.52 | 0.10 | 19.8% |
| Overall probability of detection | MRDS model | 0.07 | 0.02 | 28.9% | 0.21 | 0.04 | 20.3% |

detection probability estimates (Figure 4.9 and appendix C). With a distance distribution ranging from 70 to 100% and a routine speed ranging from 1.6 to 4.2 m/s (3.1 to 8.2 knots), the number of duplicate events increases from 14 to 35 and 3 to 37 respectively. Both $g(0)$ and the overall detection probability became stable for both models from 70% of the distance distribution. On the contrary, $g(0)$ continuously increased as the routine speed increased, and overall probability detection increased more slowly for both models.

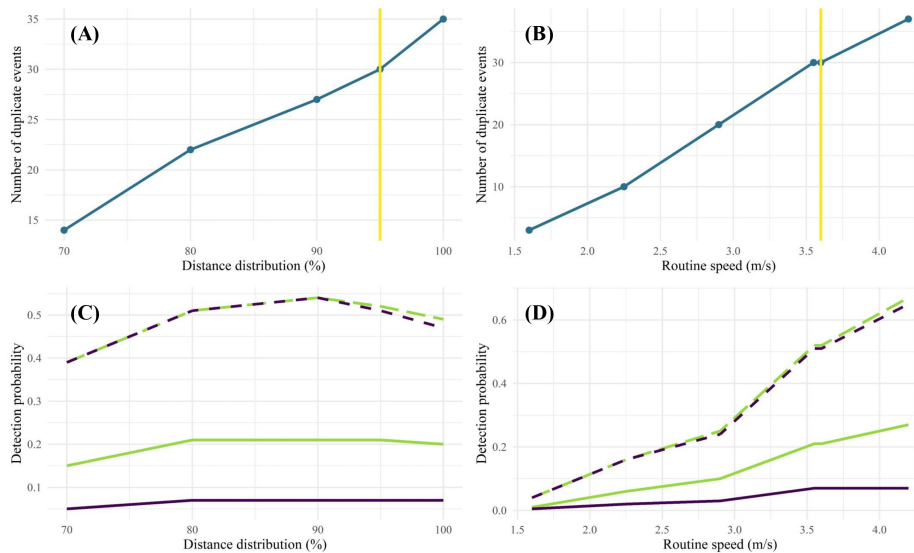


Figure 4.9: Sensitivity analysis of the two-step decision tree. The variation of the number of duplicates was explored with (A) different values of the distance distribution and (B) the routine speed. The vertical yellow line indicates the chosen value for this study. The overall detection probability (solid line) and $g(0)$ (dashed line) were estimated for each value of (C) the distance distribution and (D) the routine speed. The green and purple lines represent the models used with a half-normal and a hazard-rate key function respectively.

4.4 Discussion

The objective of this study was to estimate the detection probability of small cetaceans accounting for detection biases. Visual and acoustic data were collected simultaneously using a visual acoustic double platform in a distance sampling framework. Most studies estimate the detection probability by assuming $g(0)$ is equal to 1 with a single platform (Barlow, 2006; Øien, 2009; Dick & Hines, 2011; Hildebrand et al., 2015). To account for detection biases in abundance estimates, $g(0)$ needs to be estimated. The benefit of using a double visual-acoustic platform is to quantify the proportion of missed events to estimate $g(0)$ and thus to correctly calculate the detection probability. To do so, a method was developed first to identify duplicate events by taking the movements of the vessel and of the animal(s) into account. Then, the detection probability was estimated through an MRDS analysis by including covariates that can affect the detection.

4.4.1 Methodological considerations

4.4.1.1 Responsive movement

Performing distance sampling analysis assumes that animals are moving slower than the speed of the survey platform and are detected before any responsive movement related to the presence of the vessel, which requires detecting animals ahead of the vessel (Buckland et al., 2001). The effect of responsive movement on the detection function can be corrected by using two independent visual teams on the same vessel where one searches further ahead to detect animals before they respond (Borchers et al., 1998). When the second platform is an acoustic platform, it is more complex to account for responsive movement since small cetaceans are less easy to track with acoustic methods. For example, when they move away, they no longer face the hydrophone and may be less available for detection. Among the species studied, the three most commonly seen species were striped, common and bottlenose dolphin. These species are known to be attracted to the bow of vessels (Würsig, 2018). To reduce the bias due to responsive movement, a minimal attraction or avoidance effect from the boat was assumed because the *R/V Song of the Whale* is a quiet research vessel designed for this purpose. Second, the responsive movement was partially taken into account in the identification of the duplicate events by setting a mobility buffer based on an average cetacean routine swimming speed. Field observations during the ASI survey suggested the use of routine speed was appropriate for assessing responsive movement as animals were rarely observed ‘racing’ towards the research vessel. Additionally, a single distance was required for each duplicate event. The distance between the matching visual and acoustic events was chosen according to the first event that was detected. In general, animals were first detected visually in front of the boat and then later by the hydrophone towed 400 m behind the boat. By choosing the distance of the first detected event, the influence of any reactive motion was minimised and this partially addressed the responsive movement

problem. Martin et al. (2020) assessed responsive movement based on animal orientation and behaviour information based on visual data. They also set the trial configuration (one platform is informed about detections of the other platform) and chose the FI assumption in their model to partially address the responsive movement issue (Laake & Borchers, 2004; Burt et al., 2014). They recommended that responsive movement be properly considered in future vessel-based surveys for abundance assessments. Although responsive movement is difficult to assess and avoid, the use of a mobility buffer was believed to partially address the issue of responsive movement in the MRDS analysis with two independent platforms.

4.4.1.2 Duplicate events

The number of duplicate events plays an important role in the MRDS analysis when estimating detection probability (Evans & Hammond, 2004; Hamilton et al., 2018). Classifying unique events as duplicates will lead to an underestimation of the detection probability. In the opposite way, classifying duplicate events as unique events would result in an overestimation of the detection probability (Evans & Hammond, 2004). In the present study, only 16% of the total events were confirmed duplicates, while in other studies, they represent more than 30% of total events (35%, Dalpaz et al., 2021; 30%, Rankin et al., 2020; 48%, Richman et al., 2014). The decision tree with different values of the distance distribution in the first step and the routine speed in the second step were tested. The distance distribution was based on the data and was not an arbitrary threshold. Changing the value of the distribution did not have a great impact on detection probabilities, particularly from 80% to 100%. As for the routine speed chosen from values between 1.6 and 4.2 m/s (3.1 and 8.2 knots) found in the literature, it was an arbitrary threshold. The effect of varying this speed on detection probabilities was not negligible: the higher the routine speed, the higher the number of duplicate events and detection probabilities. By choosing the 95% quantile of the swimming speed distribution, i.e. 3.6 m/s (7 knots), we lost 7 duplicate events, which was not insignificant. The choice of a higher speed would probably correspond to an attraction or repulsion movement relative to the vessel, but it was not possible to determine whether the animals detected were being attracted or repelled or not. It seemed more appropriate to consider a routine swimming speed, with the aim of including all motivational states, including travelling, socialising, resting and foraging. The number of duplicate events in this study seemed low compared to other studies, but the approach used to identify duplicates was different from that of other studies. Dalpaz et al. (2021) used a decision tree based on three criteria: (1) less than 30 min between events, (2) less than 6 km between events and (3) taxonomic compatibility between detections of Delphinidae and Ziphiidae. Rankin et al. (2020) identified visual and acoustic detections of rough-toothed dolphins as duplicates when both detections occurred in close range. However, the authors did not explain in detail how they matched the detections and how “close” was defined. Richman et al. (2014) studied the detectability

4. Estimation of the detection probability using visual and acoustic data

of Ganges River dolphins and used a distance threshold between a visual and an acoustic detection to identify duplicates. They found the value of the distance threshold based on visual inspection of the frequency distribution of number of matched detections over distance; which was 249 m for a single animal and 349 m for a group of more than one animal. In open ocean habitats, such as in this study, hydrophones are towed as far back as possible to avoid self-boat noise. The delay between a visual sighting from in front of the vessel and the subsequent detection of the animal by the hydrophone to the rear of the vessel can be relatively long. As small cetaceans are highly mobile species, it is necessary to take their movement into account during this time. Although routine speed remains a sensitive parameter for the decision tree, the application of the mobility buffer still reduced the number of duplicate events identified by the time buffer by half, which can be considered very restrictive. However, it allowed to identify with more certainty the potentially true duplicate events, reducing the risk of false duplicates.

4.4.2 Detectability of small cetaceans

4.4.2.1 Detection process

During the survey and the analytical stage, a consistent protocol was implemented to define distinct events. However, the performance of the models tested was not perfect, as either the goodness of fit was good but the model did not seem to fit the data, or the opposite was observed. The detection function using the HR key function was unable to accurately describe the data observed close to the transect line due to a poor fit at low perpendicular distances. This indicates a possible problem associated with the detection process. Accurate distance estimation can be an issue in visual surveys (Marques et al., 2006). In this study, radial distances were estimated by naked eyes without tools, which may bias perpendicular distance estimates. For a small vessel with a low platform like the *R/V Song of the Whale*, the use of reticule binoculars or photogrammetry is complex (Leaper et al., 2023). Observers during the ASI survey had varying levels of field experience and identification skills. Thus, using the photogrammetry or reticules might have been counter-productive if being used by novice observers. Laser rangefinders can be a useful tool but only under optimal sea state conditions to avoid waves interfering with the laser and/or the motion of the vessel making reliable range-finding challenging. All of these methods would also result in a biased distance estimate. With distance estimation training conducted prior to the survey, naked eye measurements appeared to be the best approach in these conditions.

4.4.2.2 Group size estimation

During a survey, detectability between individuals may vary for multiple reasons; some animals may surface/vocalise more than others, or some may be more detectable in specific habitats such as shallow or deep waters. Due to this variability, each individual, species

or population should have its own detection probability. However, some variables that influence the detection probability cannot be observed, which corresponds to unmodelled heterogeneity and therefore does not allow a reliable estimation of detection probability and abundance (Buckland et al., 2004; Buckland et al., 2015). The first source of unmodelled heterogeneity could be related to group size estimation. Estimating group size is complex in visual and even more so in acoustic studies because animals are moving and an unknown fraction of the group might be underwater or silent at any given time (Gerrodette et al., 2019). In visual surveys, estimating the group size of a large school of active dolphins is a difficult task and the estimates can vary considerably between observers (Gerrodette et al., 2002). The average group size was estimated to be 10 individuals in this study, which was consistent with other studies averaging between 4 and 30 individuals (Notarbartolo Di Sciara et al., 1993; Bearzi et al., 2003; Cañadas & Hammond, 2008; Boisseau et al., 2010; Notarbartolo Di Sciara & Tonay, 2021) in the Mediterranean, although larger aggregations are known (Watkins et al., 1987; Boisseau et al., 2010; Notarbartolo Di Sciara & Tonay, 2021). In acoustic surveys, group size cannot be estimated directly during surveys and most studies use visual events to determine group size of the acoustic events (Barlow & Taylor, 2005; Pirotta et al., 2015). Another approach is to use cue counting to estimate the density of cues that animals produce, such as calls, that can be converted into animal density using the cue production rate of the species (Marques et al., 2009). In this study, overlapping clicks trains were used as an indicator of the number of acoustically active individuals in the group and to estimate the acoustic group size for each event, following Thomas and Marques (2012). With this methodology, the estimated visual group size was approximately three times higher than the acoustic group size. Such a discrepancy between the visual and acoustic group size suggests that the latter was underestimated. The first assumption suggests that the recordings may have captured only a subset of the group, namely those animals that were echolocating. The second assumption is that individuals moving from the front of the boat to the back were counted. It is likely that not all animals in a group were moving toward the hydrophone in the same way. As a result, only part of the group was detected and counted, while the others either moved away or did not head toward the hydrophone. The third assumption is a mixture of the two, implying that disentangling availability bias and perception bias from the acoustic method is difficult. Due to probably incorrect estimates of the acoustic group size, this covariate was not included in the model and the remaining unmodelled heterogeneity can lead to a potential overestimation of the detection probability (Borchers et al., 2006; Burt et al., 2014). With further studies of vocalisation rates, it may be possible to scale up the underestimation of acoustic group size, but there is currently insufficient meaningful data on vocal rates for small odontocetes in the Mediterranean Sea.

4.4.3 Comparison of $g(0)$ estimation with other studies

Despite the main limitations of this study, the results were statistically accurate, as shown by reasonably low CVs (20-27%), and were consistent with other studies, especially for the visual platform. Rankin et al. (2020) estimated $g(0)$ at 0.37 and 0.77 for the visual and acoustic platforms respectively and 0.84 with the combined platforms for rough-toothed dolphins. The $g(0)$ for the visual platform was similar to the results of this study (0.29, CV = 25.6% and 0.30, CV = 23.8%). For acoustics, the results of this study were lower (0.32, CV = 25.1% and 0.33, CV = 23.2%) but Rankin et al. (2020) also included other vocalisations such as whistles and burst-pulses, which resulted in a higher number of acoustic events and thus a higher estimate of $g(0)$. Additionally, echolocation clicks are highly directional and therefore if the animals are too far away or off-axis of the hydrophone, the detection probability decreases sharply (Au et al., 2012; Finneran et al., 2014), which could partly explain the low estimate of $g(0)$ from the acoustic platform in our study. Although the appropriate data are lacking for the Mediterranean, small odontocetes may be more vocal when submerged, as is typically the case for larger odontocete species including sperm whale and Cuvier's beaked whale (Akamatsu et al., 2001). This situation would preclude exact duplicates to occur. However, since dolphins can switch between the two conditions in a matter of a few seconds, and the time window for potential duplicates was within 271 s before and 1,179 s after the visual event, this left ample time for duplicates to be recorded if the individual was acoustically active during this time interval. Therefore, these methods appeared to be complementary and, as expected, we obtained a higher detection probability by combining both platforms (Laake et al., 2011; Rankin et al., 2020).

4.4.4 Implication for cetacean conservation

This study highlights the importance of using a visual acoustic double platform in multi-species line transect surveys to estimate the detection probabilities of small cetaceans, taking into account detection biases, which have a major effect on the detection probability estimates. While recognising that most cetacean conservation programs use minimum abundance estimates (Evans & Hammond, 2004), an unbiased abundance estimate is emphasised to provide a better approach to assessing the sustainability of cetaceans in the face of anthropogenic mortalities. Based on the estimates of $g(0)$ and p in this study, estimating cetacean abundance in the Mediterranean Sea without correcting for detection biases would result in an underestimation by a factor of two when using both acoustic and visual data for both models (HR and HN key functions).

5

Study of small cetacean activity rhythms

This chapter aims to study the activity rhythms of small cetaceans in relation to temporal parameters. As their acoustic behaviour is not well understood, the number of acoustic events was analysed by modelling with variables ranging from hourly to monthly resolution, including time of day, lunar cycle, lunar illumination and sea state. This chapter has been published in the journal *Frontiers in Marine Science* (Sol et al., 2024) and is available in appendix D.

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5.1 Introduction

Marine animals adapt their physiology and behaviour to environmental fluctuations and associated rhythms shaped by the marine environment (Häfker et al., 2023). These adaptations synchronise biological activity with major natural cycles governed by the Earth's orbit around the Sun (seasons), the Moon's orbit around the Earth (tides), and the Earth's rotation (nycthemeral cycle). Endogenous systems control these biological rhythms, and in some species, changes in light levels can trigger behavioural responses (Ochoa et al., 2013). Therefore, the nycthemeral cycle can be the source of daily changes and adaptations, although the exact nature of these rhythms also depends on other factors such as habitat type, coordinates, and physicochemical properties (Häfker et al., 2023). The aggregation of marine predators for feeding has been shown to be associated with primary production, bathymetry, and sea surface temperature (Hastie et al., 2004; Prieto et al., 2017; Scales et al., 2016). An example of a biological rhythm in the pelagic environment is the diel vertical migration of mesopelagic organisms, including crustaceans (euphausiids, mysids, copepods), fish (e.g., myctophids) and cephalopods (e.g., histioteuthids), which are part of the Deep Scattering Layer (DSL). These organisms migrate from depths below 200 m to the epipelagic zone (surface to 200 m) at dusk to feed, and return to the depths at dawn to avoid predators (Barham, 1966; Klevjer et al., 2016). Another example is the influence of the moon on the timing of reproductive activities in marine animals (Bentley et al., 1999). Coral spawning, for example, can be synchronized to maximise reproductive interactions between conspecifics, a process triggered by moonlight cycles (Oliver & Babcock, 1992; Lin et al., 2021; Bentley et al., 1999).

Optimal foraging theory suggests that air-breathing diving species, such as small cetaceans, develop strategies to minimize the cost of pursuing prey and maximize the energy gain during breath-holding dives to access deep resources (Pyke, 1984; Kiszka et al., 2022). Therefore, small cetaceans that consume mesopelagic prey are likely to follow DSL dynamics and adapt their feeding rhythms to nocturnal light conditions for optimal foraging efficiency (Giorli et al., 2016; Simonis et al., 2017). In pelagic habitat, cetacean activity typically increases in the evening, peaks at night and decreases in the early morning (Linnenschmidt et al., 2013). This pattern is likely due to the greater availability of prey near the sea surface at night. In demersal habitats, cetaceans such as harbor porpoises that feed on bottom-dwelling fish - many of which are not particularly active at night - tend to be less active at night and show different diel patterns from those of delphinids in pelagic habitats (Brandt et al., 2014). In the Mediterranean, where shelf habitats are limited, some studies have observed nocturnal foraging activity in small cetaceans (Giorli et al., 2016; Caruso et al., 2017). Giorli et al. (2016) highlighted that several typically offshore dwelling cetaceans (Risso's dolphin, long-finned pilot whale, Cuvier's beaked whale, and sperm whale) exhibited mostly nocturnal foraging activity. Similarly, Caruso et al. (2017)

5. *Study of small cetacean activity rhythms*

studied several delphinids (striped dolphin, bottlenose dolphin, common dolphin, Risso's dolphin and long-finned pilot whale) in the Ionian Sea and found a daily pattern in foraging activity, with greater activity at night. These findings suggest that the foraging behaviour of small cetaceans is driven by the dynamics of prey, which are more active and easier to capture at night.

Small cetaceans use echolocation clicks mainly for foraging, navigating and detection of predators (Au, 1993). Foraging involves all the activities required to reach, locate, detect and capture prey, with searching being the most time-consuming activity and this includes echolocation, which is important for both navigation and prey detection (Giorli et al., 2016). As clicks are used for navigation in a three dimensional environment, are involved in reaching favourable foraging habitat and allow prey to be detected, approached and caught, they are considered to be the most relevant acoustic indicator of foraging activity (Caruso et al., 2017). In this context, we assumed that temporal patterns in foraging activity would strongly affect click production rate. In addition, clicks are the most abundant type of sound emitted, and therefore would provide a larger sample size than the other types of vocalisations. Studying clicks can therefore help our understanding of how cetacean foraging activity changes over time.

The aim of this chapter was to investigate the pattern of foraging activity of small cetaceans in the Mediterranean Sea. Previous studies of foraging patterns in the Mediterranean Sea have typically relied on stationary acoustic devices within limited geographic areas (Giorli et al., 2016; Cascão et al., 2020). This research used acoustic data collected continuously during both day and night by the *R/V Song of the Whale*. Assuming a constant density of small cetaceans throughout the day and night, we hypothesised the existence of a distinct diel pattern with increased acoustic activity during the night. Variations in the number of acoustic events per unit of time and their correlation with candidate temporal variables were examined using a generalized additive model (GAM) framework.

5.2 Methodology

5.2.1 Data processing

Only acoustic data collected during acoustic effort (including double platform and acoustic transects) were used in this chapter. To get better resolution of variation in acoustic events in a 24-h cycle, acoustic sampling effort was divided into minutes and acoustic events were associated with the effort by date and time. Because the study area was relatively large, the time zone differed between the western and eastern Mediterranean.

To avoid time zone bias, the recorded Universal Time Coordinated (UTC) of the acoustic events was converted to solar time as (Waugh, 1973):

$$\text{solar time} = 4(\text{longitude}) + \text{UTC} \quad (5.1)$$

Longitude is given in decimal degrees, and the factor of 4 corresponds to the Earth's rotation rate. Since the Earth completes one rotation in 24 hours (or 1,440 minutes), each degree of rotation represents 4 minutes. The Greenwich meridian at 0° longitude was used as the reference. Depending on whether the acoustic event (as defined in 3) occurred east or west of this meridian, the resulting duration in minutes was either added to or subtracted from UTC to derive solar time.

5.2.2 Statistical analysis

5.2.2.1 Selection of variables

To investigate the relationship between the number of acoustic events detected per minute of effort and temporal variables using a GAM framework, variables relevant to temporal scales ranging from hourly to monthly time resolution were selected and associated with each minute of sampling effort (Table 5.1). Temporal variables included the time of day, which was treated as a circular variable to account for the continuity between 00:00 and 24:00, thereby improving the accuracy of the model and capturing significant cyclical variation in the data. In this study, daytime was defined as the period from 05:00 to 19:00, while nighttime was defined as the period from 19:00 to 05:00. The lunar cycle and the lunar illumination, which indicates the fraction of the lunar surface that is illuminated, were also included because of their influence on the diel vertical migration of the DSL. The lunar cycle, which lasts about 29.53 days (Figure 5.1), progresses through four phases: new moon (day 1), first quarter (day 8), full moon (day 15), and last quarter (day 22, DeBruyn and Meeuwigg, 2001; Wang et al., 2015). This variable was considered to be cyclical. Lunar illumination, which represents the fraction of the lunar surface that is illuminated, ranges from 0 (new moon) to 1 (full moon, figure 5.1). Both lunar phase and lunar illumination data were obtained using the 'lunar' R package (Lazzari et al., 2012), with the day of the lunar cycle calculated by dividing the lunar phase by 0.212769 (each day the lunar cycle increases by this value to complete a full cycle). Beside nocturnal illumination, the lunar cycle also determines tidal range. Although the tide is limited in the Mediterranean Sea it does exist with an amplitude from 0 around the Balearic Islands to 60 cm in the Gulf of Gabès, Tunisia. Tidal range is greater at full and new moon and is minimal at first and last quarters, following a cyclical pattern with a period of approximately 15 days. Sea state was also included as a candidate variable because it can change on an hourly timescale. Sea state was recorded during the ASI survey using the Beaufort scale from 0 to 6. Recognising the importance of spatial distribution of small cetaceans in the Mediterranean Sea (Cañadas et al., 2023), longitude and latitude were included as spatial factors rather than as explanatory variables to focus on temporal patterns.

5. Study of small cetacean activity rhythms

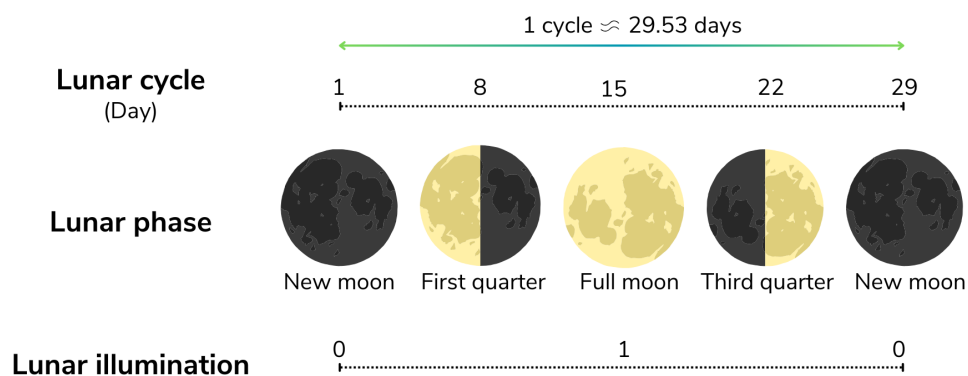


Figure 5.1: Illustration of the lunar cycle and lunar illumination with corresponding phases. The lunar cycle lasts 29.53 days. The phases of the lunar cycle are shown from left to right: new moon (day 1), first quarter (day 8), full moon (day 15), and third quarter (day 22). Lunar illumination indicates the fraction of the lunar surface that is illuminated, ranging from 0 (new moon) to 1 (full moon).

Table 5.1: Candidate temporal variables used in the model. Temporal variables included time of day (h), lunar cycle (day), lunar illumination ranging from 0 (new moon) to 1 (full moon) and sea state (measured on the Beaufort scale from 0 to 6). Longitude and latitude ($^{\circ}$) were included as spatial factors. For each variable, the type, source and reasons for selection were provided. The 'lunar' R package is from Lazzari et al. (2012)

| Variable | Variable type | Source | Description to the topic |
|------------------------------------|---------------|------------------------|---|
| Time of day | Circular | PAMGuard acoustic data | Time of acoustic events |
| Lunar cycle | Circular | Lunar R-Package | Vertical migration of organisms is associated to Lunar cycle and their illumination |
| Lunar illumination | Continue | | |
| Sea state | Category | ASI survey | Indicate the habitat use |
| Longitude, Latitude ($^{\circ}$) | Continue | | |

5.2.2.2 Generalised additive models

The variation of acoustic events was modeled using candidate variables within a GAM framework with a Tweedie distribution to account for over-dispersion in the data (Foster & Bravington, 2013). GAMs were preferred to linear models because they allow for smooth, nonlinear functions of predictor variables that are determined by the data, rather than being constrained by strict parametric relationships (Wood, 2006). Variables with Pearson correlation coefficients higher than 0.5 were excluded to avoid multicollinearity.

For the time of day and lunar cycle variables, the degrees of freedom (k) were set to 15 and 7, respectively, allowing for multiple inflection points to capture the expected nonlinear responses. Circular smoothing terms (splines, $bs = 'cc'$) were used to account for the circular nature of these variables, increasing the model's ability to capture temporal variations and cyclic patterns. For the other variables, thin-plate regression splines ($bs =$

'tp') were used for optimal results, with degrees of freedom set to 4 due to simpler expected relationships (Qian, 2016). All GAMs were fitted using the 'mgcv' R package (Wood, 2017).

All combinations of one to four variables were tested and the model with the lowest AIC (Akaike, 1998), the highest AIC weight (calculated with the 'qpcR' package from Spiess, 2018) and the highest explained deviance (Akaike, 1998) was selected. The importance of each variable was assessed by summing the AIC weights of the models in which the variable appeared, and the variables were ranked according to their individual contributions (Symonds & Moussalli, 2011). All analyses were performed using R software (version 4.1.2, Team, 2022).

5.3 Results

5.3.1 Overview of acoustic data

A total of 74,000 minutes of sampling effort were sampled between May and September 2018 with 40,000 minutes during the day and 34,000 at night. There were 161 acoustic events recorded during the day and 580 events during the night (741 events in total). Acoustic events were detected in all blocks, with a higher concentration observed in the western basin (Figure 5.2). The number of acoustic events by sea state was 80 for Beaufort 0, 62 for Beaufort 1, 225 for Beaufort 2, 246 for Beaufort 3, 83 for Beaufort 4, 45 for Beaufort 5, and none for Beaufort 6.

More acoustic events were recorded at night (shaded area, figure 5.3) with two peaks, reaching around 0.026 acoustic events per minute at 21:00/22:00 (solar time) and then around 01:00. After 01:00, the number of events decreased considerably; down to 0.0007 events per minute at 11:00 (Figure 5.3). Since the foraging activity of small cetaceans is likely influenced by DSL dynamics, the number of acoustic events over the lunar cycle was examined. Acoustic data were collected over a period of 4 months, covering approximately 4 lunar cycles. A total of 214 events were recorded during the new moon, 80 during the first quarter, 284 during the full moon, and 153 during the third quarter. After correcting for sampling effort, we observed that more acoustic events were detected during the third quarter of the lunar cycle (Figure 5.4). The highest number of acoustic events per minute of effort, 0.03, was observed on day 22, corresponding to the third quarter phase, while the lowest, 0.0008 events per minute of effort, was observed on day 8, corresponding to the first quarter phase.

5. Study of small cetacean activity rhythms

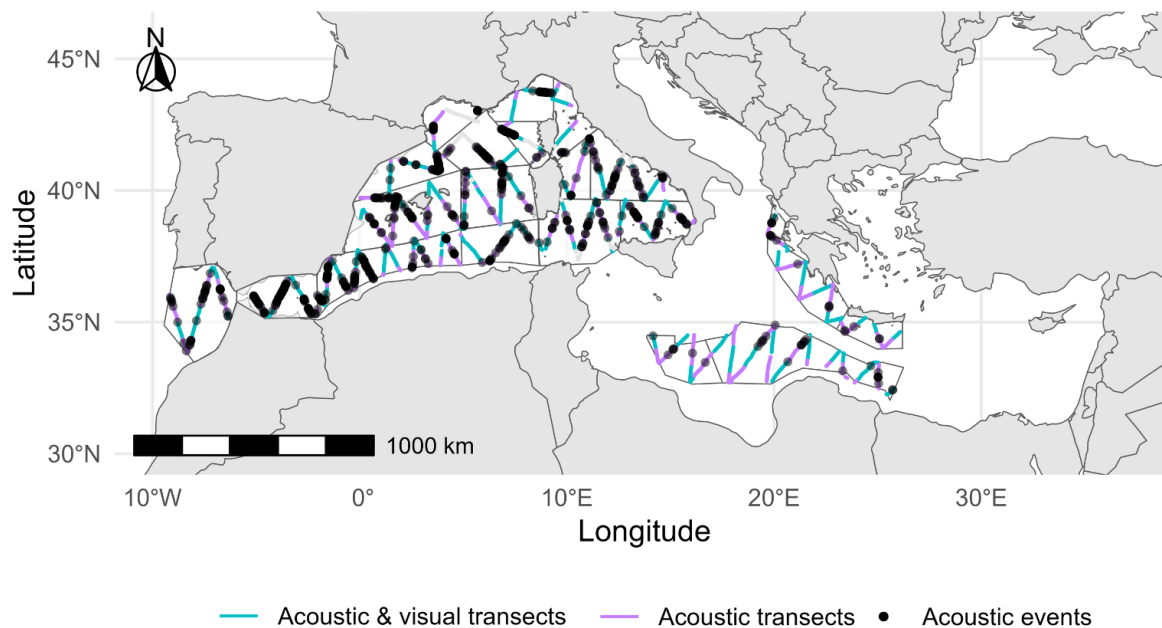


Figure 5.2: Vessel-based line transect based on acoustic effort. The map shows the linear transects sampled by the *R/V Song of the Whale*, with recorded acoustic events (black dots). The polygons represent sampled blocks. The coloured lines represent the transects used in this chapter: blue lines indicate transects where both (visual and acoustic) platforms were used, purple lines indicate transects where only the acoustic platform was used, and grey lines represent the remaining transects not used in this chapter (corresponding to visual transects only).

5.3.2 Influence of variables on the variation of acoustic event numbers

The variables showed low correlation with each other (Figure 5.5). Therefore, all the variables could be selected simultaneously in the models tested. Among the variables included, time of day and sea state were found to have the most significant influence on the variation of the number of acoustic events with Akaike weights of 99-100% (Table 5.2). They were followed by the lunar cycle with an AIC weight of 80%. In contrast, lunar illumination, had a relatively low AIC weight of 60% (Table 5.2). The best model explained 14.3% of the deviance and included all the variables tested, although lunar illumination was not significant ($p = 0.43$). The second model also explained 14.3% of the deviance and did not include lunar illumination. As the top two models were very similar ($\Delta AIC < 2$, appendix E), the second model was selected as the final model because lunar illumination was not significant. The final model included the spatial effect and the variables time of day, lunar cycle and sea state.

The number of acoustic events increased as night approached, peaking around 21:00/22:00 and at 01:00, with only a slight decrease between these two periods (Figure 5.6). The number of acoustic events then decreased to a diurnal minimum around 11:00 (Figure 5.6).

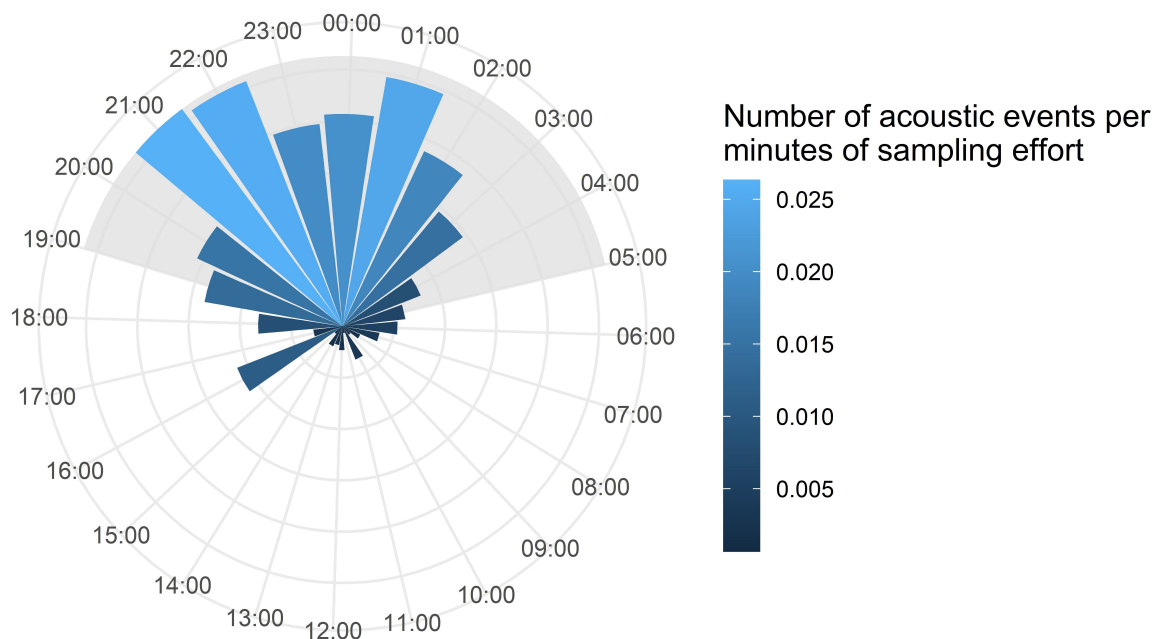


Figure. 5.3: Distribution of acoustic events corrected by sampling effort over the 24-hour cycle. The bars represent the number of acoustic events per minute occurring in each hourly slot. The highest number of acoustic events is shown in light blue, while the lowest number is shown in dark blue. The shaded area indicates the nocturnal phase, which extends from 19:00 to 05:00.

Table 5.2: Ranked variables according to their AIC weights. The count column indicates the number of times each variable appears in all the models tested, the percent column shows the associated percentage, and the Akaike weight reflects the variable's relative contribution to the model.

| Variable | Count | Percent | Akaike weight |
|--------------------|-------|---------|---------------|
| Time of day | 8 | 50 | 100 |
| Sea state | 8 | 50 | 99 |
| Lunar cycle | 8 | 50 | 80 |
| Lunar illumination | 8 | 50 | 60 |

For the lunar cycle variable, the number of events decreased from day 0, corresponding to the new moon, to a minimum on day 8, corresponding to the first quarter of the moon (Figure 5.6). The response variable then increased, reaching a maximum during the third quarter of the moon (day 22 of the lunar cycle) and decreasing again until the end of the lunar cycle (day 29, figure 5.6). The relationship with sea state was unimodal from 1 to 4 and became positive at higher sea states (above 4, figure 5.6). Longitudinal and latitudinal gradients were observed, with more frequent acoustic events in the northern part of the western and central Mediterranean sub-regions (Figure 5.6).

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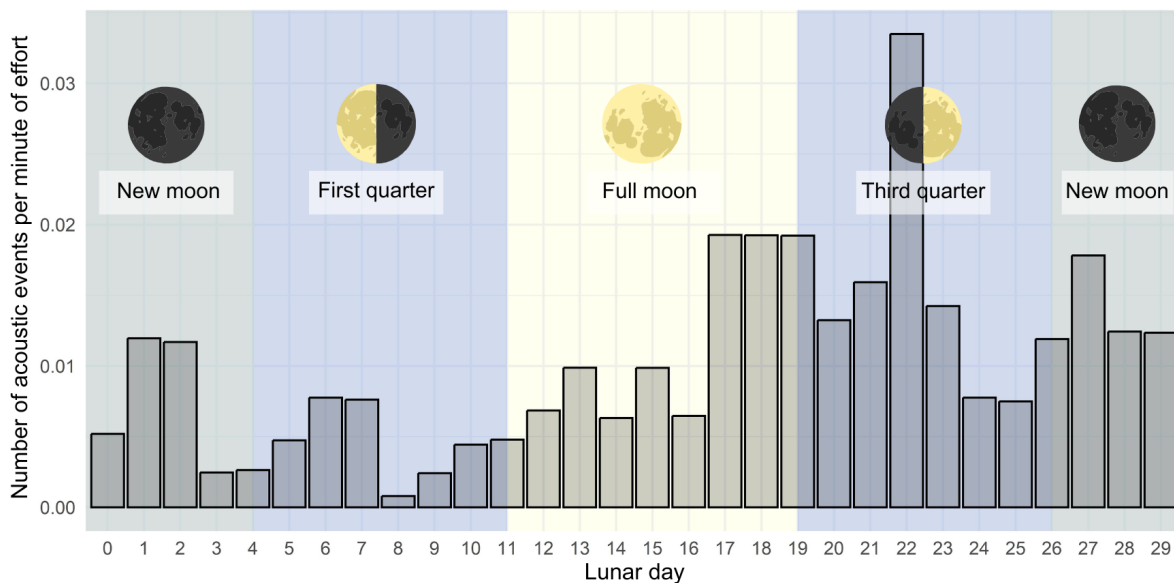


Figure. 5.4: Distribution of acoustic events corrected by sampling effort over the lunar cycle. The bars represent the number of acoustic events per minute of effort for each day of the lunar cycle. The coloured background corresponds to the phase of the moon, with the new moon in grey, the first quarter and third quarter in blue, and the full moon in beige.

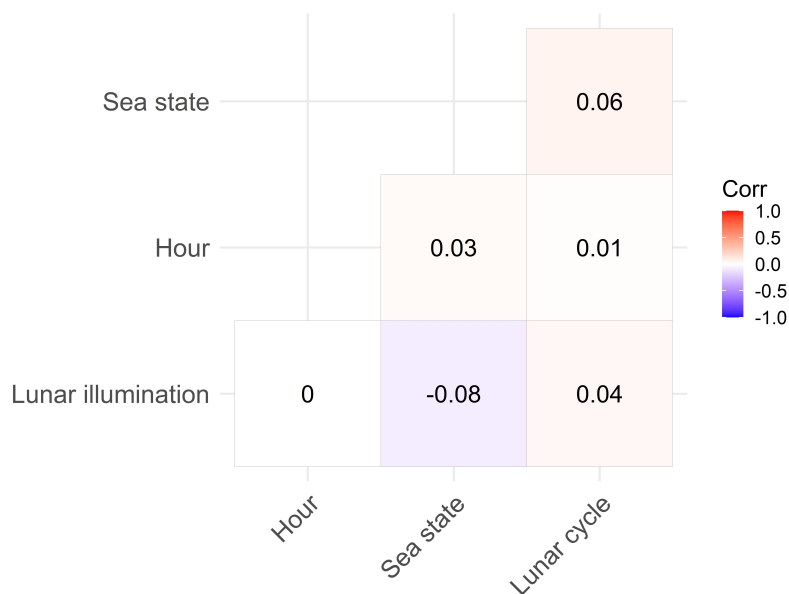


Figure. 5.5: Pearson correlation matrix including candidate variables used in the Generalized Additive Models. Positive correlations are shown in red, while negative correlations are shown in purple.

5.4 Discussion

To date, our understanding of the foraging patterns of small cetaceans throughout the Mediterranean has been somewhat patchy. Previous studies of these patterns have mainly relied on fixed PAM and focused on specific Mediterranean subregions or even local sites, such as the Ligurian sea (Giorli et al., 2016) or Sicily (Caruso et al., 2017). These studies

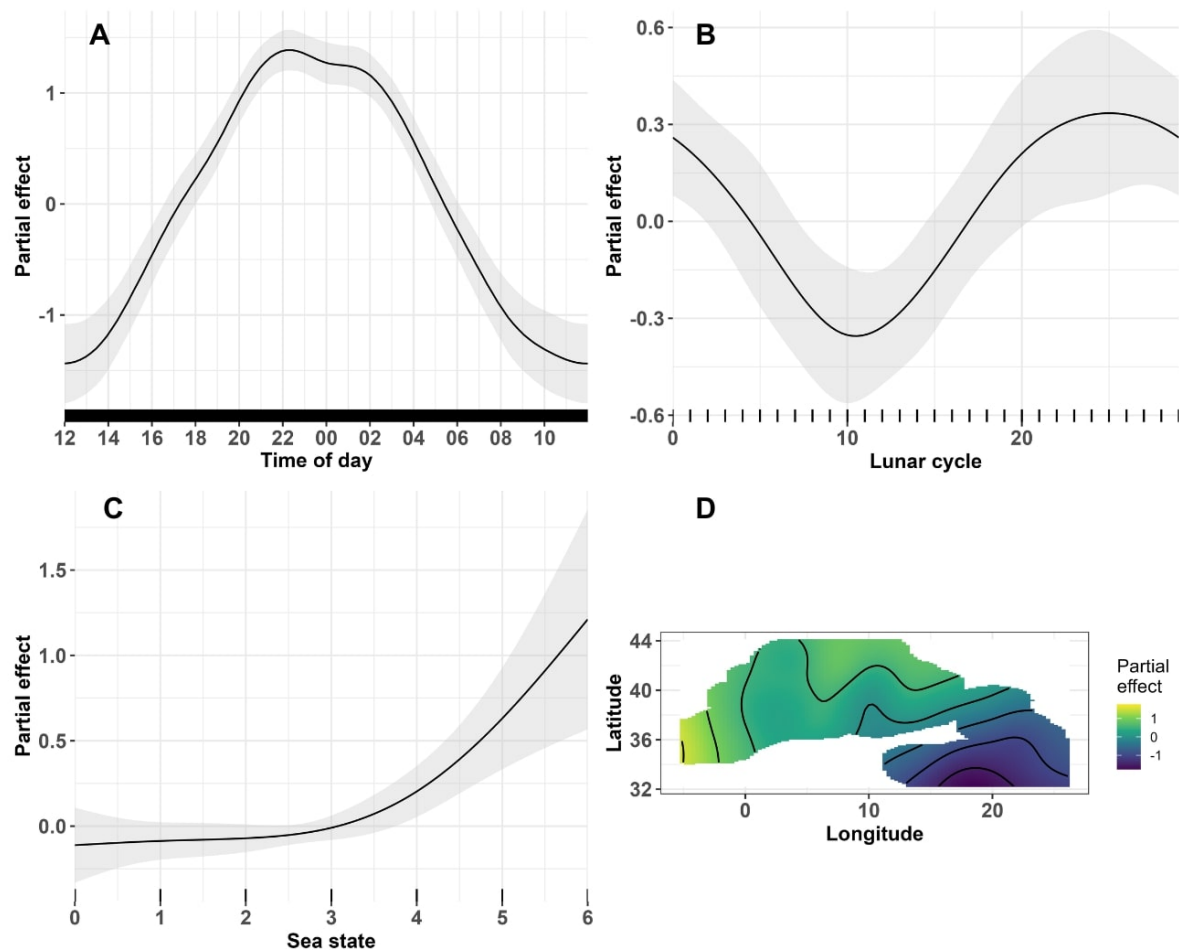


Figure 5.6: Relationships obtained between the number of acoustic events and the variables. Results of the selected GAM model with a Tweedie distribution for the variables (A) time of day, (B) lunar cycle, (C) sea state and (D) for the joint smoothing of longitude and latitude (yellow represent the highest predictions and blue the lowest). The black lines on the x-axis represent the distribution of the data. (A) time of day is a continuous variable with a resolution in minutes and labels in hours. (B) lunar cycle and (C) sea state are categorical variables. The shaded grey area represents the 95% confidence interval of the spline functions.

showed a diel foraging activity pattern with a peak at night. However, in these settings, it can be challenging to discriminate true patterns in echolocation activity around the recording stations from local movements in and out of the detection radius of these stations. The chapter provides insight into the foraging activity patterns of small cetaceans at a basin scale from a moving platform in the Mediterranean Sea. This approach assumed a constant density of small cetaceans throughout the day and night, with any changes in the number of acoustic events primarily attributed to changes in vocal behaviour related to foraging activities rather changes in their occurrence. This benefit of using basin-wide datasets helps to identify activity rhythms. Results derived from the GAM model revealed a distinct diel pattern, with a prevalence of acoustic events during nocturnal hours. The distribution of effort between day and night condition was fairly well balanced and cannot be a source of bias in the number of acoustic events per unit time. The

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lunar cycle also had a clear influence on the number of acoustic events, with more events being detected during the third quarter of the moon

5.4.1 Methodological considerations

Analysing datasets on a large scale provided an overall picture of small cetaceans activity in the Mediterranean Sea but required dealing with spatial variability and time zones. To mitigate this, UTC times were converted to solar time to remove any time zone bias (Carlucci et al., 2016). Additionally, spatial effects were incorporated into the model to mitigate the effects of animal distribution. The selected temporal variables showed a clear influence on the number of acoustic events, with minimal uncertainties associated with their relationships (as evidenced by narrow confidence intervals, figure 5.6). This suggests that the highlighted patterns were quite reliable.

However, the selected model explained only 14.3% of the deviance suggesting that variables other than those considered in the study explain the variation in the number of acoustic events. For example, tidal height and sea surface temperature may influence the number of acoustic events, as shown in the study of Gauger et al. (2022) on bottlenose dolphins in California waters. Benoit-Bird and Au (2003) analysed and compared the relative abundance and density of spinner dolphins (*Stenella longirostris*) and the mesopelagic community off three Hawaiian islands using a modified echo-sounder and showed that the dolphins followed the vertical dynamics of their prey. This lack of direct data on prey behaviour throughout the study area necessitated the use of other parameters such as time of day or lunar cycle, thought to influence prey density and catchability at dolphin foraging depths. More detailed information on local delphinid prey activity and their catchability may have allowed for a more precise explanation of delphinid activity rhythms.

5.4.2 Activity rhythms of small cetaceans in the Mediterranean Sea

The results of this study, showing that Mediterranean small cetaceans have a very distinct diel rhythm of acoustic event production, mainly displayed processes related to the striped dolphins in offshore habitats (Panigada et al., 2024). The other species present did not contribute much to the overall picture and were likely merely contributing to the uncertainty around the observed general patterns. The general pattern reflects an average across individuals, but groups within a population may show different foraging behaviour. These variations in the number of acoustic events illustrated the activity or foraging strategy of the small cetaceans, which would vary according to the availability and type of prey (Benoit-Bird & Au, 2003).

Time of day. This variable was found to be the most significant variable in the selected model. Changes in the number of acoustic events could indicate shifts in foraging behaviour that are driven by prey availability. The latter is shaped by depth distribution and density of prey. Small cetaceans assess the accessibility of prey, the potential encounter rate during foraging dives, and the associated costs in order to maximise their foraging success (MacArthur & Pianka, 1966). When prey becomes scarce or migrates to deeper waters, small cetaceans may reduce their foraging effort because it would not be profitable, resulting in fewer acoustic events (Cascão et al., 2020). When prey is abundant and easily accessible, small cetaceans may engage in more active foraging, resulting in numerous acoustic events (MacArthur & Pianka, 1966). In the latter situation, it is also possible to imagine that when prey is most abundant less foraging effort would be necessary to meet calorific requirements, whereas when there is slightly less prey but still enough for foraging to be profitable, then foraging would be greater, hence acoustic events more numerous.

In our study, small cetaceans showed increased activity and were more frequently detected at night, indicating a nocturnal peak in foraging. This behavioural pattern likely responds to nocturnal variations in prey dynamics and vertical distribution (Thompson & Miller, 1990). Prey typically migrate vertically, ascending to the surface to feed at night, where reduced visual information and increased backscatter pose a challenge to visual predators such as seabirds, and descending to deeper waters during the day to avoid predators (Marohn et al., 2021). During the ascent of the DSL to the surface, the defence mechanisms of organisms, particularly small pelagic fish, are thought to be reduced; they would be present in less aggregated schools and would have reduced individual swimming speeds (Zein et al., 2019). Furthermore, as night-time can lead to a loss of visual information and an increase in backscatter (Mass & Supin, 2018), the nocturnal increase in prey concentration near the surface would be advantageous for nocturnal air-breathing predators; this is the case for odontocetes, whose highly developed sonar allows them to detect prey regardless of light conditions.

The proximity of prey to the surface benefits nocturnal air-breathing diving species such as small cetaceans because diving deeper rapidly depletes their oxygen reserves and leads to the rapid reaching of their aerobic diving limit (Tyack et al., 2006). Therefore, to optimize foraging success while minimizing dive duration, it is advantageous for small cetaceans to concentrate their foraging activity at night, especially when the DSL rises closer to the surface (Giorli et al., 2016). During this time, prey is more abundant, easier to catch, and more accessible near the surface. This strategy allows dolphins to limit their foraging depths and maximize their hunting time (Figure 5.7). Similar nocturnal foraging strategies have been observed in small cetacean species (Simonis et al., 2017; Caruso et al., 2017). Simonis et al. (2017) have highlighted a similar diurnal pattern in certain small cetaceans,

5. Study of small cetacean activity rhythms

stating that foraging activity was mainly nocturnal, and that social behaviours tended to take place during the day. For a better understanding of this diel pattern, and given that buzz clicks are associated with prey capture and then foraging behavior, investigating these patterns in buzz clicks would be a valuable direction for future research (Nuuttila et al., 2013).

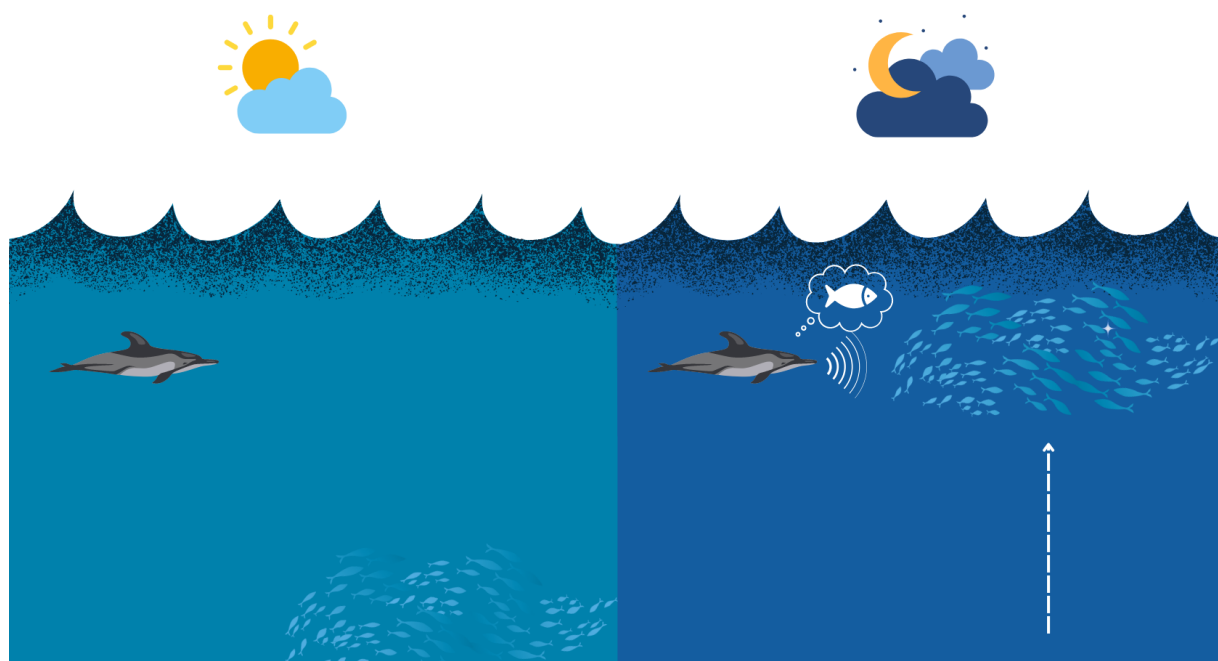


Figure. 5.7: Illustration of the foraging behaviour of small cetaceans influenced by the dynamics of the Deep Scattering Layer. Prey within the Deep Scattering Layer (DSL) typically migrate vertically (Thompson & Miller, 1990). (left) During the day, they descend to deeper waters to avoid predators, making them unavailable to small cetaceans (Marohn et al., 2021). (right) At night, they rise to the surface layer to feed, becoming accessible to small cetaceans, which then emit echolocation clicks to forage (Giorli et al., 2016).

Latitude and longitude. A spatial gradient in the number of acoustic events was observed, with more frequent events occurring in the western and northern parts of the Mediterranean. This distribution pattern is consistent with the eastward gradient of primary production, which is higher in the west than in the east due to the inflow of Atlantic waters (Gili et al., 2014). The lower primary production in the east is likely to lead to reduced prey availability for cetaceans, resulting in lower cetacean densities (see Cañadas et al., 2023 for an analysis of gradient in cetacean distribution observed during the aerial component of the ASI) and consequently fewer acoustic events in these areas.

Lunar cycle. The lunar cycle was not among the most significant variables (68% of the Akaike weight) but was included in the selected model. Acoustic events were minimal on day 8, corresponding to the first quarter moon, and maximal on day 22 during the third

quarter moon. The extent of the vertical migrations of prey would depend on the intensity of nocturnal versus diurnal illumination and would only be possible if light intensity fluctuates sufficiently during the diel cycle (Ochoa et al., 2013). During full moon nights, when lunar illumination is at its peak, migration may be delayed or attenuated to reduce the visibility of prey to surface predators, making prey less available (Ochoa et al., 2013).

As a result, small cetaceans may reduce their foraging behaviour, resulting in fewer acoustic events. However, the results of this study are inconsistent with previous research that observed minimal acoustic foraging activity during the full moon. Simonis et al. (2017) found that common dolphin echolocation activity in the Southern California Bight was the lowest during the full moon and the highest during the third quarter phase. They suggested that the brightness of the full moon delayed or shortened vertical migrations to avoid predators, causing predators to reduce foraging or switch to visual predation. During the third quarter, an extended period of darkness after sunset allows mesopelagic prey to migrate to the surface before the moon rises, making them more vulnerable and available to predators. In the Mediterranean Sea, Caruso et al. (2017) found no evidence of a relationship between echolocation activity and the lunar cycle in a pelagic area. These mixed results suggest that the response of small cetaceans to the lunar cycle is more complex than previously thought (Cohen et al., 2023; Shaff & Baird, 2021; Benoit-Bird et al., 2009; Caruso et al., 2017; Simonis et al., 2017). Therefore, in our study, lunar illumination alone cannot explain the variation in the rhythm of small cetaceans activity as maximum acoustic activity was found close to the third quarter of the moon and not at full moon. The interaction of the mesopelagic community with the lunar cycle involves more than just the nighttime light, which affects the vertical migration of DSL and the density of prey at the surface during a full moon. Detailed studies show that the major taxonomic groups within the DSL (fish, squid, and crustaceans) exhibit complex variations related to the lunar cycle that significantly affect prey availability for top predators (Battaglia et al., 2020). For example, bluefin tuna (*Thunnus thynnus*) in the Strait of Messina showed different prey compositions during the lunar cycle: mesopelagic prey dominated during the first quarter and full moon, mesopelagic squid after the first and third quarters, and other invertebrates during the third quarter and full moon (Figure 5.8). If different prey types are available at different times of the lunar cycle, small cetaceans may adapt their foraging strategies and acoustic behaviour accordingly, including variable echolocation rates, to cope with the potentially different acoustic reflectivity of these organisms. Organisms with structures of contrasting density, such as bones, swim bladders, and lipid-rich elements, are expected to have greater acoustic reflectivity and therefore require less echolocation to be detected than organisms that are uniformly close to the density of the surrounding water.

Sea state. Sea state was also selected in the best model. This variable may have an influence on cetacean sound production activity. The number of acoustic events increased

5. Study of small cetacean activity rhythms

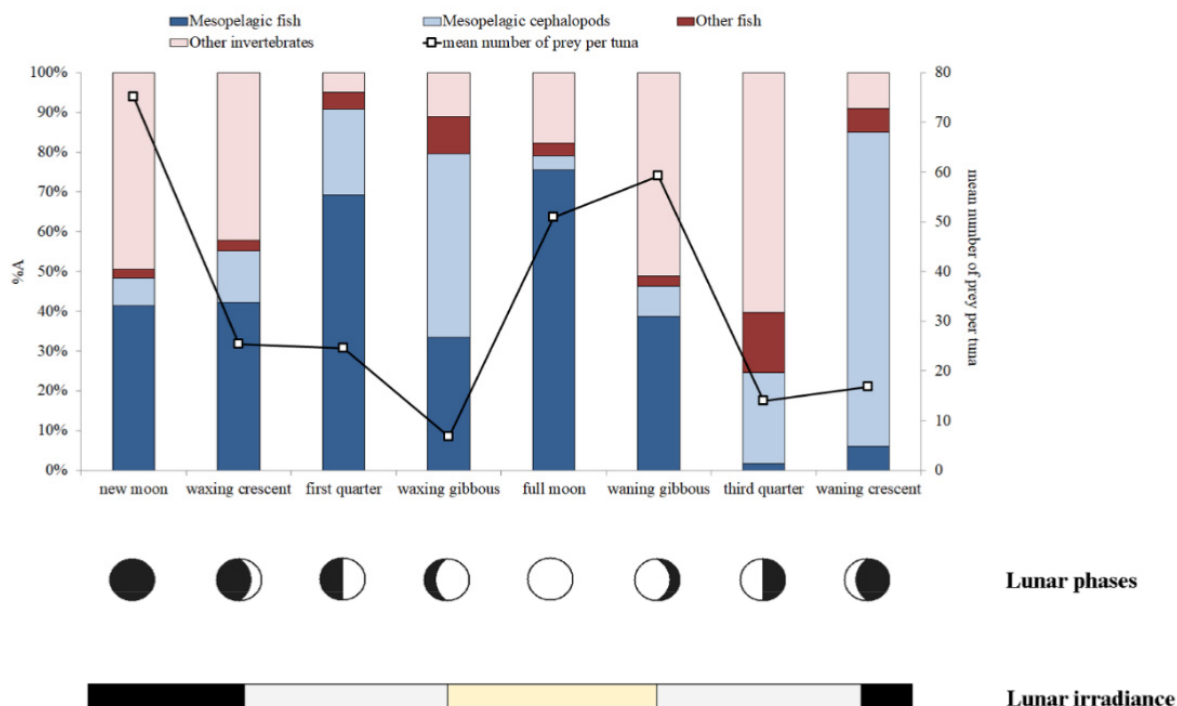


Figure 5.8: Relative percentage abundance (%A) of food categories consumed by *Thunnus thynnus* during the different moon phases. The mean number of prey per tuna over the lunar cycle (bar plots) is also present (line). The lunar irradiance is also shown for the entire lunar cycle. Lunar irradiance: black = low intensity; grey = medium intensity; yellow = high. Adapted from Battaglia et al. (2022).

from Beaufort 4. However, it is difficult to interpret this trend due to the limited data coverage in these conditions. This pattern may indicate an adaptive strategy in which cetaceans increase amplitude or shift frequency in response to significant ambient noise either natural or anthropogenic (Isojunno et al., 2022; Martin et al., 2018). Increased ambient noise can also affect the detection range of a hydrophone array, reducing the probability of detection (Ward et al., 2011). An independent measure of ambient noise may be useful in future surveys to explore whether dolphins adjust their sound activity to ambient noise.

5.4.3 Monitoring and conservation implication

The results revealed a strong diel pattern in the acoustic activity of small cetaceans, which has important implications for monitoring with passive towed hydrophones. Assuming that cetacean densities are similar during day and night, the increased events at night indicate that detection probability varies throughout the diel. Therefore, an uniform acoustic detection probability over the diel cycle would not be appropriate. Instead, a variable detection probability that accounts for the diel pattern, or at least day/night differences, should be used when estimating the abundance of small cetaceans to account for their acoustic behaviour. This would apply to the analysis of data from towed passive

acoustic surveys following a linear transect strategy. In contrast to stationary passive acoustic surveys using moored hydrophones, changes in dolphin activity on the one hand and small scale movements affecting local dolphin density within the detection range of the hydrophone on the other hand, determine together the number of acoustic detection per unit time and are hard to disentangle.

The existence of these activity rhythms may also have conservation implications. While fishing may occur day or night (Levy et al., 2015), depending on the diversity of fishing practices, increased foraging activity at night could make dolphins more vulnerable to fisheries bycatch as they would be more focused on foraging and less alert to environmental hazard (Todd et al., 2020). Anthropogenic sound sources in the same frequency bands as dolphins can have a masking effect on these signals (Marian et al., 2021) which can affect foraging success and, indirectly, the survival of the species.

5.5 Conclusion

This chapter focuses on understanding the acoustic behaviour of small cetaceans through the analysis of acoustic events identified by echolocation clicks. A diel rhythm of acoustic activity was shown, with small cetaceans exhibiting a predominantly nocturnal foraging pattern, as evidenced by significantly higher acoustic events at night. This rhythm of foraging activity was associated with temporal variables such as time of day, lunar cycle and sea state. The results are consistent with available knowledge on the DSL vertical migration, while the effect of the lunar cycle is more complex. This study has important implications for cetacean abundance estimation, as it shows that the behaviour of small cetaceans differs between day and night, making an uniform detection probability inappropriate.

6

Assessment of the effects of detection probability on abundance estimates

The aim of this chapter was to investigate different methods for accounting for detection biases inherent to acoustic and visual platforms. To achieve this, abundance estimates were derived using different datasets (visual and/or acoustic) and different scenarios accounting for detection biases, based on all blocks surveyed by the *R/V Song of the Whale*. In addition, abundances were estimated using previous scenarios and compared with corrected ASI aerial abundance estimates from blocks surveyed by both components. This chapter is based on an article that is currently in preparation.

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6.1 Introduction

Abundance estimation using line-transect distance sampling typically assumes $g(0) = 1$, i.e. perfect detection on the transect line, only because estimates of true $g(0)$ are often not available (Øien, 2009; Hammond et al., 2013; Lauriano et al., 2014). This assumption often leads to biased abundance estimates due to availability bias and perception bias (Laake & Borchers, 2004). Availability bias corresponds to the unavailability of animals for detection, either because they are below the sea surface, which depends on the time spent at depth by the species and the platform speed, or because they are not acoustically active, which depends on the vocalisation rate of the species. Perception bias accounts for the non-detection of available animals by observers or recorders due to imperfect observer vigilance or unfavourable conditions for detection (e.g. high sea states). Addressing these biases has been an active area of research for many years (Fais et al., 2016; Laake et al., 1997; Martin et al., 2020). Some studies have corrected abundance estimates for either perception bias or availability bias, and rarely for both. Double-platform surveys effectively quantify these biases (Barlow, 1995; Barlow & Forney, 2007). In visual surveys, the availability bias can also be quantified using dive data (Fais et al., 2016) although it is likely to be less of an issue for small cetaceans that make shorter dives, surface frequently, and display conspicuous surface behaviour; making them more likely to be detected in the observation time window (Leonard & Øien, 2020; Panigada et al., 1999). In this case, an approach based on the double platform framework aimed to estimate perception bias. Estimating $g(0)$ can be logistically and financially challenging, so most studies correct their abundance estimates using $g(0)$ correction factors derived from other studies (Boisseau et al., 2024). Others have designed survey protocols to estimate $g(0)$ based on their specific survey conditions and have used this value to produce unbiased abundance estimates (Martin et al., 2020; Gerrodette et al., 2011; Hammond et al., 2021b; Cañadas et al., 2004). As a result, estimates of $g(0)$ were often found to be less than 1, highlighting the importance of estimating $g(0)$ (Forcada et al., 2004; Rankin et al., 2020).

Detection probability may vary between species, between environments or over space and time (Callaghan et al., 2024). It is widely recognised that detectability varies between species and therefore $g(0)$ are often species-specific (Hammond et al., 2013; Martin et al., 2020). Some species are more easily detected due to their size, behavior, or when found in large groups. In the vessel component of the SCANS survey, $g(0)$ values were estimated to be 0.216 (CV = 0.16) for harbour porpoises, 0.550 (CV = 0.17) for common dolphins, 0.565 (CV = 0.27) for white-beaked dolphins (*Lagenorhynchus albirostris*) and 0.544 (CV = 0.29) for minke whales (Hammond et al., 2013). Another example is in the study of Barlow (2015), which showed that $g(0)$ varied with sighting conditions, assuming that the true density did not vary with sighting conditions. The author developed a method to

6. Assessment of the effects of detection probability on abundance estimates

estimate $g(0)$ values under different Beaufort sea state conditions by comparing Beaufort-specific density estimates of 20 cetacean taxa from different surveys in the eastern and central Pacific Ocean from 1986 to 2010. The results showed that $g(0)$ decreased with increasing Beaufort sea state. Detection probability may also be influenced by species behaviour, which may change over time. Miller et al. (2010) demonstrated a seasonal behavioural pattern in bottlenose dolphins, with more socialising behaviour in the spring and more foraging behaviour in the autumn. Such behavioural changes may affect acoustic detectability, especially if it is based on echolocation clicks, which are primarily associated with foraging behaviour. Therefore, comparisons of abundance estimates between seasons should be made with caution when species behaviour is known to change seasonally.

Estimating $g(0)$ for abundance estimates from acoustic data is more challenging because the vocal behaviour of most species is poorly understood. As a result, most studies have not corrected abundance estimates from an acoustic platform (Gordon et al., 2020; Hastie et al., 2003). Recent studies have successfully estimated $g(0)$ for the acoustic platform using the MRDS framework with a visual platform, despite the challenge of identifying duplicate events (Martin et al., 2020; Rankin et al., 2020, chapter 4). However, using acoustic data collected during the day, in parallel with visual data, may not take full advantage of acoustic methods that can also collect data at night. The vocal behaviour of small cetaceans can change with the time of day (Giorli et al., 2016).

The ASI design, complementary to the aerial surveys, allowed for optimal use of the visual and acoustic platforms during the vessel-based surveys, with acoustic data being collected continuously day and night, and visual data being collected during the day within the double-platform framework. As both acoustic and visual methods have inherent detection biases, these must be accounted for in the statistical analysis to estimate absolute abundance. To properly combine data for abundance estimates, $g(0)$ must be estimated for each platform. Chapter 4 provided $g(0)$ estimates for each platform but the double-platform surveys were conducted only during the day, while many acoustic data were also collected at night. The results in chapter 5 showed that the number of acoustic events varied between day and night, with more acoustic events occurring at night. Assuming that true abundance remains constant between day and night on a large scale and that a moving platform would not be affected by daily animal movements, this implies that detectability should increase at night. The $g(0)$ estimated for the acoustic platform in chapter 4 was based on daytime data, so this value may not accurately reflect acoustic detectability at night.

The present chapter aims to assess how the abundance estimate changes when different datasets are combined, and to assess how considering a $g(0)$ that varies with platform and/or time of the day influences this abundance estimate. To do this, several scenarios

were constructed, in which the number of data available for abundance estimation is gradually increased by using data from different sources, but also by considering a $g(0)$ that varies according to platform and time (Figure 6.1). On this occasion, a novel methodology was developed to account for the detection biases inherent in each method to estimate the absolute small cetacean abundance in the Mediterranean Sea based on the ASI survey. As the ASI survey was designed to allow blocks to be surveyed by both vessel and aerial components, abundance estimates were compared with the aerial estimate, which is totally independent from the vessel estimate while being spatially and temporally fully consistent.

6.2 Methodology

The design of the ASI vessel component was developed to allow the vessel *R/V Song of the Whale* to operate continuously day and night, with portions of transects surveyed using either the visual platform alone, the acoustic platform alone, or both platforms together. The acoustic and visual data used here come from the formatting process described in chapter 3.

6.2.1 Testing the effect of correction biases on abundance estimates

6.2.1.1 Effect of combining acoustic and visual data: creation of datasets

To assess the effects of combining acoustic and visual data on abundance estimates, three different datasets were built (Figure 6.2). The first dataset, named "visual dataset" included the effort segments and visual events collected during the visual transects and the visual component of the acoustic-visual transects. The second dataset, labeled "double-platform dataset", included visual dataset with the addition of the acoustic component of the acoustic-visual transects. In this case, the acoustic-visual transects were duplicated to separate the visual effort from the acoustic effort, and the transects were treated as if they had been surveyed twice (once per platform). The third dataset, labeled "full dataset", extended the diurnal double-platform dataset by incorporating effort segments and acoustic events collected during acoustic transects, mostly including the acoustic events recorded at night. By progressively adding effort through these three datasets, the sample size increased. We hypothesised that the precision of the estimates would increase as more samples were added, which would be indicated by a lower CV.

6.2.1.2 Consideration of $g(0)$ variability in estimating abundance

The aim was to assess how accounting for different $g(0)$, and hence detection biases, affects abundance estimates. Four scenarios were defined.

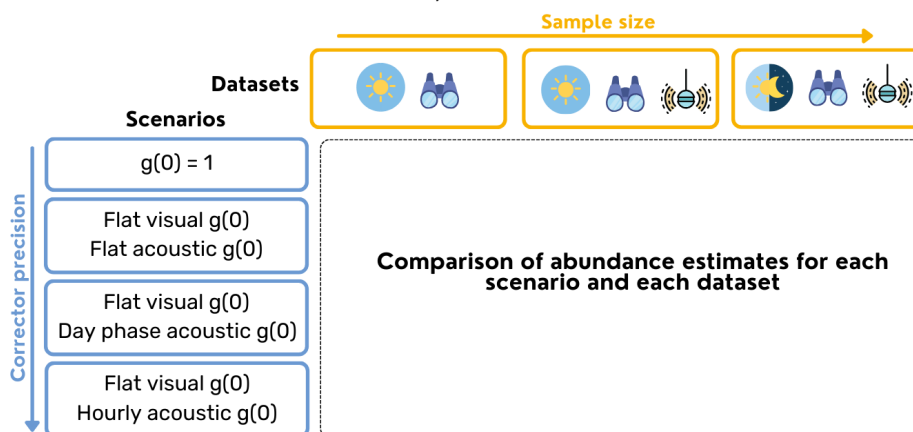
Scenario 1 assumed perfect detection of animals on the transect line, i.e. $g(0) = 1$.

Effect of variability in detection probability on abundance estimates - Experimental strategy

PROBLEMATIC
 How can the detection biases inherent in each method be taken into account when estimating abundance?

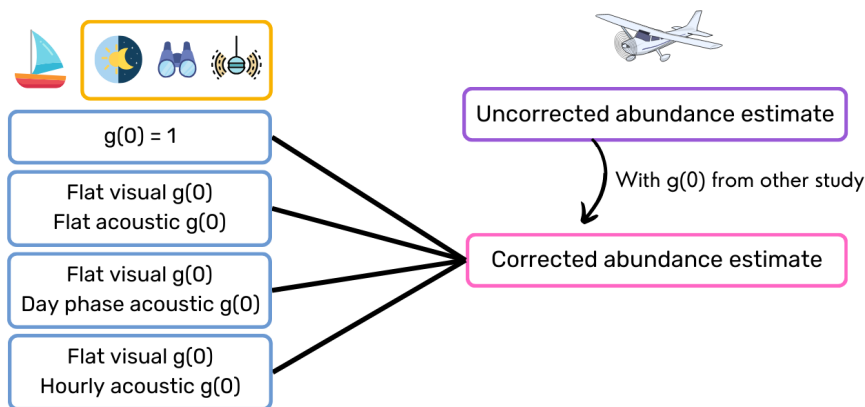
1. Testing effect of correction of detection biases on abundance estimate

Study area: Western Mediterranean (blocks 2 to 15), as this is a region totally surveyed by the vessel



2. Comparison with aerial abundance estimates

Study area: Mediterranean blocks surveyed by both vessel and aerial surveys



Comparison of vessel-based abundance estimates for each scenario with corrected aerial abundance estimate

Figure. 6.1: Experimental strategy of the chapter 6. The methodology in chapter 6 was divided into two parts. The first part of the analysis focused on assessing the effects of combining visual and acoustic data (using different datasets) and testing the effects of different methods (scenarios) for accounting for detection biases on abundance estimates. Abundance estimates were made for each dataset and scenario, and these estimates represented the western Mediterranean. The second part of the methodology tested the validity of the different scenarios by comparing the results with abundance estimates obtained from the aerial component of the ASI, conducted synchronously and in the same series of blocks as the vessel component. The aerial estimates from Panigada et al. (2024) were corrected for availability and perception biases before any comparisons were made.

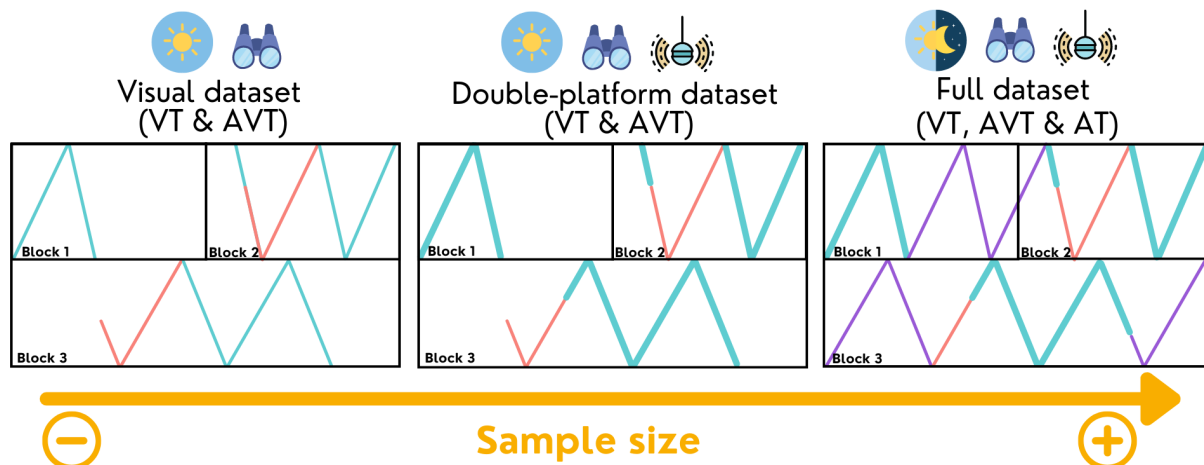


Figure 6.2: Schematic representation of the three datasets using visual and acoustic data for abundance estimates. The black box represents the study area with a simplified survey design for visualization. Three blocks were designed for this schematic, with the *R/V song of the whale* moving continuously along the transects day and night. The transects were divided into three types: visual transects (red lines), acoustic transects (purple lines), and acoustic-visual transects (blue lines). From left to right, the figure shows the three different datasets used in this study. The visual dataset included only visual transects and the visual component of the acoustic-visual transects. The double-platform dataset included the visual dataset and the acoustic effort from the acoustic-visual transects. The blue lines are doubled to represent the duplicated transects for each platform. The full dataset extended the double-platform dataset by including additional effort from acoustic transects. Adding effort progressively from left to right increases the sample size of the datasets.

In **scenario 2**, platform-specific $g(0)$ values were used to estimate abundance. The $g(0)$ values for the acoustic and visual platforms were those estimated in chapter 4 using a half-normal key function. They were set to $g(0)_a = 0.33$ (SE = 0.08) for the acoustic platform and $g(0)_v = 0.30$ (SE = 0.07) for the visual platform.

In **scenario 3**, a temporal variation of $g(0)$ values was considered for the acoustic platform. Indeed, it was shown in chapter 5 that the number of acoustic events varied with time, with a peak at night. Assuming that the animal population remained constant between day and night throughout the northwestern Mediterranean basin, the increased number of events at night would be due to an increase in nocturnal vocalisations rather than an increase in nocturnal occurrences, hence an increased detection probability at night. Thus, the $g(0)$ estimated during the day cannot be used for the night. This scenario proposed a methodology to estimate $g(0)$ for the acoustic platform based on the phase of the day. This was done by plotting the number of acoustic events against time and fitting a cosine function to the data distribution (Figure 6.3). The cosine function was chosen because of its sinusoidal nature, which fitted the data well. The fitted function was then used to derive $g(0)$ values over time, assuming that $g(0) = 1$ at the peak number of events at night. The function was scaled to have a mean $g(0)$ value of 0.33, as estimated during the day with the

6. Assessment of the effects of detection probability on abundance estimates

acoustic platform between 5:00 and 19:00 and $g(0)$ values were capped at 1 during the night. A mean $g(0)$ and SE were calculated for each phase of the day, with day defined between 5:00 to 19:00, night defined between 21:00 to 3:00, and transition periods defined between 19:00 to 21:00 and 3:00 to 5:00. The day-phase specific $g(0)$ value for the acoustic platform were estimated to be $g(0)_{day} = 0.33$ (SE = 0.15), $g(0)_{night} = 0.98$ (SE = 0.05) and $g(0)_{transition} = 0.78$ (SE = 0.16). For the visual platform, $g(0)$ was assumed to be constant and set to 0.30.

Scenario 4 used the same methodology as in scenario 3, but the $g(0)$ values were determined on an hourly basis. A mean and SE were calculated for each hour, resulting in 24 $g(0)$ values (Table 6.1), and used for the acoustic platform. For the visual platform, $g(0)$ was assumed to be constant and set to 0.30. We did not explore possible hourly variation in visual events during the day.

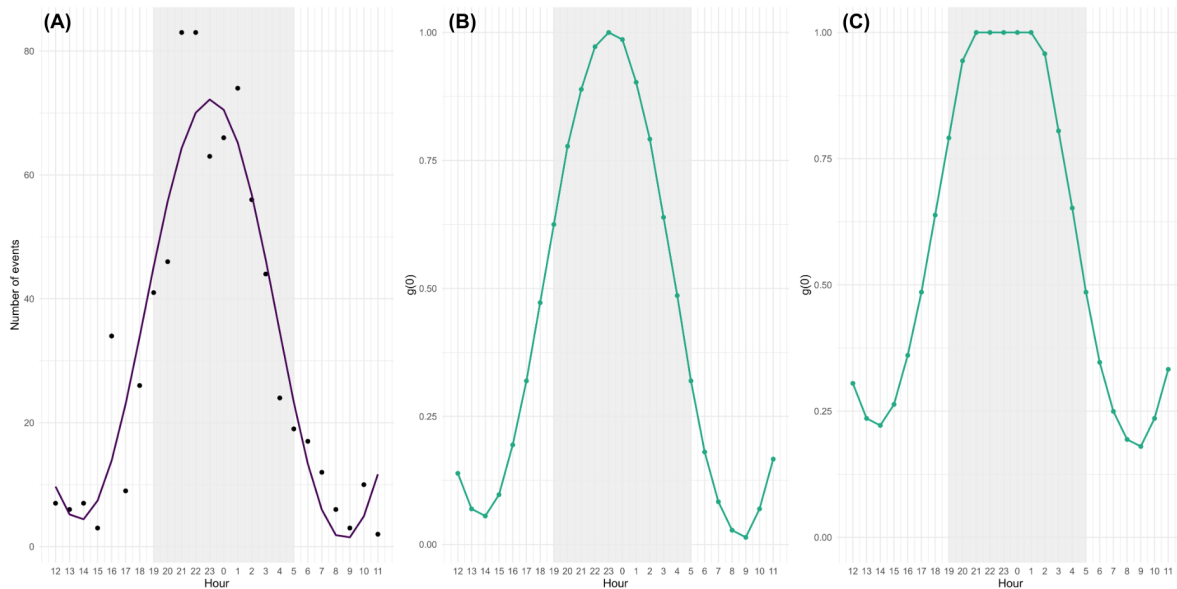


Figure. 6.3: Estimation of $g(0)$ for the acoustic platform as a function of time. (A) A cosine function was fitted to the distribution of the number of acoustic events per hour. **(B)** The fitted function was then used to derive $g(0)$ values over time, assuming that $g(0) = 1$ at the peak number of events at 23:00 **(C)** The function was scaled to have a mean $g(0)$ value of 0.33, as estimated during the day with the acoustic platform between 5:00 and 19:00. The shaded area indicates the night phase, which extends from 19:00 to 05:00.

6.2.1.3 Comparison of abundance estimates

As mentioned in chapter 3, abundance of individuals was calculated as:

$$\hat{D} = \frac{nS}{2wLpg(0)} \quad (6.1)$$

where n is the number of events, S is the estimated group size in the population, p the overall detection probability over $0 - w$, L the total length of the transect surveyed and $g(0)$

Table 6.1: Values of $g(0)$ estimated per hour for the acoustic platform. The mean $g(0)$ and associated standard error (SE) are shown for each hour slot in a 24h-cycle.

| Hour | Mean $g(0)$ | SE $g(0)$ |
|------|-------------|-----------|
| 0 | 1 | 0 |
| 1 | 0.99 | 0.01 |
| 2 | 0.88 | 0.04 |
| 3 | 0.73 | 0.05 |
| 4 | 0.57 | 0.05 |
| 5 | 0.42 | 0.04 |
| 6 | 0.30 | 0.03 |
| 7 | 0.21 | 0.02 |
| 8 | 0.18 | 0.00 |
| 9 | 0.20 | 0.01 |
| 10 | 0.27 | 0.03 |
| 11 | 0.38 | 0.04 |
| 12 | 0.26 | 0.02 |
| 13 | 0.22 | 0 |
| 14 | 0.24 | 0.01 |
| 15 | 0.3 | 0.03 |
| 16 | 0.41 | 0.04 |
| 17 | 0.54 | 0.05 |
| 18 | 0.7 | 0.05 |
| 19 | 0.85 | 0.04 |
| 20 | 0.98 | 0.02 |
| 21 | 1 | 0 |
| 22 | 1 | 0 |
| 23 | 1 | 0 |

the detection probability on the transect line. From the estimated density, the abundance \hat{N} is calculated as the product of \hat{D} and the searched area A:

$$\hat{N} = A \cdot \hat{D} \quad (6.2)$$

Group size

Abundances were estimated at individual levels, and therefore required reliable estimates of group sizes. As shown in chapter 4, the mean acoustic group size was about three times smaller than the mean visual group size, but this was not true across the whole observed range of visual estimates. The relationship between acoustic and visual group sizes was investigated and showed no correlation between visual and acoustic group sizes (Appendix F). This led to the conclusion that acoustic group size could not be used to estimate abundance. Consequently, the mean group size of visual events from each block was assigned to the acoustic events recorded in the same block. If no visual events occurred in a block, the mean group size of visual events from all blocks was used (Appendix F).

Detection functions

Before estimating abundance, it was necessary to fit detection functions for all datasets and scenarios. Each block was surveyed using different platform types (scenario 2), day-phase type (scenario 3) or hourly type (scenario 4). Each platform, day-phase and hourly type had different estimates of $g(0)$. The survey and analysis design implemented here included two forms of stratification: first, geographic stratification by block, and second, within each block, further stratification by category type (platform type, day-phase type, and hourly type). However, the *Distance* software cannot handle this particular situation. Therefore, the geographical stratification by block was ignored and the data from blocks 2 to 15 were pooled. These blocks were selected as they represent the western Mediterranean, as this is a region that was fully surveyed by the vessel. As a result, the focus was on category type alone to fit the detection function and derive abundance estimates for each dataset and scenario. To allow comparison of abundance estimates, detection functions were fitted with a truncation distance of 1.5 km, no covariates, and half-normal key functions without adjustment using the 'ds' function from the 'Distance' package (Miller et al., 2019).

Abundance estimates

Scenario 1: the uncorrected abundance was estimated using the 'ds' function.

For the remaining scenarios, the 'dht2' function from the 'Distance' package (Miller et al., 2019) was used to estimate abundance at individual levels. This function allows for the inclusion of multipliers, such as specific values of $g(0)$ (depending on the scenario and datasets used), and stratification that divides the survey data into different replicates (e.g., for the platform-type stratification, acoustic platform and visual platform were considered as separate effort and treated as two replicates). The function estimates the abundance or density of each replicate, which can then be combined to give an overall estimate. Uncertainty in the multiplier can be accounted for by providing the SE of $g(0)$.

Scenario 2: Abundance was estimated using platform-specific $g(0)$ values with the associated SE and stratification by replicate (specified as 'stratification = "replicate"' in the 'dht2' function). Stratification by replicate refers to surveys conducted using acoustic and visual methods, treated as two separate efforts (replicates). They were set to $g(0)_a = 0.33$ (SE = 0.08) for the acoustic platform and $g(0)_v = 0.30$ (SE = 0.07) for the visual platform. The overall abundance estimate was calculated as a weighted average, with weights proportional to the effort associated with each platform.

Scenario 3: Abundance was estimated using day-phase specific $g(0)$ values with the associated SE and stratification by replicate (specified as 'stratification = "replicate"' in

the ‘dht2’ function). Stratification by replicate refers to surveys conducted during different phases of the day (day, transition, and night), which are treated as three separate efforts (replicates). They were set to $g(0)_{day} = 0.33$ (SE = 0.15), $g(0)_{night} = 0.98$ (SE = 0.05) and $g(0)_{transition} = 0.78$ (SE = 0.16) for the acoustic platform and $g(0)_v = 0.30$ (SE = 0.07) for the visual platform. The overall abundance estimate was calculated as a weighted average, with weights proportional to the effort associated with each phase of the day.

Scenario 4: Abundance was estimated using hourly-specific $g(0)$ values with the associated SE and stratification by replicate (specified as ‘stratification = "replicate"’ in the ‘dht2’ function). Stratification by replicate refers to surveys conducted at different hours of the day, which are treated as 24 separate efforts (replicates). They were set using the hourly $g(0)$ values referenced in the table 6.1 for the acoustic platform and a constant $g(0)_v = 0.30$ (SE = 0.07) for the visual platform. The overall abundance estimate was calculated as a weighted average, with weights proportional to the effort associated with each hour.

6.2.2 Comparison of corrected estimates between the vessel-based survey and the ASI aerial survey

To test the validity of the different scenarios, I compared the results with the abundance estimate obtained from the aerial component of the ASI, conducted synchronously and in the same series of blocks as the vessel component, which constitutes the only fully independent dataset available. The aerial estimates from Panigada et al. (2024) need to be corrected for availability and perception biases before any comparison can be made.

6.2.2.1 Common blocks between the ASI vessel and aerial components

The methods used in each of the scenarios presented in the previous sections were to produce abundance estimates which were eventually compared with estimates from the aerial survey in blocks surveyed by both components. The ASI survey was designed to ensure that both vessel and aerial components surveyed the same blocks (ACCOBAMS, 2021). However, some blocks were only surveyed by one component due to political and jurisdictional constraints. The aerial component of the ASI surveyed from the Alborán Sea to the northeastern Mediterranean, while the vessel component surveyed mainly the Alborán Sea and the western and central Mediterranean. Panigada et al. (2024) provides uncorrected abundance estimates from the aerial component for each block and species.

To facilitate a proper comparison of abundance estimates between the aerial and vessel-based surveys, only data from blocks surveyed by both components were used. These included blocks 3 to 5, 7 to 15, 22w, 22c and 22e. Block 3 was retained because only a small portion was not covered by the aerial survey, which was unlikely to affect the comparison of abundance estimates (Figure 6.4).

6. Assessment of the effects of detection probability on abundance estimates

6.2.2.2 Vessel-based detection functions and abundance estimates

The detection functions and abundance estimates, as previously described, were re-estimated using only the blocks common with the aerial survey. In the same way, data from these blocks were pooled and category type was used to fit the detection function and derive abundance estimates. The method for estimating abundance for scenarios 1 to 4 followed the same approach used in the previous section (6.2.1). The truncation distance was also set at 1.5 km, and half-normal key functions without adjustments and covariates were used to fit the detection function using the 'ds' function from the 'Distance' package (Miller et al., 2019). In contrast, only full dataset were used to estimate abundance for each scenario because this included all transects and provided a better representation of the study area.

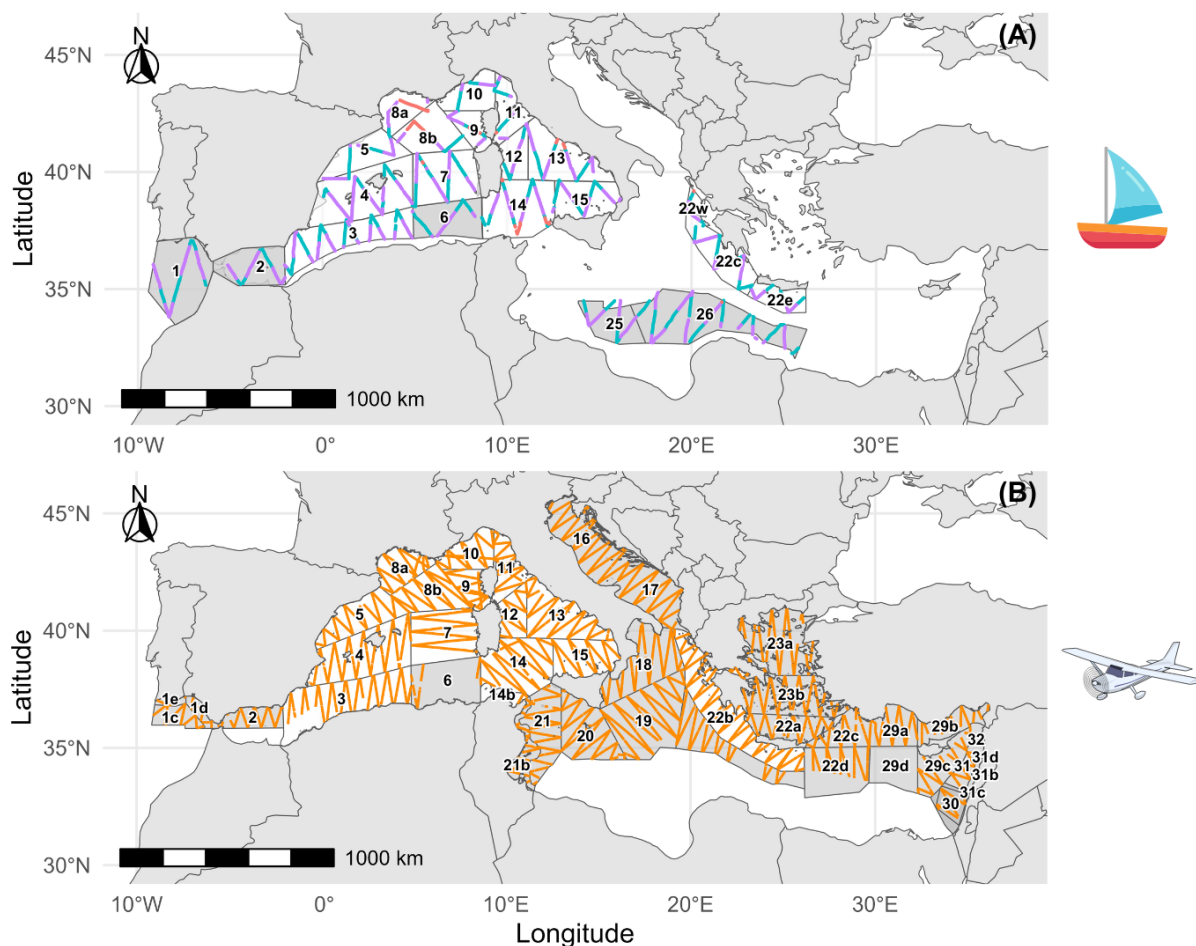


Figure. 6.4: Common blocks surveyed by vessel and aerial components of the ASI survey. (A) The vessel *R/V Song of the Whale* surveyed mainly the western Mediterranean, covering 21 blocks. The transects were categorised into three types: visual transects (red lines), acoustic transects (purple lines) and acoustic-visual transects (blue lines). (B) The aircraft mainly covered the northern Mediterranean Sea and surveyed 42 blocks. Surveyed transects are shown in orange. Blocks with white backgrounds were common to both survey components and data collected in these blocks were used to compare abundance estimates.

6.2.2.3 Aerial abundance estimates

Aerial abundance estimates from Panigada et al. (2024) were summed by selecting the appropriate blocks and surveyed species, which included Risso’s dolphins, bottlenose dolphins, long-finned pilot whales and small dolphins (including striped dolphins, common dolphins and unidentified dolphins belonging to either of these two species). However, the aerial abundance estimates were not corrected initially. The summed estimate was corrected by dividing by a $g(0)$ value chosen from the literature (Appendix G). The choice of the $g(0)$ value was based on survey conditions similar to those of the ASI survey, such as altitude, speed and species surveyed. The ASI aerial survey was conducted at an altitude of 183 m and a speed of 100 knots using aircraft equipped with bubble windows. The $g(0)$ value of 0.77 from Palka (2005) was chosen due to similarities in the survey conditions and species studied.

6.3 Results

6.3.1 Testing the effect of correction biases on abundance estimate

6.3.1.1 Summary of the survey data

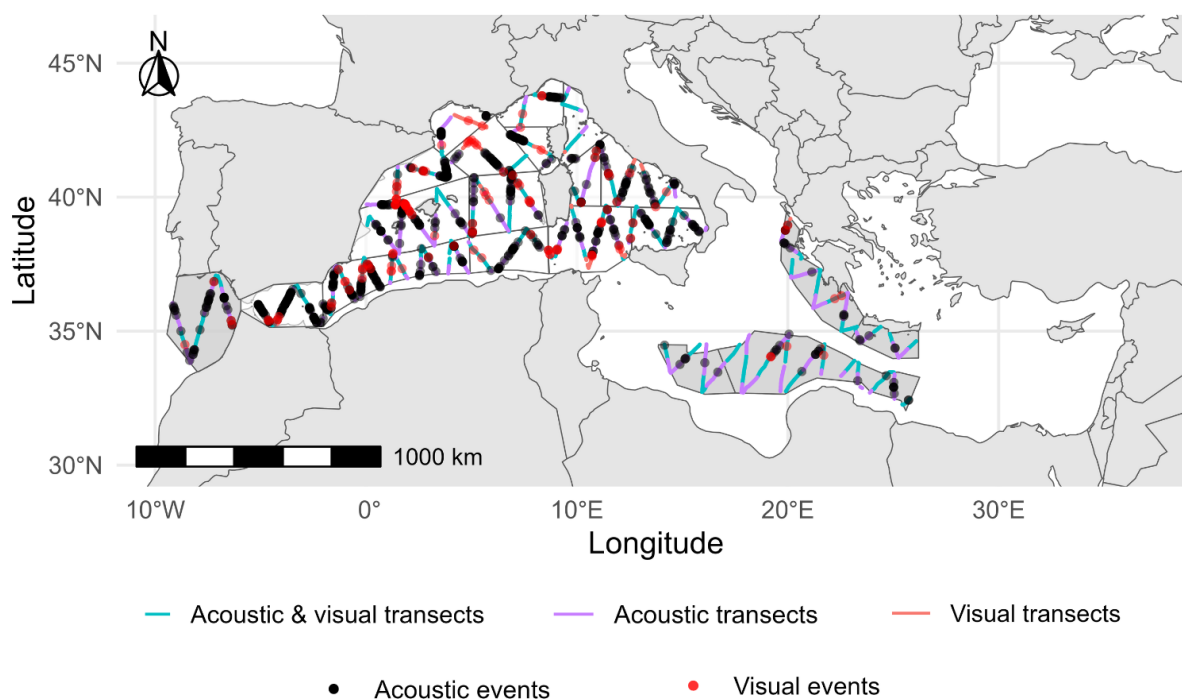


Figure 6.5: Effort and sightings collected by platform during the ASI vessel-based survey. The map shows the linear transects sampled by the *R/V Song of the Whale*, with recorded acoustic (black dots) and visual (red dots) events. Polygons represent sampled blocks. Blue lines represent the acoustic-visual transects, purple lines represent the acoustic transects and orange lines represent the visual transects. Blocks with grey backgrounds were not used in the analysis.

6. Assessment of the effects of detection probability on abundance estimates

Transects conducted under favourable conditions (Beaufort Sea State ≤ 4) covered a total of 4,759 km for the visual dataset, 9,022 km for the double-platform dataset and 13,522 km for the full dataset in blocks 2 to 15. A total of 109 visual events and 670 acoustic events (110 during the day and 560 during the night) were recorded (Figure 6.5). Most of these events occurred in the western Mediterranean Sea. A truncation distance of 1.5 km was set, which removed 10 visual events and 23 acoustic events during the night. This resulted in 99 visual events being retained, together with 109 acoustic events during the day and 537 during the night. As a result, the visual dataset included 99 visual events, the double platform dataset included 99 visual and 109 acoustic events, and the full dataset included 99 visual and 646 acoustic events to fit the detection functions.

6.3.1.2 Comparison of abundance estimates between scenarios and datasets

Abundance was estimated at individual levels for each dataset and scenario, resulting in 12 estimates (Figure 6.6). Results are presented scenario by scenario and within each scenario, the three datasets are compared.

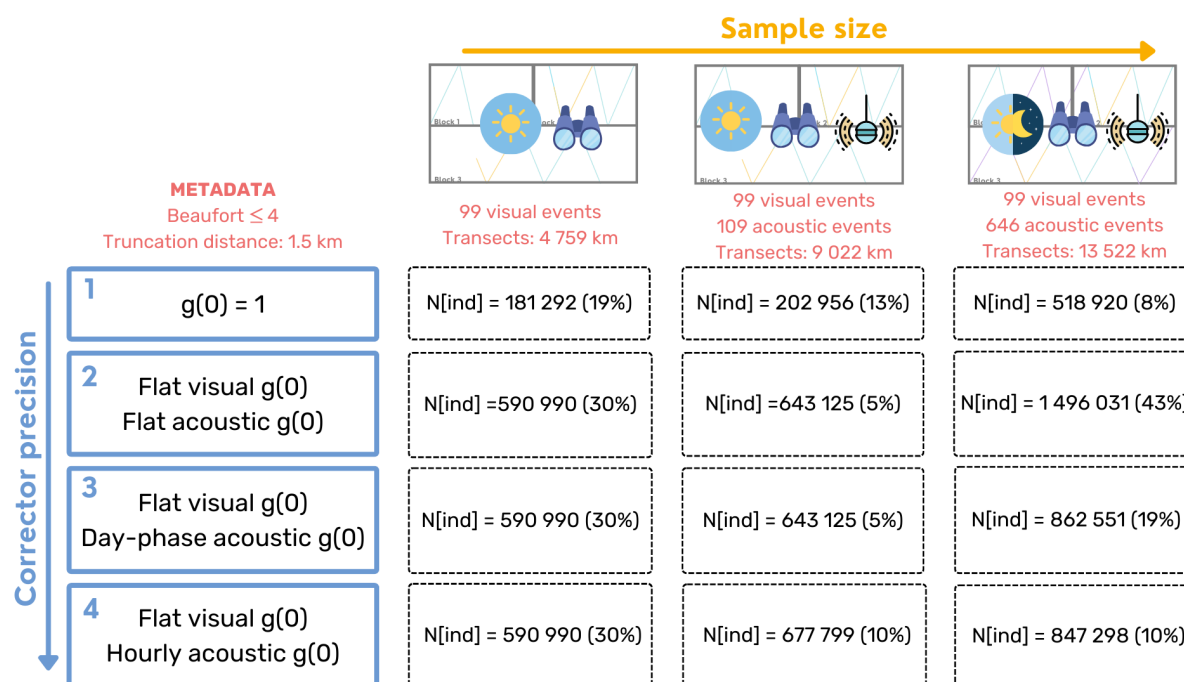


Figure. 6.6: Abundances estimated for each dataset and scenario. Abundances were estimated for the three different datasets, from left to right: visual dataset (visual effort only), double-platform dataset (visual and acoustic effort during the day) and full dataset (visual and acoustic effort during the day and night). By progressively adding effort from left to right, the sample size of the datasets increases. For each dataset, abundances were estimated under four scenarios, from the top to the bottom: scenario 1 ($g(0) = 1$), scenario 2 (constant platform-specific $g(0)$ for the acoustic and visual efforts), scenario 3 (day-phase-specific $g(0)$ for the acoustic effort and constant $g(0)$ for the visual effort), and scenario 4 (hour-specific $g(0)$ for the acoustic effort and constant $g(0)$ for the visual effort). Abundances were estimated at individual levels with the associated coefficient of variation (CV).

Scenario 1: Abundance was estimated using CDS, assuming $g(0) = 1$, and was therefore an uncorrected abundance estimate. It increased with the sample size of the dataset. Individual abundance estimates were estimated to be 181,292 (CV = 19%, 95% CI = 125,946 - 260,959) for the visual dataset, 202,956 (CV = 13%, 95% CI = 158,063 - 260,599) for the double-platform dataset and 518,920 (CV = 8%, 95% CI = 440,735 - 610,975, appendix H) for the full dataset, showing a 2.9 ratio between the visual and full datasets. The higher estimate obtained for the full dataset reflected the fact that by adding nocturnal events, the number of events increased by a factor 3.6, while effort only doubled up. The CV gradually decreased with increasing sample size, indicating a better precision of the estimates with increasing sample size.

Scenario 2: Abundance estimates were corrected using platform-specific $g(0)$ values estimated in chapter 4. The $g(0)$ values (0.33 and 0.30 for the acoustic and visual platform respectively) remained constant throughout the survey. The pattern of increasing abundance estimates with increasing sample size was similar to that observed in scenario 1. Individual abundance estimates increased from 590,990 (CV = 30%, 95% CI = 330,637 - 1,056,353) for the visual dataset only to 643,125 (CV = 5%, 95% CI = 583,915 - 708,340) for the double-platform dataset and 1,496,031 (CV = 43%, 95% CI = 13,913 - 160,865,677, appendix H) for the full dataset. The ratio of the estimates between the visual and full datasets was approximately 2.5. Overall, abundance estimates in scenario 2 are 3 times higher than in scenario 1 because of $g(0)$ values close to 0.3. However, the CV did not decrease consistently with the sample size and remained low for the double-platform dataset.

Scenario 3: For this scenario, abundance estimates were corrected using day-phase-specific $g(0)$ values for the acoustic effort and a constant $g(0)$ for the visual effort. Abundance estimates increased with sample size, following the same pattern as described in scenarios 1 and 2. Individual abundance estimates increased from 590,990 (CV = 30%, 95% CI = 330,637 - 1,056,353) for the visual dataset to 643,125 (CV = 5%, 95% CI = 583,915 - 708,340) for the double-platform dataset and 862,551 (CV = 19%, 95% CI = 549,807 - 1,353,192, appendix H) for the full dataset. The ratio of the estimates between the visual and full datasets was 1.5. Compared to scenario 2, the abundance from the full dataset is considerably reduced because of the higher nocturnal acoustic $g(0)$. Similar to scenario 2, the CV did not show a consistent decrease with sample size and was low for the double-platform dataset.

Scenario 4: Abundance estimates were corrected using hourly-specific $g(0)$ values for the acoustic effort and a constant $g(0)$ for the visual effort. This scenario used the most refined correction procedure for detection biases, to account for the variability of acoustic event production rate over a 24-hour cycle. Estimates and precision increased with sample

6. Assessment of the effects of detection probability on abundance estimates

size. Individual abundance estimates were 590,990 (CV = 30%, 95% CI = 330,637 - 1,056,353) for the visual dataset, 677,799 (CV = 10%, 95% CI = 551,459 - 833,084) for the double-platform dataset and 847,298 (CV = 10%, 95% CI = 702,862 - 1,021,415, appendix H) for the full dataset, with an approximate ratio of 1.4 between the visual and full datasets. Here, abundance estimated from the full dataset was only slightly different from scenario 3, probably resulting from the hourly tuning of acoustic $g(0)$. The CV decreased between the visual and double-platform datasets and then remained constant at 10% for the double-platform and full datasets.

6.3.2 Comparison of corrected estimates between the ASI vessel-based and aerial surveys

6.3.2.1 Summary of the survey data

Transects conducted in favourable conditions (Beaufort Sea State ≤ 4) covered a total of 14,163 km (full dataset) in blocks surveyed by both vessel and aerial surveys (3 to 5, 7 to 15 and 22c, 22e, 22w). A total of 105 visual events and 543 acoustic events (103 during the day and 440 during the night) were recorded. A truncation distance of 1.5 km was set, which removed 10 visual events and 13 acoustic events during the night. As a result, a total of 95 visual events, 103 acoustic events during the day and 427 during the night were used to fit the detection functions.

6.3.2.2 Vessel-based abundance estimates

Abundance was estimated for each scenario using the full dataset as reported in appendix H. The lowest abundance was estimated from scenario 1 at 429,093 individuals (CV = 9%, 95% CI = 358,732 - 513,255) and the highest was estimated from scenario 2 at 1,226,736 individuals (CV = 40%, 95% CI = 18,959 - 79,375,592). For scenario 3, the abundance was estimated to be 726,617 individuals (CV = 16%, 95% CI = 519,188 - 1,016,921) and for scenario 4, it was estimated to be 699,439 individuals (CV = 10%, 95% CI = 577,598 - 846,975, figure 6.7).

6.3.2.3 Comparison with ASI aerial-based estimates

The total uncorrected abundance estimate from the aerial survey was 535,224 individuals (CV = 12%, 95% CI = 471,168 - 599,280) within blocks surveyed by both aerial and vessel components (Panigada et al., 2024). Using a correction factor of 0.77 (Palka, 2005), the corrected aerial abundance was calculated to be 695,096 individuals (CV = 12%, 95% CI = 611,685 - 778,508). This corrected estimate was very close to the scenario 4 estimate (N = 699,439), differing by approximately 4,300 individuals, i.e. less than 1%.

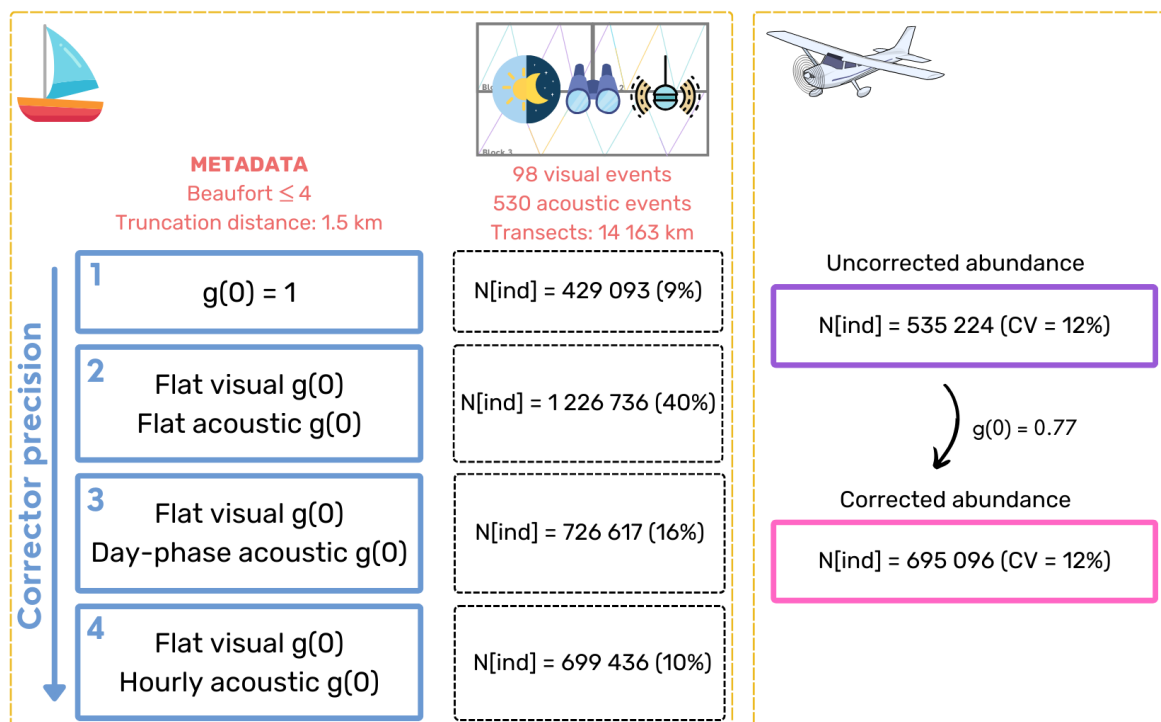


Figure 6.7: Comparison of vessel-based and aerial abundance estimates. Vessel-based abundance was estimated for each scenario using the full dataset (day and night visual and acoustic effort). The uncorrected aerial abundance estimate was calculated from Panigada et al. (2024) and corrected using the $g(0)$ value from Palka (2005). Abundance was estimated at the individual levels with the associated coefficient of variation (CV).

6.4 Discussion

The aim of the chapter was to evaluate the benefits of combining visual and acoustic methods, while addressing the detection biases inherent to each, to improve cetacean abundance estimates. To achieve this, three different datasets were created: a visual dataset (visual effort only), a double-platform dataset (visual and acoustic effort during the day), and a full dataset (visual and acoustic effort during both day and night). For each dataset, four scenarios with varying degrees of correction for detection biases were considered:

- Scenario 1: $g(0) = 1$.
- Scenario 2: platform specific $g(0)$.
- Scenario 3: day-phase specific $g(0)$ for the acoustic effort and a constant $g(0)$ for the visual effort
- Scenario 4: hourly $g(0)$ for the acoustic effort and a constant $g(0)$ for the visual effort.

6. Assessment of the effects of detection probability on abundance estimates

Abundances were estimated and compared at individual levels for each dataset and scenario. The results showed that combining acoustic and visual data increased the sample size for all scenarios and the precision of the estimates for scenarios 1 and 4. Using the full dataset, the estimated abundance of small cetaceans in the western Mediterranean was 518,920 (95% CI = 440,735 - 610,975) for scenario 1, 1,496,031 (95% CI = 13,913 - 160,865,677) for scenario 2, 862,551 (95% CI = 549,807 - 1,353,192) for scenario 3 and 847,298 individuals (95% CI = 702,862 - 1,021,415) for scenario 4. The abundance estimate using scenario 4 (699,439 individuals, 95% CI = 577,598 - 846,975) was very close to the corrected aerial estimate (695,096 individuals, 95% CI = 611,685 - 778,508) in the blocks surveyed by both components of the ASI.

6.4.1 Methodological considerations

While numerous studies have corrected for detection biases due to surfacing behaviour and sighting conditions in visual surveys (Danilewicz et al., 2010; Martin et al., 2020; Forcada et al., 2004), accounting for acoustic detection biases remained challenging due to limited research on the vocal behaviour of small cetaceans. This study presents an approach to test different methods for correcting detection biases in acoustic surveys. The primary bias addressed here is the availability bias, as the detection probability over time (scenarios 3 and 4) was based on the number of acoustic events recorded during a 24-hour cycle. Assuming constant abundance between day and night, detection probability is inferred to be higher at night, as a result of small cetaceans being more vocal and therefore more available for acoustic detection at night (Giorli et al., 2016, chapter 5). As discussed in chapter 5, this assumption may only be valid when estimating abundance in large geographic areas, such as at the basin scale or subregional scales, where the occupation of the study area by small cetaceans is likely to be uniform throughout the day. The availability bias of the acoustic platform was accounted for by using a function derived from the distribution of the number of acoustic events in a 24-hour cycle to represent $g(0)$ as a function of time. It was assumed that the highest number of acoustic events, observed at 23:00, corresponds to $g(0) = 1$. Studies have shown that animals tend to vocalize more at night (Casção et al., 2020; Caruso et al., 2017; Simonis et al., 2017), making them more detectable, suggesting that $g(0)$ could be close to 1. However, it may exceed 1 during periods of high vocal activity due to overlapping signals, which could lead to an overestimation of vocalizing individuals. Nonetheless, $g(0)$ could still be less than 1 at night due to residual acoustic perception bias, as animals facing away from the hydrophone would not be detected. As a result, abundance estimates may be slightly underestimated. In the future, an acoustic double platform could be used to quantify the detection biases of the acoustic platform at night. During the day, the decision to scale the function with a mean $g(0)$ of 0.33 serves as a minimum cap because it was highly unlikely for $g(0)$ to be close to 0 at 9:00. The $g(0)$ of the acoustic platform was estimated with

the double-platform framework in chapter 4 and was believed to be a robust estimate. Therefore this value was used as a reference for the daytime. However, this study is the first attempt to use a variable $g(0)$ as a function of time, and future efforts should focus on obtaining more data improving the precision of scaling $g(0)$ between day and night as well as more flexible way to incorporate a variable $g(0)$ in the Distance Sampling framework.

Other covariates that affect the detection of acoustic events, such as sea state and background noise levels, may be important to consider. Gordon et al. (2000) used PAM fixed stations and towed hydrophones and found that detection rates of small cetaceans decreased with increasing wind speed, sea state, and background noise. However, in chapter 5, an opposite pattern was observed, with the number of acoustic events increasing with sea state. This relationship is still not well understood. While these covariates are important for acoustic detectability, sea state and wind speed were not included in the detection function to facilitate comparisons between datasets and scenarios without masking the effect of $g(0)$ on abundance estimates. Except for the $g(0)$ of the acoustic platform where perception bias was accounted for with a negative effect of distance and swell height on acoustic detectability during the day (chapter 4), perception bias during the night was not accounted for. However, it was more important to account for availability bias when present, as it can be a substantial source of bias with a much larger impact than perception bias (Laake & Borchers, 2004). Nonetheless, future analyses should attempt to measure levels of background noise, including water background noise, ship noise, and noise generated by the survey vessel, and test their effect on acoustic detectability (Gordon et al., 2000).

Another methodological issue to consider in this study is the group size. When individuals in a study population occur in groups, accurate measurement of the group size of an event becomes critical (Buckland et al., 2001). As shown in appendix F, acoustic group size estimates did not appear to correlate at all with visual group size, suggesting that the definition of group size may differ between acoustic and visual methods. Estimating abundance at the cluster level eliminates the problem of estimating group size, but the definition of a cluster may not be consistent. This is evident in visual surveys, where the definition of a cluster varied between aerial and vessel surveys - a large group detected by aerial survey could appear as two separate clusters from a vessel. In this study, acoustic group size was replaced by the mean visual group size of the corresponding block, and abundance was estimated at individual levels for comparison. Using a mean visual group size for acoustic events may affect abundance estimates, particularly in blocks with few visual events. In such cases, a high group size from visual events might be attributed to the mean group size of acoustic events, which may not accurately represent group dynamics throughout the block. Nevertheless, group size significantly influences abundance estimates and using actual acoustic group sizes *versus* those inferred from visual events can lead to

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substantial differences in estimates. Estimating acoustic group size remains challenging, especially for detections involving large groups, such as small cetaceans often detected in large numbers (Frasier et al., 2021). Boisseau et al. (2010) estimated group sizes of different species using the same vessel, *R/V Song of the Whale*, in the southwest of the Mediterranean basin, finding mean group sizes of 8 for striped dolphins, 5 for bottlenose dolphins, and 10 for common dolphins. Therefore, the best approach would be to use an acoustic-cue-rate based method, where the sounds produced by small cetaceans are converted into animal density using a cue production rate (Marques et al., 2009). Therefore, methods to combine acoustic cue rate data with individual-based visual data for abundance estimates need to be developed.

It should be noted that this study represents comprehensive basin-wide effort to estimate small cetacean populations in the Mediterranean Sea using a vessel-based survey, which makes direct quantitative comparisons with existing knowledge difficult. (Forcada et al., 1994) conducted a vessel-based survey in the western Mediterranean in 1991, but did not cover the Tyrrhenian Sea and only estimated the abundance of striped dolphins. Consequently, the only viable comparison available is with the ASI aerial component, as number of blocks were surveyed by both components of the ASI (ACCOBAMS, 2021). However, this aerial abundance estimate was not corrected and assumed $g(0) = 1$ (ACCOBAMS, 2021). It is essential to correct this estimate for a proper comparison with the corrected vessel-based survey estimates in this study. Therefore, it was necessary to select an appropriate $g(0)$ value from the literature based on similar survey conditions and species as the ASI aerial survey. The $g(0)$ value from Palka (2005) was considered the most appropriate due to similarities in survey methodology, including flight altitude, speed, use of bubble windows to detect animals on the transect line, and the circle-back method for estimating $g(0)$. However, this study was conducted in the Northwest Atlantic, where environmental conditions and species behaviour may differ from the current study area. Although Forcada et al. (2004) and Gómez De Segura et al. (2006) surveyed areas in the Mediterranean Sea and estimated $g(0)$ values of 0.78 and between 0.68 and 0.79 respectively, these estimates were not selected because they did not use bubble windows and were based on dive data. Despite these differences, the above $g(0)$ values are in a similar range and we believe that the corrected estimate of aerial abundance would likely result in minimal changes and remain within a comparable confidence interval.

6.4.2 Accounting for variability in detection biases

Abundance estimates were compared across different datasets and scenarios. The difference in the estimates resulted from the different methods used to account for detection biases. The overall results showed that estimates at the individual levels increased with sample size from the visual dataset to the full dataset. However, these estimates should be used

with caution as we hypothesised an increase in precision (interpreted as a decrease in CV) with increased sample size across these three datasets. This was evident in scenarios 1 and 4, but the CV varied unpredictably in scenarios 2 and 3. The CV was unrealistically low for the second dataset in scenarios 2 and 3.

From the visual to full datasets, different data sources were added, and thus detection biases inherent to each method were introduced. Scenarios 1 through 4 accounted for variability in acoustic detection probability with increasing refinement. Scenario 1 assumed $g(0) = 1$ and did not account for detection biases, resulting in the lowest abundance estimates. This is consistent with the hypothesis that assuming $g(0) = 1$ underestimates abundance due to uncorrected detection bias. Estimates from the visual dataset in scenarios 2 to 4 were the same because $g(0)$ remained constant as visual data were solely collected during the day, and we did not explore possible variation in visual detection probability during daylight hours. However, the number of visual events may vary throughout the day, and if these variations need to be accounted for in the same way as acoustic events, different abundance estimates might be obtained. Scenario 2 used platform-specific $g(0)$ and estimates were equal to those in scenarios 3 for the double-platform dataset because only acoustic and visual data collected during the day were used. However, scenario 2 produced the highest estimates with 1,496,031 individuals when the nighttime acoustic effort was included. Estimates decreased to 862,551 and 847,298 individuals for scenarios 3 and 4, respectively. These scenarios used a temporal $g(0)$ variation for acoustic effort based on the small cetacean acoustic behaviour (Giorli et al., 2016; Gordon et al., 2000). In scenario 2, the $g(0)$ of the acoustic platform was estimated during the day and applied uniformly to all acoustic data, including at night, which did not account for detection biases at night and resulted in an overestimation of abundance. Therefore, the use of a temporal $g(0)$ was likely to take account of the acoustic availability bias on abundance estimates. Consequently, scenarios 3 and 4 were considered the best approaches for estimating abundance because accounting for detection biases at the day-phase or hourly scale was consistent with small cetaceans being more acoustically available at night (Chapter 5). Scenario 4 provided the finest temporal resolution with lower CV, reflecting the acoustic behaviour of small cetaceans primarily associated with foraging, while scenario 3 was easier to apply with fewer $g(0)$ values. As a result, the number of small cetaceans in the Mediterranean Sea was estimated to be 847,298 individuals (95% CI = 702,862 - 1,021,415) based on the vessel-based survey using the methodology from scenario 4.

This study has shown that using a constant $g(0)$ throughout a survey, as is common practice, can result in a major biases in the estimated abundance. It is crucial to consider the behaviour of small cetaceans when estimating their abundance. Sucunza et al. (2018) assessed the availability bias to correct aerial abundance estimates of Franciscana dolphins (*Pontoporia blainvillei*) in Batibong Bay, southern Brazil, using helicopter surveys. Due

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to regional differences in the surfacing behaviour of this species, they recommended conducting surveys to estimate the availability bias if the population occurs in habitats other than Batibong Bay. This bias may vary between habitats and potentially lead to inaccurate abundance estimates if availability differs significantly. In other taxa, James et al. (2005) showed that the availability of leatherback sea turtles (*Dermochelys coriacea*) varied between periods spent in high latitude foraging areas and during migration to lower latitude breeding areas, with the surfacing time decreasing as turtles moved to lower latitudes. Thomson et al. (2013) studied variation in detection biases associated with habitat depth and seasonal water temperature for marine turtles, such as green turtles (*Chelonia mydas*) and loggerhead turtles (*Caretta caretta*) in Shark Bay, Western Australia. They found that using constant detection bias values could lead to overestimates of abundance in shallow waters during warmer seasons and underestimates in deeper waters during colder seasons.

6.4.3 Comparison with the ASI aerial component

Abundance estimates were compared between vessel-based and aerial surveys using data collected in the blocks surveyed by both components. The corrected aerial abundance estimate was 695,096 individuals (Panigada et al., 2024; Palka, 2005), which was very close to the vessel estimate of 699,436 individuals derived from the scenario 4 method based on hourly specific $g(0)$. While it is unknown whether the aerial abundance estimate is closer to the 'true' abundance, this comparison further supports scenario 4 as the best approach to account for detection bias in both acoustic and visual platforms. The ASI survey is the first large-scale survey in the Mediterranean Sea, and comparisons of abundance estimates with other studies that have conducted vessel-based surveys of small cetaceans in different parts of the region are challenging due to differences in the areas surveyed, which complicates comparisons with existing knowledge (Cañadas & Hammond, 2006; Forcada et al., 1995; Forcada et al., 1994; Forcada & Hammond, 1998; Lauriano et al., 2014). Future recommendations include estimating abundance per block to facilitate comparisons at a more local scale with previous vessel-based surveys and achieving uniform coverage of the Mediterranean to obtain the most accurate abundance estimates of small cetaceans (Mannocci et al., 2018).

Although surveys using both vessel and aerial components were limited (Sucunza et al., 2022), this study provided an opportunity to compare abundance estimates derived from both components. The results showed that vessel-based surveys can provide estimates comparable to those obtained from aerial surveys, indicating a similarity in their ability to estimate abundance. When financial constraints are an issue, using the same type of vessel as *R/V Song of the Whale* may offer several advantages over aerial surveys. Logistically, vessels may be more manageable than aircraft, allowing for continuous monitoring over long periods of time and the detection of temporal patterns in cetacean presence and

behaviour (Boisseau et al., 2010; Lewis et al., 2007). Using a small vessel may also be more cost-effective than using multiple aircraft for the same purpose. In addition, the *R/V Song of the Whale* generally produces fewer carbon emissions than repeated aerial surveys and therefore has a more favorable environmental footprint (R. McLanaghan, personal communication). Modern vessels such as the *R/V Song of the Whale* can integrate renewable energy technologies such as solar panels or wind turbines, further reducing their environmental impact. The vessel can also accommodate 10 to 12 people, whereas aircraft are typically limited to three to four observers. During the ASI survey, the vessel hosted over 30 participants from 10 countries, providing valuable training and field experience that is difficult to replicate with aerial surveys (ACCOBAMS, 2021, O. Boisseau personal communication). Vessel-based surveys also provide significant opportunities for public outreach by organising port calls for advocacy and awareness-raising events.

6.5 Conclusion

This chapter focused on assessing the effects of combining visual and acoustic data and testing the influence of different methods for accounting for detection biases on abundance estimates. The study compared abundance estimates for three datasets: (a) visual effort, (b) visual and acoustic effort during the day, and (c) visual and acoustic effort during both the day and night. For each dataset, abundance was estimated under four different scenarios to account for detection biases: (1) $g(0) = 1$, (2) platform-specific $g(0)$, (3) day-phase specific $g(0)$ for acoustic effort and a constant $g(0)$ for the visual effort, and (4) hourly $g(0)$ for the acoustic effort and a constant $g(0)$ for the visual effort. This study demonstrates the benefit of combining data to increase sample size while accounting for the detection biases inherent in each method. Small cetaceans were more likely to be detected at night, resulting in a higher detection rate at night. The best approach was to use an hourly $g(0)$ to account for this diel pattern in small cetacean behaviour, resulting in accurate abundance estimates. Using a constant $g(0)$ results in an overestimation of abundance. This study highlights the importance of accounting for small cetacean behaviour when quantifying detection biases. Using this approach, we provide the first estimate of the corrected abundance of small cetaceans from a vessel-based survey in the Mediterranean Sea. This estimate was similar to corrected aerial abundance estimates in blocks surveyed by both components. This study represents an important step forward in calculating more reliable correction factors for vessel survey estimates, ultimately leading to more accurate absolute abundance estimates.

7

The benefits and challenges of combining visual and acoustic data in cetacean monitoring surveys

This final chapter concludes this thesis with a comprehensive discussion of the strategy adopted, its impact on abundance estimates and the limitations encountered. It examines the benefits and challenges of integrating acoustic and visual data and compares these with other research that combines visual and acoustic data for different taxa or uses novel technologies to improve animal detection and wildlife monitoring.

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7.1 Overview of the thesis dissertation

As mentioned in chapter 1, monitoring cetacean populations is challenging due to their elusive nature. Estimates of absolute abundance, or 'true' population size, are essential for determining acceptable levels of human-caused mortality. Bycatch poses a major threat to small cetaceans, highlighting the urgent need to reduce mortality rates (Reeves et al., 2013). However, these estimates are often subject to error and uncertainty which depend on the detectability of the species and the sampling intensity of the survey (Callaghan et al., 2024). Estimating absolute abundance typically requires extensive fieldwork, and different techniques can be used, such as marking individuals (capture-recapture) or distance sampling to estimate detectability without marking. The latter method provides reliable absolute abundance estimates only if certain assumptions are met (Buckland et al., 2001). Detections are assumed to be certain on the transect line ($g(0) = 1$) but are generally not due to availability and perception biases (together detection biases). The true value of $g(0)$ must be estimated to account for detection biases and provide absolute abundance estimates. Most studies use $g(0) = 1$ because estimates of $g(0)$ are often not available and estimating $g(0)$ can be logistically challenging. Some studies correct abundance estimates for either perception bias, availability bias, or both. In visual vessel-based surveys, availability bias is likely less of an issue for small cetaceans, which exhibit shorter dives, tend to surface frequently, and display conspicuous surface behaviour; they are therefore more likely to be detected in the time observation window (Leonard & Øien, 2020; Panigada et al., 1999). To address perception bias, studies typically used a double platform configuration with two independent observer teams, either with an additional vessel or a second observer team on the same vessel (Calambokidis & Barlow, 2004; Barlow, 1995; Gilles et al., 2023; Leonard & Øien, 2020; Pike et al., 2010; Barlow & Forney, 2007). With advances in technology, acoustic surveys are increasingly being used to detect cetaceans, offering advantages where visual methods are inappropriate. More studies are combining visual and acoustic methods to exploit the strengths of both, using parallel sampling platforms to monitor cetacean populations (Rankin et al., 2020; Richman et al., 2014; Martin et al., 2020; Gerrodette et al., 2011; Dalpaz et al., 2021).

This approach was implemented during the vessel component of the large-scale ASI survey in the Mediterranean during the summer of 2018. The *R/V Song of the Whale* moved continuously along transects within the survey area using independent acoustic and visual platforms. Transects were surveyed with both platforms whenever possible. Some portions of transects were surveyed using either a visual platform (during daylight hours and under suitable viewing conditions, i.e. Beaufort Sea State ≤ 4) or an acoustic platform (when Beaufort Sea State was less than 5 and local water depths were greater than 50 m, subject to approval by the bordering states). This thesis aimed to investigate the optimal combination of acoustic and visual cues, the two main types of presence indicators

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used in cetacean population monitoring surveys while accounting for detection biases. The developed methodology consisted of three steps: (1) estimating visual and acoustic detection biases, (2) investigating temporal variation in acoustic detectability, and (3) accounting for variation in detectability to improve abundance estimates when detections collected day and night are used jointly in the same analysis.

Chapter 4 aimed to estimate $g(0)$ with a double acoustic and visual platform. Acoustic and visual data collected simultaneously during daylight periods in the ASI survey were analyzed to quantify the proportion of missed events and to estimate $g(0)$ for each platform separately and for the combined platforms under an MRDS framework. A decision tree based on time and distance thresholds was constructed to identify duplicate events. The temporal threshold was determined based on the time window between the acoustic and visual platforms, which were 400 m apart, each with a specific detection radius, and moving at an average speed of 3.2 m/s. The detection radius for both acoustic and visual platforms were calculated as 95% of their respective perpendicular distance distributions recorded during the study. The distance threshold was determined based on the animal's movement between detection by the acoustic and visual platforms. An animal mobility buffer, calculated with an average routine swimming speed of 3.6 m/s, was applied to the first detection by either platform. This buffer represented the area where the target animal(s) could be located when detected by the second platform. As a result, only 16% of the total events were identified as duplicates, a low value compared to other studies that reported more than 30% duplicate events (Dalpaz et al., 2021; Rankin et al., 2020; Richman et al., 2014). Although the decision tree appeared restrictive, it allowed for more accurate identification of true duplicate events, thereby reducing the risk of false duplicates. This method may be applicable in other contexts using a double platform with towed hydrophones but by changing parameters such as vessel speed and the routine speed of the species being studied. Thus, the chosen MRDS model with a Half-Normal (HN) key function estimated the overall detection probability at $p = 0.21$ and $g(0)$ to be 0.52 (CV = 19.8%) for the combined platform, significantly lower than the assumed $g(0) = 1$. This finding highlights the importance of estimating $g(0)$ values for the platforms used to provide absolute abundance estimates. The model also estimated $g(0)$ values of 0.33 (CV = 23.2%) for the acoustic platform and 0.30 (CV = 23.8%) for the visual platform, which were used for the abundance estimates in chapter 6.

Given the importance of accounting for detection biases, it is crucial to understand their sources to determine how detectability may vary. In visual surveys, detection biases are known to vary with observation conditions and surfacing behaviour. For example, surfacing rates may differ between seasons or habitats, resulting in heterogeneous availability of animals (Hagihara et al., 2018; Miller et al., 2010). However, the sources of detection

biases in acoustic surveys are less well understood. Previous studies have reported that the acoustic behaviour of small cetaceans may exhibit diurnal rhythms (Giorli et al., 2016; Caruso et al., 2017). Hence the rate of vocalisation production, which is likened to the cue rate for acoustic monitoring in a distance sampling framework, would vary on a diel pattern as would the acoustic availability of the dolphins. To investigate this further, chapter 5 aimed to understand the variability in the number of events detected by the acoustic platform during day and night. GAM models were fitted to explore variations in acoustic events and their correlation with temporal variables such as hour, lunar cycle, lunar illumination and sea state. The results clearly showed a strong diel pattern, with more acoustic events occurring at night (0.026 events per minute at 21:00/22:00) compared to only 0.0007 events per minute at 11:00. In addition, these events were more frequent during the third quarter of the moon (0.033 events per minute on day 22 of the lunar cycle) compared to 0.0008 events per minute on day 8, corresponding to the first quarter of the moon. However, the selected model, including the hour and lunar cycle, had a low deviance (14.3%), suggesting that other variables may also contribute to the variation in the number of acoustic events. Because acoustic events were recorded over a large study area, other factors contributing to the variation in the number of events could also indicate animal density, rather than animal activity rhythm. Future studies should investigate habitat models based on acoustic data to better understand the variation in the number of acoustic events. This approach has been applied for example to sperm whales (Lerebourg et al., 2023). Nevertheless, the present study showed that the acoustic behaviour of small cetaceans in the Mediterranean Sea was strongly influenced by diurnal and lunar rhythms, making them more detectable at night and during the third phase of the lunar cycle. This provides a first understanding of the availability of these animals in an acoustic survey, indicating that the $g(0)$ estimated for the acoustic platform during the day is not constant and shows a strong diel pattern.

In chapter 6, the final step was to account for the variability in acoustic availability biases reported in chapter 5 to optimally combine acoustic and visual data for absolute abundance estimation in this ASI vessel survey design. Several combinations of acoustic and visual data were evaluated to determine how data integration and different ways to cope with biases might affect or improve abundance estimates. These combinations included using only visual data, visual and acoustic data collected during the day only, and all data collected at day and night. For each dataset, abundance estimates were compared across scenarios with different correction of acoustic detection biases ($g(0) = 1$, platform-specific $g(0)$ values, day-phase-specific $g(0)$ values and hour-specific $g(0)$ values). Abundance estimates using the full dataset were then compared to aerial survey estimates. Results showed that the most consistent estimates were obtained using day-phase specific $g(0)$ values (862,551 individuals, CV = 19%, 95% CI = 549,807 - 1,353,192) and hour-specific

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$g(0)$ values (847,298 individuals, CV = 10%, CI = 702,862 - 1,021,415) because diel effects were accounted for in the estimates. When diel effects were not taken into account and the $g(0)$ from the acoustic platform estimated during the day was used instead, abundance estimates nearly doubled. However, these results should be interpreted with caution as the CV in the estimates appeared to be inconsistent across scenarios and datasets. Comparison with corrected abundance estimates from the aerial survey in the same survey blocks as the vessel component, (695,096 individuals, CV = 12%, 95% CI = 611,685 - 778,508; with $g(0) = 0.77$), showed very close estimates between the aerial and vessel-based components of the ASI. This study highlighted the importance of accounting for variability in detection biases to obtain absolute abundance estimates. In this case, vessel-based surveys may have advantages over aerial surveys in terms of cost, logistics, carbon footprint and communication.

In this study, six different species of small cetacean were pooled without taking into account species heterogeneity. In fact, small cetaceans have different group sizes, dive durations, vocalisation rates or preferred habitats. For example, the three most observed species in the Mediterranean Sea have different distributions. The bottlenose dolphin is patchily distributed with hotspots on the continental shelf (Cañadas et al., 2023; Bearzi et al., 2009), while the striped dolphin is an oceanic species that is usually found in open waters with a strong longitudinal gradient following the gradient of marine productivity (Cañadas et al., 2023; Notarbartolo Di Sciara & Tonay, 2021). The common dolphin can be observed in both inshore and offshore waters (Bearzi et al., 2003) in the southern part of the western Mediterranean (Cañadas et al., 2023). Other delphinids set include the long-finned pilot whale and the Risso's and rough-toothed dolphins, three species with much lower abundance in the area (Panigada et al., 2024) and therefore considered here to contribute little to the pattern found in the present acoustic data set. In acoustic studies, the common spectral features of the species studied and the characteristics of the clicks (i.e. directionality, high frequency) contribute to click variability and complexity in classification. Although ongoing research is opening avenues for improved classification (Oswald et al., 2003; Soldevilla et al., 2008; Bittle & Duncan, 2013; Pedersen et al., 2021), species identification from echolocation clicks remains limited and we had to pool the different species. By grouping species together, a single detection function was fitted for all species. However, the striped dolphin is the dominant species in the Mediterranean Sea as shown by its prevalence in the visual sightings from either the vessel or the aerial components of the ASI (63% and 8% respectively; ACCOBAMS, 2021; Panigada et al., 2024). Pooling of species is a common practice in aerial surveys because some species can be difficult to tell apart from short-duration and vertical sightings (e.g., striped dolphin/common dolphin; ACCOBAMS, 2021). As striped dolphins were highly dominant in the study area, I consider that the patterns observed are mostly from that species.

The study showed that combining visual and acoustic data is mostly useful and effective when detection biases inherent to each method are properly taken into account. The double-platform approach allows these biases to be estimated and improves abundance estimates. By integrating acoustic and visual methods, researchers can overcome the limitations of single platforms and gain a comprehensive understanding of cetacean populations (Figure 7.1).

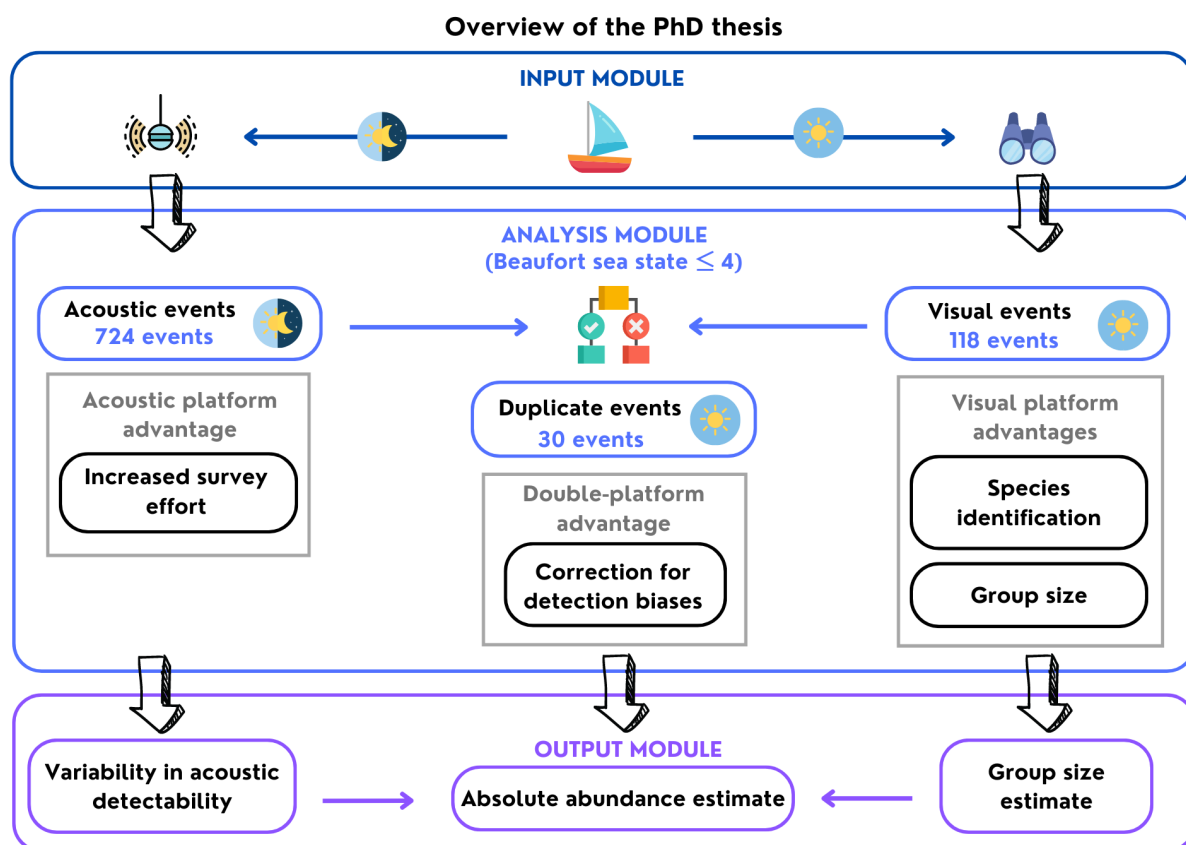


Figure 7.1: Overview of the PhD thesis. The analysis involved detecting small cetaceans either from an acoustic platform equipped with a towed hydrophone or from a visual platform with observers. When data were collected simultaneously from both platforms, duplicate events could be identified. The advantages of each platform, as well as the double-platform approach, were highlighted and used to improve abundance estimates with the ASI design of the vessel component.

7.2 Combining acoustic and visual method across taxa

The combination of visual and passive acoustic methods has been attempted for a variety of taxa, and the level of integration of both types of data varies widely between cases. In addition to cetaceans, other mammals, birds, amphibians, fishes and arthropods produces sounds (Bradbury & Vehrencamp, 1998). The use of PAM in terrestrial environments is relatively new compared to its well established implementation in marine environments

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and has only recently received significant attention (Sugai et al., 2019). Efforts to integrate visual and acoustic data have been less developed and numerous in terrestrial studies compared to marine mammal research.

7.2.1 Species inventories

Biodiversity assessment is a central task in conservation biology and quantifying species diversity can be used either visually or acoustically. Here I discuss how the joint implementation of acoustic and visual detection methods helps assessing species diversity and improving sound libraries across various taxa.

Barnes and Quinn (2023) used both acoustic recordings and visual observations to detect reptiles and amphibians in an urban area in the southeastern United States. While acoustic surveys increased the number of detections and identified nine different anuran species, visual observations were essential for detecting less-vocal species such as snakes, turtles and skinks (Barnes & Quinn, 2023). For bird assemblages, comparisons of species composition between data collected by acoustic recorders and human observers have shown mixed results. Some studies found that PAM recorded more species than observers did (Celis-Murillo et al., 2009), while others found the opposite (Leach et al., 2016; Kulaga & Budka, 2019). In addition, results from acoustic monitors can provide a different perspective on overall community composition compared to direct observations, offering a complementary approach to bird monitoring (Blake, 2021). The combination of acoustic and visual methods helped to develop sound libraries by identifying the species of interest when emitting that sound (Gibb et al., 2019). For example, the FishSounds website (<https://fishsounds.net/>) provides a global inventory of fish species for which sound production has been documented in the scientific literature. These sounds are categorised from category 1 (unknown/undetermined) to categories 4 to 6 (validated acoustic documentation, Looby et al., 2023). If a sound is likely to be produced by a fish species without visual confirmation, the sound is placed in category 3 (no known acoustic documentation to confidently validate). However, if a sound is confirmed by visual sighting, it can be placed in the higher categories as validated acoustic documentation (Looby et al., 2023). In this context, the combined use of acoustic and visual methods allows more reliable identification of species from their sounds, thereby improving the sound libraries of fish species.

Researchers have also aimed to compare acoustic and visual methods to estimate species richness. In amphibian studies, Boullhesen et al. (2021) measured anuran species richness in the Yungas forests of Argentina using PAM with autonomous recording units (ARUs) and traditional visual encounter surveys (VES). The results showed similar levels of species detection, with 19 species detected by the visual method and 18 by the PAM. The authors suggested that the similarity in results may be due to the heterogeneous landscape of

the Yungas forest, which may affect the detection probability of anuran survey methods. In contrast, other studies conducted in more homogeneous landscapes found significant differences in species richness between the two methods (Acevedo & Villanueva-Rivera, 2006; Madalozzo et al., 2017). Comparing these methods helps researchers to understand the strengths and limitations of each approach, and to determine the best method to be used in different contexts.

The complementary use of acoustic and visual methods is beneficial for identifying a wide range of species that are difficult to see or hear in a given area. In cetacean monitoring, the use of both methods allows more species to be detected in the vast marine areas. Boisseau et al. (2010) reported cetacean encounter rates in the Mediterranean Sea and adjacent Atlantic Ocean using visual and acoustic platforms with the *R/V Song of the Whale*. The visual platform was particularly effective in detecting species such as small cetaceans, while the acoustic platform primarily detected sperm whales. This study documented new species in Libyan waters, including sperm whales, striped dolphins and rough-toothed dolphins. The use of both methods extends and clarifies some of the known distributions of cetaceans in a study area (Simard et al., 2015; Boisseau et al., 2010). Duporge et al. (2023) took a different approach to use visual and acoustic methods. The authors relied on visual surveys to identify species during the day, while using PAM on another boat to detect dolphin encounters at night, as PAM cannot identify dolphin at the species level. The combined use of visual and acoustic methods to study cetacean presence served as a preliminary reference for monitoring cetacean populations in less studied areas, such as the Gulf of Aqaba and the northeastern Red Sea (Duporge et al., 2023). In the present study, the species inventory was only possible with visual platform. The species inventory based on acoustic events was feasible when duplicate events were identified during the double platform framework, allowing species seen to be assigned to the corresponding acoustic events. This is one advantage of acoustic monitoring compared to visual monitoring. Only the former produces archives that can be rerun when more efficient classifiers are available. The same applies to digital imagery that can be re-examined later when AI allows a better use of large image archives.

7.2.2 Behavioural determinant of acoustic cue rates

The combined use of acoustic and visual events often helps understand how detection probability varies over time and space, as a result of behavioural patterns and variations in group sizes.

The use of simultaneous visual and acoustic methods reveals important insights into bat behaviour and vocalisation patterns. Gorresen et al. (2017) recorded the flight activity of Hawaiian hoary bats (*Laiurus semotus*) using simultaneous thermal video cameras

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and acoustic detectors to understand whether bats consistently call during flight. Their comparison showed that only a third of visual detections were accompanied by a call, suggesting that bats do not always vocalize during flight, with implications for ecological research. Another study demonstrated the need for visual observations to study the vocal repertoire of the little brown bat (*Myotis lucifugus*) at night in an abandoned mine in Ontario, Canada (Barclay, 1982). Using remote low-light imaging cameras, social behaviour was associated with different types of bat calls. For example, they found that short squawks, described as 'irritation buzzes', were produced when bats were disturbed while forming clusters and when females fought during copulation attempts.

For group size, the combination of visual and acoustic data can be beneficial to investigate relationship between calling rates and number of individuals. For example, Thompson et al. (2010) collected simultaneous visual and acoustic data from African forest elephants (*Loxodonta africana cyclotis*) to locate and assign calls to individuals and determine their calling rate. The results showed a significant linear relationship between call rates and elephant numbers, providing a reliable index of elephant abundance and supporting the use of PAM for long-term monitoring.

In a more in-depth study in terms of analysis, a novel study design and analytical approach were developed to allow data from autonomous recording units (ARU) to be calibrated with visual data to estimate bird density/abundance from both types of surveys while accounting for imperfect detection and species availability (Van Wilgenburg et al., 2017). Bombaci and Pejchar (2018) applied this method to estimate the density of New Zealand's forest birds and found that the bias in density estimates between ARU and human observer counts was negative for most species.

In cetacean studies, combining acoustic and visual methods can provide insights into the behavioural dynamics of cetacean communities (Whitehead & Weilgart, 1991; Rankin et al., 2008). For example, Rankin et al. (2008) collected simultaneous acoustic and visual data over seven years through line transect surveys in the eastern and central Pacific Ocean. They found that vocalisation patterns and behaviours of dolphins vary with group size, which impacts species detection and identification. A significant correlation was observed between group size and vocal behaviour, suggesting that species in larger groups are more readily detected. Furthermore, dolphin schools that predominantly produce clicks were found in smaller groups compared to those that produce whistles. These findings underscore the importance of considering vocal behaviour when using passive acoustic methods. This was evident in chapter 5, where a strong diel pattern in acoustic events was observed during the study of temporal patterns. With a better understanding of acoustic vocal behaviour, I developed a method to account for this pattern

in abundance estimates. Without this adjustment, the abundance estimates would have been overestimated. Additionally, I compared acoustic group sizes with visual group sizes of duplicate events identified through the double-platform framework. The results indicated that acoustic group sizes did not correlate with visual group sizes. This finding led me to exclude acoustic group sizes from abundance estimates, as their reliability could be compromised. However, this analysis was based on only 30 duplicate events, suggesting that further data collection is needed. The understanding of acoustic group sizes in this study remains limited, as it is difficult to determine how many individuals are present based on acoustic recordings. However, one hypothesis considered is that in large dolphin groups, some individuals may be eavesdropping on the echolocation clicks and their echoes of their conspecifics (Gregg et al., 2007). This behavior could allow dolphins to gather environmental information without actively producing their own calls, potentially complicating the interpretation of acoustic data and the estimation of group size based on sound alone (Barluet de Beauchesne et al., 2022; Gregg et al., 2007).

7.2.3 Limitations of PAM

Limitations of PAM in the context of abundance estimation include the difficulty to identify individual calling animals, making it hard to determine acoustic group size for most taxa (Gibb et al., 2019). When individual identification is possible, it often requires extensive manual analysis (Petrušková et al., 2016; Root-Gutteridge et al., 2013). In addition, many animals, such as birds, cetaceans and bats, produce multiple call sequences that must be merged into individual detections (Gibb et al., 2019). Thus, estimating abundance from PAM is often difficult due to the lack of a comprehensive understanding of the relationship between animal density and call counts (Gibb et al., 2019). Although methods such as cue counting by estimating call rates have been developed to address these issues (Marques et al., 2013), little has been done in terrestrial areas (Gibb et al., 2019). In this context, the combination of visual and acoustic data can be beneficial by providing estimates of the group size of visual events.

Another limitation is species identification, as much remains unknown about the diversity of inter- and intra-specific calls (Kershenbaum et al., 2016). In bird studies, species identification using PAM is generally effective. However, some species are not very vocal; for example, hummingbirds (Trochilidae), swallows (Hirundininae), bluebirds (Sialia), American robins (*Turdus migratorius*) and dark-eyed juncos (*Junco hyemalis*) are more likely to be detected visually than acoustically (Hutto & Stutzman, 2009). These less-vocal species may be under-represented if only acoustic autonomous recorders are used. Identifying species based on the echolocation calls of cetaceans and bats is also challenging (Gibb et al., 2019). Visual surveys can complement acoustic data by providing direct species identification and group size estimates. When used together, these methods can validate and enhance each other's data, thereby reducing uncertainties. Visual methods can confirm species identifications and group sizes that acoustic methods may miss or misinterpret.

7.3 To become mature tools novel technologies need to undergo a calibration process via a double platform approach

7.3.1 Development of PAM: a reliable tool for cetacean monitoring

Although not new, the development of passive acoustic survey methods is more recent than that of visual survey methods. Visual surveys using dedicated marine mammal observers on vessels or aircraft have been used to monitor cetaceans for several decades and have become standard practice since the 1970s, when systematic efforts to study and conserve cetacean populations became more widespread (Kaschner et al., 2012). Over the years, improvements to this traditional method have helped to improve cetacean detection and reduce detection biases in estimates. For example, changes in field methods or modeling approaches for estimating $g(0)$ have been topics of interest for many researchers to improve the accuracy of abundance estimates (Oedekoven et al., 2018; Laake et al., 2011). As technology advances, researchers continue to push the boundaries of science by exploring alternative approaches based on passive acoustics and high-resolution imagery that enhance traditional surveys and provide new insights (Lennert-Cody et al., 2018).

Passive acoustic monitoring has been used as an alternative to traditional surveys since the late 1980s (Zimmer, 2011). This method has grown in importance with technological advances and offers significant advantages over visual surveys, particularly in challenging conditions such as night, bad weather or deep water (Zimmer, 2011). In addition to detecting animal presence, it provides unparalleled insight into the soundscape and anthropogenic noise. To improve the use of PAM for cetacean monitoring, efforts have focused on the development of vocalisation catalogues. These catalogues, often developed in conjunction with visual surveys, aid in the detection and classification of cetacean vocalisations (Oswald et al., 2003). An example of a classifier developed for passive acoustic monitoring is ROCCA (Real-time Odontocete Call Classification Algorithm), available as a module in PAMGuard (Oswald et al., 2007; Gillespie et al., 2008). ROCCA extracts delphinid whistle contours from spectrograms and analyzes features such as duration, frequencies, slopes and variables describing the shape of the whistle. These features are then used as input to a random forest-based classifier to identify the species of each whistle (Oswald & Oswald, 2013). This tool assists in species identification and helps to monitor species occurrence. For example, (Howe & Lammers, 2021) used ROCCA for species identification and investigated the diel occurrence of odontocetes around the Maui Nui region, finding that smaller species have stronger acoustic activity at night, while larger species have less pronounced diel patterns. This research can inform management practices that take into

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account interspecies differences in use of the Maui Nui basin.

Advances in technology have led to the development of more effective instruments, such as autonomous acoustic recorders, which allow long-term data collection in remote and harsh environments (Wiggins & Hildebrand, 2016; McDonald et al., 1995). For example, autonomous acoustic recorders have been used to identify seasonal vocalisation patterns of blue and fin whales in the Western Antarctic Peninsula (Širović et al., 2004). Today, acoustic methods are highly advanced and serve as powerful tools to identify population structures, migration patterns and relative population trends (Szesciorka et al., 2020; Širović et al., 2015; McDonald et al., 2006). Improvements in this method now allow estimation of parameters such as abundance from acoustic surveys alone, without the need for visual surveys for some species (Marques et al., 2012). While acoustic methods continue to advance, new technologies are emerging, including digital imagery and genetic approaches (Lennert-Cody et al., 2018) and would need calibration against traditional survey methods when technologically mature.

7.3.2 Emerging technologies applicable to a line transect approach

New technologies that can be used in line-transect approaches include unmanned aerial vehicles (UAVs), which are aircraft or drones remotely controlled by a pilot from the ground or a vessel via a communications system linking the UAV to the pilot (Ferguson et al., 2018). Developed primarily to improve aerial surveys, UAVs eliminate safety issues, reduce noise and carbon emissions, and improve the accuracy and precision of counts (Hodgson et al., 2017). They are particularly useful in areas away from airfields and in unsafe conditions for manned aircraft. For example, Sweeney et al. (2016) conducted a study along the high winds and cliffs of the Aleutian Island chain, far from airfields, and found that using UAVs along with traditional aerial surveys provided a more comprehensive survey to estimate the density of Steller sea lions (*Eumetopias jubatus*). UAVs also have important implications in behavioural studies when behavioural observations from a vessel-based surveys are typically limited to records of animal surfacings obtained from a horizontal perspective (Torres et al., 2018). UAVs can provide high-resolution imagery for species identification, group size estimation and body condition assessment. However, the use of UAVs is more costly than traditional aerial line-transects due to increased logistical complexity, more equipment and extensive post-processing (Ferguson et al., 2018). In addition, UAVs are often limited in terms of radius of actions (Hodgson et al., 2017), making them unsuitable for large-scale surveys such as SCANS or ASI.

Satellites represent a major advance in terms of action range and can provide spatial resolution in the meter range and are capable of detecting individual animals. Initially

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developed for terrestrial species, attempts to monitor cetaceans using satellite imagery have increased since 2002 (Abileah, 2002; Fretwell et al., 2014). Very high-resolution (VHR) satellite imagery allows access to remote regions and facilitates large-scale surveys (Cubaynes et al., 2019). This technology has also been used to study movement patterns, such as tracking humpback whales with satellite tags in the Southern Ocean to study their movements and habitat use (Dalla Rosa et al., 2008). This research revealed variability in movement distances between feeding areas and provided comprehensive information on whale population structures (Dalla Rosa et al., 2008). However, the acquisition of VHR satellite imagery is expensive, especially for large study areas covering several thousand square kilometers. This high cost limits the potential use of VHR satellite imagery to study cetaceans (Höschle et al., 2021). In addition, satellite imagery struggles to differentiate between baleen whale species compared to *in situ* surveys due to the limitation of image resolution (Bamford et al., 2020) and therefore it is still not possible to observe small cetaceans with VHR using satellite imagery, let alone identify their species.

In both cases, these technologies can provide permanent recording of video/images that can be reviewed as needed (Brown et al., 2023) but analysis is typically labor-intensive and time-consuming when manually analysing large datasets (Baumgartner & Mussoline, 2011; Höschle et al., 2021). Efforts to develop automated image analysis through machine learning and artificial intelligence have been underway for many years and continue to advance (Borowicz et al., 2019; Gray et al., 2019). In Fretwell et al. (2014), southern right whales (*Eubalaena glacialis*) were successfully identified in Argentine waters using both manual methods and supervised and unsupervised classification algorithms with satellite imagery, although the method may be sensitive to variations in ocean colour and turbidity. Borowicz et al. (2019) enhanced detection by creating an automated system to identify images containing whales, reducing the need for expert annotation. They achieved a 100% success rate in classifying whale images and 94% for images containing only water. Ongoing improvements to the whale detection training models will further expand the use of VHR imagery in cetacean monitoring. However, costs remain very high today, both for the platform and for image analysis. For example, in the SAMM (Suivi Aérien de la Mégafaune Marine, Aerial Survey of Marine Megafauna) survey, the expenses associated with using digital cameras and analysing the images double the hourly acquisition costs per aircraft (Laran et al., 2022; V. Ridoux, personal communication).

In the field of acoustic studies, this has led to significant progress in the automatic detection and classification of cetacean sounds. For example, Oswald et al. (2007) developed a method for real-time acoustic identification of delphinid whistles that extracts, measures and classifies whistles to species in real time, reducing the need for extensive post-field data analysis. Rankin et al. (2017) used their system to classify whistles of cetaceans in the

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California current and achieved a correct classification for individual whistles ranged from a low 38% for bottlenose dolphin and long-beaked common dolphin to a high of 75% for killer whales. Successful assignment of echolocation clicks to species has been also demonstrated using data from the Gulf of Mexico for several delphinid species (Frasier et al., 2017). However, machine learning models require training on known species vocalisations and may not be universally applicable, especially if delphinids produce different clicks in different study areas. In the PhD work, the identification of acoustic events was quite laborious and time-consuming. The classifiers used were not specifically designed to identify and group sequences of clicks produced by individual animals into distinct events (Gordon et al., 2020). To minimise false positives, I manually assigned click sequences that followed a consistent temporal trajectory across time gaps to individual small cetaceans. I believe that advances in machine learning will greatly improve the identification of individual click sequences in the future.

As stated in the introduction, the implementation of new technologies holds significant potential for abundance estimation, although they are not yet as mature as acoustic surveys, which are already quite advanced. Availability and perception biases are still not well understood, and these technologies cannot yet independently assess populations. Satellite imagery continues to face challenges in estimating detection probability and biases (Fretwell et al., 2014). Meanwhile, UAVs have shown great promise in estimating availability bias, which can improve abundance estimates from aerial surveys (Hodgson et al., 2017; Brown et al., 2023). For example, Brown et al. (2023) used aerial video of diving and surfacing behaviours to estimate the availability bias and group size error of Australian humpback dolphins (*Sousa sahulensis*) in Australia. However, it is too early to replace traditional aerial surveys with UAVs for large-scale cetacean abundance studies (Ferguson et al., 2018).

While novel technologies offer many advantages, they often require calibration with traditional visual-based surveys to ensure accuracy and reliability. This involves implementing the novel method and the traditional visual surveys in a double platform approach. This calibration process is essential to validate the use of the novel method to produce comparable and consistent results, thereby increasing its credibility and utility in long-term monitoring programs. Visual surveys, despite their inherent biases, provide essential baseline data against which the results of newer technologies can be validated. The use of double platform surveys allows for direct comparisons and identification of their respective strengths and weaknesses (Buckland et al., 2012). For example, Fettermann et al. (2022) used drones and visual vessel surveys to detect groups of bottlenose dolphins around Great Barrier Island, New Zealand, and found that drone-based counts identified 26.6% more individuals per group than vessel-based counts. This suggests that drones provided the best group size estimates, especially when studying large groups of animals within a fairly small study area. The use of multiple survey platforms could facilitate the calculation of correction factors that refine abundance estimates over larger areas.

7.3.3 Emerging technology applicable to a stationary approach

A new method developed in the last decade is environmental DNA (eDNA) analysis, which allows species identification using environmental samples such as water to collect genetic material shed by cetaceans (Parsons et al., 2018). Cetaceans are well suited to this tool because they shed cellular DNA through skin shedding, faecal plumes, and blowing. Because eDNA degrades rapidly in seawater, it is a good indicator of recent presence. DNA can be collected from the environment, concentrated and amplified by PCR using specific DNA sequences (primers, figure 7.2, Parsons et al., 2018). This method has been tested on cetaceans such as harbour porpoises, killer whales and bowhead whales (Parsons et al., 2018; Baker et al., 2018; Székely et al., 2021). It can detect the presence of species without direct observation, providing data on species diversity and distribution, as well as prey and population genetic data. Current studies aim to improve eDNA catalogs by identifying taxon-specific primers and understanding species identity and behaviour in the environment (Alter et al., 2022). However, DNA in seawater can degrade rapidly due to abiotic or biotic factors such as UV radiation, temperature and microbial activity, which can affect detection rates (Suarez-Bregua et al., 2022).

Integrating vessel-based visual with eDNA sampling helps to determine the feasibility of using eDNA to detect visually observed cetacean species (Alter et al., 2022). According to Alter et al. (2022), using eDNA alongside other survey methods helps to understand its capabilities and limitations. eDNA seems to be fairly well developed for species inventories to complement visual and acoustic surveys (Baker et al., 2023), in which has led to the detection of species in areas where they were previously unreported or poorly reported (Suarez-Bregua et al., 2022), but much remains to be done to understand the mechanisms that determine the quantities of eDNA present in the water with a view to possibly using this method to produce abundance estimates (Alter et al., 2022). The specific identification capacity appears to be high but has not been extensively tested and paired with other survey methods (Alter et al., 2022). Generally speaking, this methodology is still at the technology development and validation stage before being used on a full scale to assess the conservation status of a cetacean species.

7.4 Future recommendations

7.4.1 The use of double acoustic and visual platforms in small cetacean population surveys

This PhD dissertation demonstrated the importance of using both acoustic and visual methods as a double platform for cetacean population monitoring. The double platform approach allowed the quantification of detection biases inherent to each method and

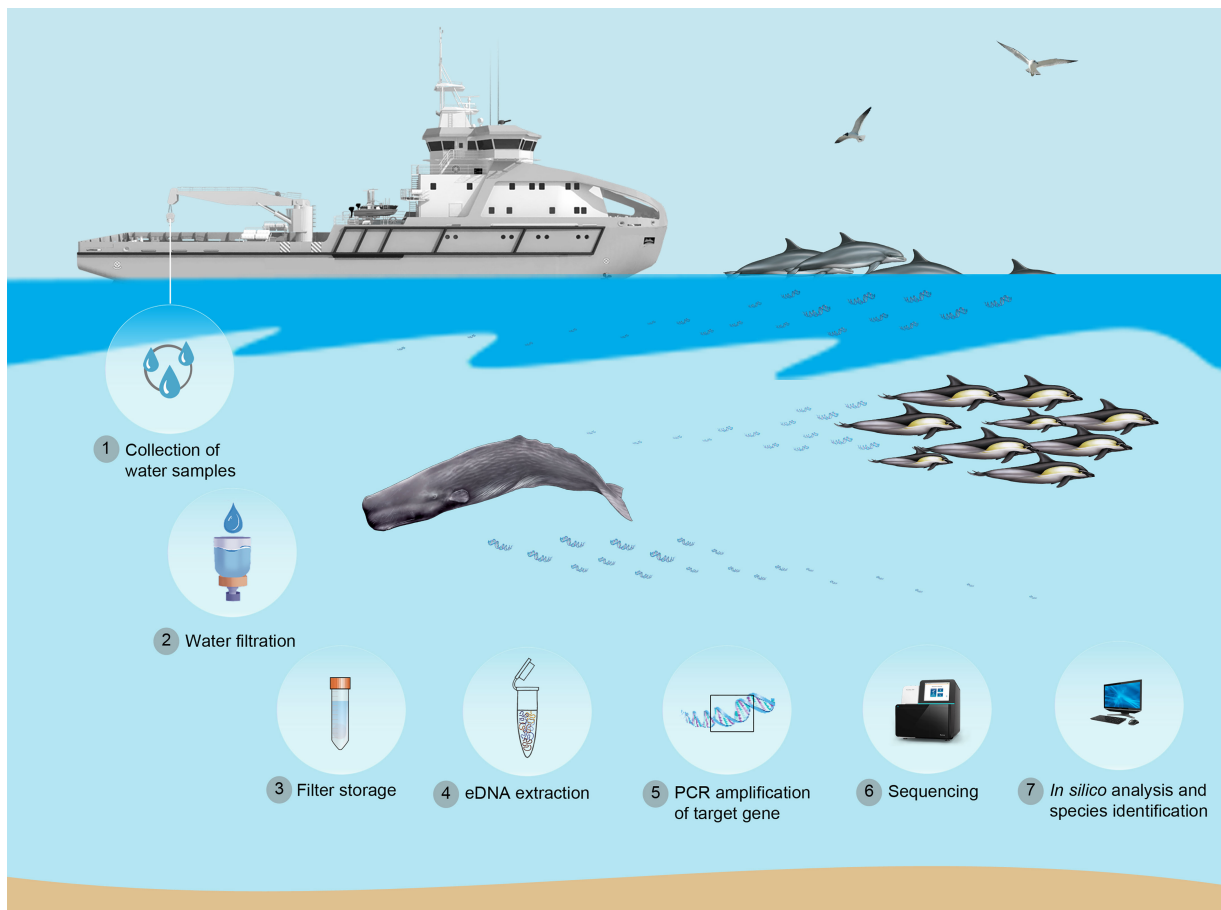


Figure. 7.2: Application of eDNA methodology for marine mammal monitoring.

facilitated the calibration of the acoustic and visual data. These methods effectively complemented each other, with the visual platform providing species identification and group size estimates, while the acoustic platform was invaluable for night-time surveys, approximately doubling the effective time and distance sailed in effort by the research vessel. While simultaneous acoustic and visual data collection is common in cetacean surveys, it is often used to study occurrence, compare methods, or estimate abundance from a single type of data (Duporge et al., 2023; Barlow & Taylor, 2005). Few studies have conducted analyses in a real double-platform context to estimate detection probability or density/abundance with combined data (Gerrodette et al., 2011; Martin et al., 2020). Future surveys aiming to estimate abundance should use a double-platform approach with the objective of combining data at the analysis stage. This will increase the robustness of the results and allow for more comprehensive comparative analyses. The application of rigorous protocols is essential to estimate $g(0)$ and to achieve absolute abundance estimates. Here, I provide some recommendations for future studies to improve field methods and analysis when combining acoustic and visual data.

One recommendation is to include reticle binoculars or photogrammetry to reduce distance measurement errors. When measuring perpendicular distances, errors and rounding

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problems can occur when estimating distances by eye. For small vessels with low platforms, such as the *R/V Song of the Whale*, the use of reticle binoculars or photogrammetry is complicated (Leaper et al., 2023). Radial distance estimation by eye was found to be most effective in such situations. Future surveys should consider the height of the platform to facilitate the use of reticle binoculars or photogrammetry to improve the accuracy of distance estimation.

Responsive movement is a major issue when estimating absolute abundance with vessel line-transect surveys. One key assumption of distance sampling is that animals are detected before they move. This assumption should be given as much attention as the $g(0)$ assumption. It is recommended that the behaviour of small cetaceans should be rigorously quantified when first detected by the visual platform, for example by observing the swimming direction (Palka & Hammond, 2001). Observers should also measure the time that groups spend bow riding until they pass abeam, allowing for a more thorough analysis of duplicate events between the acoustic and visual platforms. For example, Martin et al. (2020) described the behaviour of Heaviside's and dusky dolphins, noting their orientation ('towards', 'away', 'left', 'right') and concluded that they were mostly attracted to the vessel. If reactive movement is a concern, it should be taken into account in statistical analyses (Burt et al., 2014).

Another recommendation is to establish consistent times for switching between effort types during the day and night (i.e. from acoustic transects to acoustic-visual transects in the morning and vice versa at night) to ensure consistent data collection. For example, the double-platform effort should begin and end at specific times (depending on latitude and date), in the morning and evening respectively, and the acoustic-only effort should be relayed during the night. Maintaining consistent timing will increase data reliability and allow for more robust implementation of $g(0)$ specific to day phases or hours for the acoustic platform.

Last but not least, when using an acoustic-visual double platform, it is important to consider the identification of duplicate events at the analysis stage to assign species to acoustic events. A whistle repertoire has been developed for small Mediterranean cetaceans (Azzolin et al., 2014), allowing species identification based on whistles but echolocation clicks of small cetaceans are difficult to distinguish and a reliable species repertoire and classifier for dolphin clicks is still lacking (Roch et al., 2011; Azzolin et al., 2014). By associating visual events to acoustic events, this approach could expand the regional vocal repertoire of echolocation clicks for a variety of small cetaceans. With more data, machine learning models could be trained to detect clicks at the species level, allowing species abundance to be estimated.

The following is an advisory note rather than a recommendation. The detection biases of the acoustic platform are still not well understood. Information on the click production rates of small cetaceans, particularly striped dolphins - the most abundant in the Mediterranean Sea - would be extremely valuable in quantifying acoustic availability bias. Independent data using digital acoustic recording tags (DTags) would be beneficial (Johnson & Tyack, 2003), but deploying DTags on free-ranging small cetaceans is more challenging and ethically complex compared to larger cetaceans (Nowacek et al., 2016). Nevertheless, with information on click production rates, it would be possible to estimate acoustic density based on cue rates.

7.4.2 Recommendations for ASI 2

ACCOBAMS has agreed that conducting synoptic surveys of the entire ACCOBAMS area every six years provides the right balance between monitoring costs and regularly updated information on the abundance and distribution of cetacean species (Panigada et al., 2024). In anticipation of a second ASI survey using the vessel component, I make several recommendations for future surveys, in addition to those mentioned above.

Firstly, to estimate the absolute abundance of small cetacean communities in the Mediterranean, the ASI protocol should be expanded to include a section on double-platform line transect methodology during the day, as the previous ASI protocol did not mention the use of a double-platform approach for the vessel component. This methodology should provide $g(0)$ estimates of each platform and account for reactive animal movements, similar to the protocols used in the SCANS surveys for harbour porpoises (Hammond et al., 2013; Gilles et al., 2023). For example, the following sentence was included in the SCAN survey protocol "The method used was a double platform line transect survey with two teams of observers on each ship to generate abundance estimates that were corrected for animals missed on the transect line and also for the effects of movement of animals in response to the ship". The aim is to apply the same rigour to the visual platform as to the acoustic platform and to ensure the independence of the two platforms. Conducting a pilot study to train cruise leaders can help ensure consistent implementation of the study methodology when several research vessels are used simultaneously.

As the vessel component has primarily been used to estimate the abundance of sperm and beaked whales (ACCOBAMS, 2021), I suggest explicitly including small cetaceans in the rationales for the vessel component of the ASI to complement the data on deep-diving species. In addition, I recommend maintaining overlapping survey blocks between the aerial and vessel components to facilitate future comparisons and extending the vessel effort to the entire Mediterranean to provide a more comprehensive picture of small cetacean

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communities. Given the lengthy nature of large-scale vessel surveys, the use of a second vessel similar to the *R/V Song of the Whale* could help cover the entire study area during the summer.

Another recommendation is to organise a workshop before the survey to revise and improve protocols and design platforms for the vessel component to be able to estimate the absolute abundance of small cetaceans from the future survey.

7.5 Conclusion

Monitoring cetacean populations is a challenging task and requires innovative approaches to overcome the limitations of each detection method. The combination of acoustic and visual data represents a promising advance in this field. Acoustic methods offer the advantage of being able to monitor cetaceans both day and night, while visual observations allow species identification and group size estimation, but are limited to daytime hours. This PhD project provides a comprehensive overview of studies that combine passive acoustic and visual data for cetacean monitoring. It highlights the different degrees of combination of these methods, from simple comparisons to fully combined data for abundance estimates. To date, the joint use of acoustic and visual data has been rare due to complexities such as differences in detection radius, detection biases and temporal use. The methodology presented here allowed the strengths of each method to be used to improve the monitoring of small cetaceans by using all available data collected by the *R/V Song of the Whale* during the ASI survey, i.e. acoustic data collected during the day and night and visual data collected only during daytime. This study showed that combining visual and acoustic data is mostly useful and effective when detection biases inherent to each method are properly taken into account. The detection biases in abundance estimates were considered when estimating $g(0)$ of each platform during a double-platform framework and $g(0)$ in function of time to account for the diel pattern in vocal behaviour of small cetaceans. Although this analysis involved pooling different cetacean species, future research should take into account species-specific characteristics to further refine abundance estimates. This study demonstrates the benefits of using a double acoustic-visual platform-based survey to monitor cetaceans with additional advantages in terms of cost-effectiveness, logistical feasibility, record archiving and reduced environmental impact. By adjusting estimates to account for detection biases, this methodology not only aids in refining acceptable levels of human-caused cetacean mortality but also improves our understanding and management of cetacean populations, thereby addressing key conservation challenges.

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Appendices



Article - Matching visual and acoustic events
to estimate detection probability for small
cetaceans in the ACCOBAMS Survey
Initiative



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Matching visual and acoustic events to estimate detection probability for small cetaceans in the ACCOBAMS Survey Initiative

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Estimating the detection probability of small cetaceans using either visual or acoustic surveys is difficult because they do not surface or vocalise continuously and can be imperceptible to an observer or hydrophone. Animals seen at the surface may have lower vocalisation rates, while submerged individuals may be more vocally active. This study aims to estimate visual, acoustic and combined detection probability by using Mark-Recapture Distance Sampling (MRDS) methodology. We used vessel-based visual sightings and acoustic data (based on click identification) collected simultaneously during the ACCOBAMS Survey Initiative in summer 2018 onboard the *R/V Song of the Whale*. This study focused on small cetaceans in the Mediterranean Sea, including the most commonly-encountered species, the striped dolphin (*Stenella coeruleoalba*). We identified duplicate events between visual and acoustic platforms using a decision tree based on time and distance thresholds to estimate $g(0)$ (the detection probability on the trackline) for small cetaceans. A total of 30 duplicate events were identified from 107 and 109 events identified by the visual and acoustic platforms respectively. We tested the models with two key functions. With a hazard-rate key function, the $g(0)$ was estimated at 0.52 (CV=21.0%) for both platforms combined, 0.29 (CV=25.6%) for the visual platform and 0.32 (CV=25.1%) for the acoustic platform. With a half-normal key function, $g(0)$ was estimated at 0.51 (CV = 21.7%) for both platforms combined, 0.29 (CV = 25.6%) for the visual platform and 0.33 (CV = 23.2%) for the acoustic platform. Our results illustrate that passive acoustic monitoring can be used as an independent platform in MRDS to estimate the detection probability. Our estimate of $g(0)$ was well below 1, far from the perfect detection commonly assumed for abundance estimation. Without correction for detection biases, total abundance would be underestimated by a factor of two when using both acoustic and visual data. This highlights the importance of using dual-platform surveys to estimate detection probability in order to improve abundance estimates and conservation efforts.

KEYWORDS

detection probability, duplicate events, mark-recapture distance sampling, dual platform, passive acoustic monitoring, line-transect surveys

1 Introduction

Marine megafauna species, which have long life spans, low fecundity rates and high longevity (McCauley et al., 2015; Sequeira et al., 2019), are particularly sensitive to anthropogenic pressures and consequently face conservation risks (Bossart, 2011). Although positive actions have been taken for the conservation of populations (Alves et al., 2022), they are still exposed to a wide range of anthropogenic threats such as over-exploitation, underwater noise or bycatch, which affect their vital rates and population viability (Bossart, 2011; New et al., 2014; Pirotta et al., 2018). As a result, many populations of marine megafauna currently have a critical conservation status (Lascelles et al., 2014).

Conservation status assessment is based on information on the abundance, population status and natural history of the species, as well as anthropogenic pressures, all of which may vary over time. Estimating cetacean abundance is a difficult task, as they are mobile and elusive species that spend most of their time below the sea surface, over extended home ranges. Due to these difficulties, opportunities to detect cetaceans in a study area (hereafter called events once detected) may be missed, leading to a biased estimate of population abundance. While most cetacean conservation programs use minimum abundance estimates to take conservation measures (Evans and Hammond, 2004), unbiased absolute abundance is essential to identify acceptable levels of human-caused mortality for cetaceans (Punt et al., 2021). For example, bycatch is the most common source of cetacean mortality (Reeves et al., 2013) and assessing the sustainability of cetacean bycatch can allow the development of effective conservation and management measures (Parra et al., 2021).

Line-transect and mark-recapture methods are two well-known techniques for estimating cetacean population abundance (Buckland et al., 2001; Hammond, 2018). Mark-recapture methods can be applied using different techniques such as acoustic devices (Marques et al., 2012), DNA sampling (Mills et al., 2000) or photo-identification (Genov et al., 2008). The latter is the most commonly used technique, using natural markings on animals to identify cetaceans, and patterns of recaptures in the form of capture histories to estimate the number of undetected animals and hence population size (Hammond, 2018). Photo-identification based mark-recapture technique is effective for studying small coastal populations of cetaceans in a limited study area. In contrast, the line transect method, which is based on distance sampling techniques, does not require the identification of individuals and is generally applied over large study areas, while allowing for the simultaneous monitoring of several species (Buckland et al., 2004; Daura-Jorge and Simões-Lopes, 2017). This method relies on the visual and/or acoustic detection of events collected by observers/recorders on a platform moving along a predetermined linear route in a study area. Observers record visual and/or acoustic detection events, i.e. each event in which an individual or group of individuals is encountered, the radial distance of the event from the observer/recorder and the angle between the vessel's bow and the animals. For each event, the radial distance and angle are used to calculate the perpendicular

distance from the transect line. A detection function $g(x)$, which is the probability of detecting an animal given its distance x from the line, is estimated from the distribution of the perpendicular distances. Knowing this probability of detection, the number of events and the size of the covered region, density and abundance of the population and the effective strip width (ESW; the number of objects detected beyond this distance is equal to the number of objects missed before this limit) can be estimated (Buckland et al., 2015). Conventional Distance Sampling (CDS) usually requires three assumptions to be met: (1) all animals on the transect line are detected, usually referred to as $g(0) = 1$, (2) animals are detected at their initial location and (3) distance measurements are accurate. The assumption $g(0)=1$ has been commonly used to estimate cetacean abundance (Barlow, 2006; Øien, 2009; Dick and Hines, 2011; Hildebrand et al., 2015) despite the fact that many animals spend a significant proportion of the time submerged and might hence be missed, potentially inducing a negative bias in abundance estimates.

Abundance estimation is indeed closely linked to the detectability of individuals during surveys (McCarthy et al., 2013). Detectability can be affected by both an availability bias and a perception bias (Laake and Borchers, 2004), constituting together the detection biases. Availability bias corresponds to the unavailability of animals for detection, either because they are below the sea surface, which depends on the time spent at depth by the species and the platform speed, or because they are not acoustically active, which depends on the vocalisation rate of the species. Perception bias accounts for the non-detection of available animals by observers or recorders due to imperfect observer vigilance or unfavourable conditions for detection (e.g. high sea states). Multi-Covariate Distance Sampling (MCDS) partially addresses detection biases using covariates in the detection function (Marques and Buckland, 2003). However, estimating the detection probability of small cetaceans remains difficult and the assumption that all animals are detected on the transect line can be violated due to both availability and perception biases. If they are not accounted for, the estimated abundance will be negatively biased (Saavedra et al., 2018).

To provide more accurate abundance estimates, the Mark-Recapture Distance Sampling (MRDS) method deals with missed detections at distance zero by estimating $g(0)$. This method requires two independent platforms scanning the same area simultaneously, which are used to 'mark' animals (Laake and Borchers, 2004). The $g(0)$ and overall detection probability are estimated by using the number of animals seen by each platform and by both platforms (duplicate events). Most dual platform line-transect surveys use two visual platforms, either with a single survey platform or with two separate survey platforms (Cañadas et al., 2004; Hammond et al., 2013; Laran et al., 2017; Lambert et al., 2019). The number of surveys using an acoustic platform with a towed hydrophone array as a second platform has increased in recent years (Barlow and Taylor, 2005; Boisseau et al., 2010; Richman et al., 2014; Martin et al., 2020; Rankin et al., 2020; Dalpaz et al., 2021). The acoustic platform has the advantage of detecting cetaceans even when they are not visible at the surface, and thus not available to the visual platform. These two methods are complementary and can improve the overall detection efficiency (Verfuss et al., 2018). This kind of

analysis can however be challenging due to the complexity of identifying events; acoustic events are typically validated during post-field analysis, while visual events are recorded directly during the survey.

The ACCOBAMS Survey Initiative (ASI) vessel component, conducted in the summer of 2018 with the *R/V Song of the Whale* in the western and central Mediterranean Sea, was a unique survey using a visual-acoustic dual platform (ACCOBAMS, 2021). The ASI was carried out under the auspices of the Agreement on the Conservation of Cetaceans of the Black Sea Mediterranean Sea and Contiguous Atlantic Area (ACCOBAMS) to estimate cetacean abundance in the entire Mediterranean Sea. This region is exposed to increasing levels of anthropogenic impacts (Coll et al., 2012) and is home to cetacean populations that are often distinct from their nearby Atlantic counterparts. Numerous studies have been conducted in the Mediterranean Sea to estimate the abundance of cetaceans (Laran et al., 2017; Panigada et al., 2017; Lewis et al., 2018) but survey efforts have been recognised as heterogeneous across the basin (Mannocci et al., 2018). Some species, like the Risso's dolphin (*Grampus griseus*) or the rough-toothed dolphin (*Steno bredanensis*), have received less attention than others (Boisseau et al., 2010; Kerem et al., 2012; Luna et al., 2022) and some areas have been studied more extensively, especially within the western basin (Mannocci et al., 2018). Therefore, the ASI project aimed at filling these data gaps.

In this study, we aimed to use this visual-acoustic dual platform to estimate the detection probability of small cetaceans in the Mediterranean Sea. Small cetaceans studied here include the bottlenose dolphin (*Tursiops truncatus*), the long-finned pilot whale (*Globicephala melas*), the Risso's dolphin, the rough-toothed dolphin, the common dolphin (*Delphinus delphis*), the striped dolphin (*Stenella coeruleoalba*) and unidentified dolphins. This diverse community is largely dominated by the striped dolphin (ACCOBAMS, 2021). We only included transects from the ASI survey where visual and acoustic data (based on echolocation clicks) of small cetaceans were collected simultaneously. In this study, we did not go as far as estimating cetacean abundance because the transects where visual and acoustic data were collected simultaneously did not cover the study area uniformly, and therefore these transects were not a representative sample of the species distribution (Buckland et al., 2004). In addition, we did not estimate group size in our study, which is necessary for absolute abundance estimation. Although group size is a key aspect of abundance estimation, we did not fully address it in this study as it was primarily focused on estimating detection probabilities. To estimate detection probability, we first developed a new methodology to identify duplicate events based on a decision tree (rule-based classification). Then, we implemented an MRDS approach with covariates affecting detectability on the prior identification of visual/acoustic event duplicates. The MRDS analysis allowed the detection probability and ESW of the visual, acoustic and combined platforms to be estimated, taking detection biases into account. We expected to obtain a $g(0)$ lower than 1, since detection cannot be considered as perfect for either platform, with a number of the animals on the transect

line inevitably being missed. This paper aims to provide estimates of detection probabilities to be used to estimate the abundance of small cetacean populations, and to demonstrate the benefits of systematically using a dual platform in multi-species line-transect surveys.

2 Materials and methods

2.1 Studied species

This study focused on small cetaceans in the Mediterranean Sea which included: the bottlenose dolphin, the long-finned pilot whale, the Risso's dolphin, the rough-toothed dolphin, the common dolphin and the striped dolphin. The echolocation clicks of these species share similar frequency ranges (Table 1), making species identification difficult (Soldevilla et al., 2008), hence all studied species were pooled for the MRDS analysis. In addition, there were likely too few encounters with species other than striped dolphin to generate robust detection functions for individual species. Striped dolphins, with 52% of the sightings during the vessel survey (ACCOBAMS, 2021) and 85% during the aerial survey (Panigada et al., in review), were the most prevalent small odontocetes in the Mediterranean Basin. These species do not share the same behaviours (i.e. group size, habitat preference, dive duration, responses to the boat) and by grouping all small odontocetes in the same analysis, we assumed that all species behave in the same way in terms of visual and acoustic events; this simplification will be discussed later on.

TABLE 1 Frequencies of peaks energy characteristics (kHz) for each studied species.

| Species | Peak(s) energy (kHz) | References |
|--|---|---|
| Bottlenose dolphin | 120-130 60-140 35-60 33-109 40-80 24-30 40-120 | Au et al., 1974* Akamatsu et al., 1998* Diercks et al., 1971 Wahlberg et al., 2011* Soldevilla et al., 2008 Baumann-Pickering et al., 2010 Finneran et al., 2014* |
| Long-finned pilot whale Short-finned pilot whale (behaviourally similar sp.) | 50 40 | Eskesen et al., 2011* Pedersen et al., 2021* |
| Risso's dolphin | 22-39 50 | Soldevilla et al., 2008 Madsen et al., 2004* |
| Rough-toothed dolphin | 18-30 | Rankin et al., 2015 |
| Common dolphin | 40-80 23-67 | Soldevilla et al., 2008 Evans, 1973 |
| Striped dolphin | Striped dolphin clicks have not been described but we assumed they produce in the same frequency range as bottlenose and common dolphin | |

*Studies that included only "on-axis" signals.

2.2 Survey design

The study area covered the Alborán Sea/Strait of Gibraltar, the Algero-Provençal Basin, the Tyrrhenian Sea/eastern Ligurian Sea, the Strait of Sicily/Tunisian Plateau/Gulf of Sirte, and the Ionian Sea/Central Mediterranean (from 6°W to 36°E and from 30°N to 46°N; [Figure 1](#)). The survey area was divided into 21 blocks. It was conducted using *R/V Song of the Whale*, a 21 m acoustically quiet vessel. The vessel operated with minimal disturbance to marine life by using noise-reduction devices, including vibration-damping mounts for the main engine and a five-bladed propeller. Some transects were surveyed using either a visual or an acoustic platform, while others were surveyed using with both platforms. In this study, we focused on data collected with both platforms between May and September 2018 at an average speed of 3.2 m/s (6.2 knots; [Figure 1](#)). Transects were designed with the *Distance* software ([Thomas et al., 2010](#)) as equal-spaced zig-zag transects to provide uniform coverage probability. The ASI survey used a line-transect sampling protocol and visual observers recorded the location, environmental conditions, group size and perpendicular distance to the animal(s) from the transect line ([Buckland et al., 2001](#)). Transects were divided into legs with constant environmental conditions, and each leg was finally divided into 5 km segments for analysis.

2.3 Visual data collection

Visual data were collected during daylight hours, whenever the observation conditions were appropriate (i.e. Beaufort sea state ≤ 4). During the visual effort, two observers were positioned on a 5 m elevated platform to search for cetaceans. Each observer was on either side of the platform: the first observer scanned the starboard side from 340° to 90° and the second observer scanned the port side from 270° to 20° with 0° representing the bow. They observed the respective areas with naked eye and used binoculars to confirm species identity if required. For each visual event, observers

provided information to a dedicated data logger using the Logger software package (www.marineconservationresearch.org). Information about species, group size, bearing angle and distance from the boat (between the observer and the centre of the group) were recorded for each visual event. Bearings and distances were estimated by eye and group sizes were reported as best, high and low estimates of the number of animals for each visual event. In order to improve effectiveness of and consistency between the observers, distance trials and training on the survey protocol were carried out prior to the survey. Additional information was recorded on cue type and animal behaviour. When necessary, the vessel interrupted the transect line to approach animals for species identification or photo-identification before returning to the transect line at the point where it was left. Information on environmental conditions i.e. Beaufort sea state (out of 9), wave and swell heights (m), cloud cover (percentage scale; out of 10), glare, visibility (from 1 low visibility to 3 good visibility), wind direction and speed (m/s) and boat speed (m/s) were logged every hour or whenever conditions changed by the data logger member. The Logger software automatically registered the GPS position, heading and boat speed every 10 seconds. The visual survey team, consisting of at least 5 members, rotated between different roles that lasted no more than one hour: port observer, starboard observer and data logger for three hours, followed at least by two hours of rest to avoid fatigue. Any duplicate sightings made by both observers in the overlap area have been removed.

2.4 Acoustic data collection

The acoustic survey was conducted 24 hours a day with a towed hydrophone array capable of detecting all cetacean species. A 400 m tow cable was used to avoid any boat self-noise; at this distance, any vessel noise, such as propeller cavitation, was imperceptible to both human ear and the detection algorithms described below. Acoustic effort took place when Beaufort sea state was below 5 and local water depths were above 50 m. The hydrophone array was housed

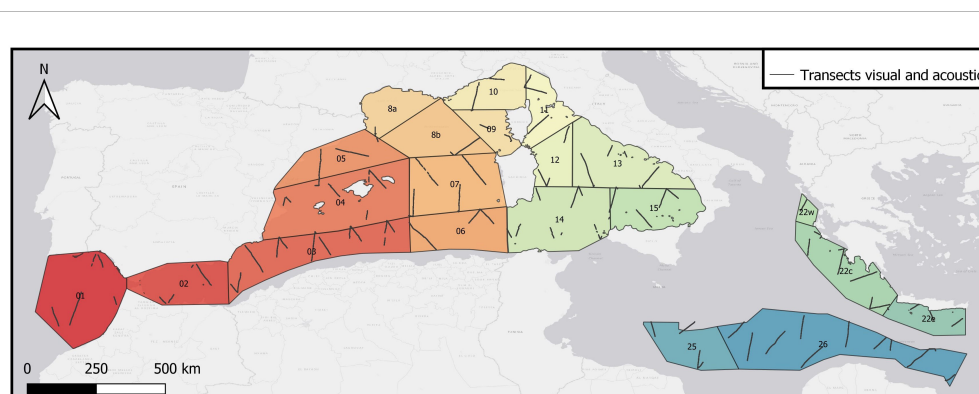


FIGURE 1

Study area covered by the ASI survey in 2018. The area was divided into 21 blocks: 1) Gulf of Cadiz, 2) Alborán, 3) Algeria West, 4) Balears, 5) North East Spain, 6) Algeria East, 7) West Sardinia, 8a) Gulf of Lion shelf, 8b) Gulf of Lion deep, 9) Pelagos South West, 10) Pelagos North West, 11) Pelagis East, 12) Tyrrhenian Central West, 13) Tyrrhenian Central East, 14) Tunisia North, 15) Tyrrhenian South East, 22w) Hellenic Trench West, 22c) Hellenic Trench Central, 22e) Hellenic Trench East, 25) Libya East and 26) Libya East. The black lines represent the transects sampled in dual-platform mode (simultaneous visual and acoustic effort).

in an oil-filled tube and was composed of a pair of hydrophones in a linear configuration. The two hydrophone elements (Magrec HP03), spaced 0.25 m apart, had a sensitivity of -204 dB re 1V/ μ Pa with a flat frequency response (± 3 dB) from 1 to 100 kHz in the frequency band of most odontocete vocalizations. Pre-amplifiers with 29 dB gain were used to prevent voltage drop between the array and the research vessel. The outputs of the pair of hydrophones were digitised at a sample rate of 192 kHz and were monitored in real-time using a click detector in PAMGuard, a passive acoustic monitoring software package (Gillespie et al., 2008). Audio recordings were stored as 16-bit wav files. Outputs from the click detector were compressed into binary storage files in PAMGuard and these files were manually analysed *post-hoc* with a focus on small odontocetes.

2.5 Acoustic data analysis

2.5.1 Echolocation click identification

The small cetaceans considered here have a rich vocal repertoire, producing clicks, whistles, burst pulses and many other vocalisations (Janik, 2009). Here we focused only on echolocation clicks for multiple reasons. Echolocation clicks are produced by all odontocetes and are the predominant vocalizations of toothed whales (Klinck and Mellinger, 2011). Echolocation click trains can be used to derive an estimation of the perpendicular

distance which is key when applying a distance sampling framework (see below). In contrast, whistles are omnidirectional vocalizations (Jensen et al., 2012) without clear onset/offset, and as such are less suitable for estimating perpendicular distances (Amorim et al., 2022).

We defined an acoustic event as a sequence of clicks that was produced by the same animal or group of animals and showed a consistent change in bearing (e.g. when a vocalising cetacean passed from in front to behind the hydrophone array; Figure 2). Sequences of clicks that did not show a consistent trajectory of bearings (e.g. clouds of clicks) or did not cross the 90° line (e.g. detections that did not move past the array) were not considered as acoustic events.

To confirm that an acoustic event was likely produced by a small cetacean, clicks were identified by eye based on peak frequency, the width of the peak frequency, and the number of zero crossings. We hypothesized that impulsive signals between 10 and 80 kHz were most likely produced by a cetacean. Echolocation clicks are short, broadband pulses varying from 10 to 150 kHz for many species (Au, 1993). Odontocetes emit echolocation clicks in a narrow beam projected forward from the melon and the signal energy is more focused in the forward direction (“on-axis”) than to the sides (“off-axis”; Au et al., 1978). Most studies focus on understanding clicks produced “on-axis” (Table 1), i.e. when the animals are facing the hydrophone where the transmission loss of the signal is minimal, which is not typically applicable to the field conditions when recording free-ranging cetaceans (Soldevilla et al.,

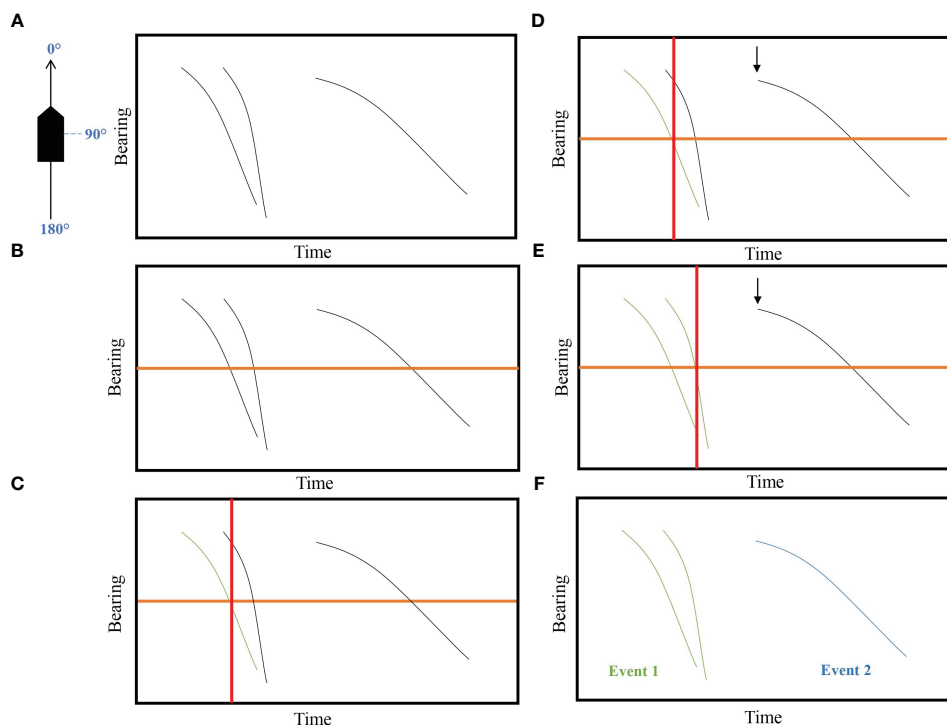


FIGURE 2
 Protocol for determining acoustic events using PAMGuard Click detector module. (A) Determination of the number of events. (B) Set a 90° reference line representing the bearing of 90° of the boat. (C) Set a perpendicular line where the first track is crossing the 90° reference line. (D) If the followed track starts before the perpendicular line of the 1st track, it will be considered as the same event. (E) If we set a perpendicular line on the 2nd track, the 3rd track starts after the perpendicular line, this would be considered as a distinct event. (F) In conclusion, the first two tracks are the same event but probably from two different animals and the 3rd one is another acoustic event.

2008; Baumann-Pickering et al., 2010). Signal waveforms can vary strongly between “off-axis” and “on-axis” clicks. As the higher frequencies attenuate faster than lower frequencies, the higher frequency peaks in clicks recorded “off-axis” (or clicks recorded from distant animals) may not be evident. Although acoustic events, in this study, can be either recorded “off-axis” or “on-axis” depending on the swimming direction of the animals relative to the hydrophones, most free-ranging animals are not likely to produce clicks “on-axis” of the hydrophone (Miller, 2002). Therefore, we expected to record echolocation clicks with lower bandwidths than those reported in Table 1 (marked by *), which included only “on-axis” clicks. The frequency range expected from small cetaceans corresponded to those of the ASI hydrophones which recorded sounds up to 92 kHz.

2.5.2 Localisation

A sequence of clicks can be used to derive an estimation of the perpendicular distance using the Target Motion Analysis (TMA) module’s 2D simplex method implemented in PAMGuard. The bearing angle of each detected click was determined using the time delay of arrival of a signal detected by the pair of hydrophones. Convergence of successive bearing lines was used to locate the sound source and allows the estimation of the distance perpendicular from the crossing point. The TMA module attempted to resolve left/right ambiguity using variation in the vessel’s course.

The number of acoustically active individuals per acoustic event was determined as the number of tracks that occurred at the same time. This method allowed the number of vocalising animals to be counted instead of the number of vocalisations (Akamatsu et al., 2018; Richman et al., 2014). As for visual events, acoustic group sizes were reported as best, high and low estimates of the number of animals for each event.

2.6 Identification of duplicate events

For this study, transects where visual and acoustic data were simultaneously collected were retained to identify duplicate events collected by the visual and acoustic platforms. The MRDS analysis is based on the reliable identification of duplicate events between the two platforms. Two events are considered duplicates when the same group of individuals is detected both visually and acoustically. For this purpose, a two-step decision tree (i.e. a rule-based classification system) was elaborated based on a set of temporal and spatial criteria determining how close in time and space a visual and an acoustic event were recorded. A putative duplicate was a pair of events consisting of a visual and an acoustic event to be tested with the decision tree. A putative duplicate became a potential duplicate then a confirmed duplicate when the first and the second step of the decision tree were respectively passed successfully.

2.6.1 1st step of the decision tree: time threshold

The time window in which a pair of visual and acoustic events can originate from the same group of individuals was defined by

considering that the two platforms, visual and acoustic, were 400 m apart, had a specific detection radius and were moving at the vessel speed (Figure 3). The visual buffer was defined as the 270°-90° sector scanned by the observers in front of the vessel with a radius calculated as 95% of the distribution of the visual perpendicular distances recorded during the survey (here 2,107 m). The acoustic buffer was a disk centred on the hydrophone array with a radius calculated as 95% of the distribution of the acoustic perpendicular distances recorded during the survey (here 1,266 m).

When a first event was identified by either platform, we calculated the minimum and maximum time lags (Δt_1 and Δt_2) for an event from the second platform to be identified in the corresponding buffer, assuming that the detected animal was stationary.

The time lag Δt (in s) was determined by:

$$\Delta t = \frac{L}{v}$$

where L is the maximum distance (in m) travelled by the vessel between an acoustic event (v_s visual event) and a subsequent visual event (v_s acoustic event) forming a putative duplicate. It was estimated as 866 m (1,266 m – 400 m) when the acoustic event came first and 3,773 m (1,266 m + 400 m + 2,107 m) when the visual event came first. Based on an average speed boat of 3.2 m/s (6.2 knots), $\Delta t_1 = -271$ s and $\Delta t_2 = 1,179$ s. Hence any pair of records in which the acoustic event occurs within 271 s before and 1,179 s after the visual event was considered as a potential duplicate.

2.6.2 2nd step of the decision tree: distance threshold

Once potential duplicates have been identified with the temporal criteria related to the platform structure and movement, another threshold was applied to account for the potential movement of the target animal(s) between the two events of the potential duplicate. A mobility buffer was thus estimated based on published values of the routine swimming speeds of small cetaceans. This mobility buffer represented the area centred on the first record of the potential duplicate in which the target animal(s) could be at the time of the second record if they were moving at a routine swimming speed, assuming no responsive movement relative to the vessel. If the location of the second record of a potential duplicate fell within the mobility buffer, the potential duplicate became a confirmed duplicate (Figure 4). The radius of the mobility buffer (in m) was calculated as:

$$r = \Delta t \times v_r$$

where Δt was the time lag (in seconds) between a visual and an acoustic event and v_r the routine swimming speed of the animal (in m/s). The routine speed was determined from the literature and the value corresponding to the 95% quantile of the distribution was chosen, i.e. 3.6 m/s (7 knots; Supplementary Table 1; Pilleri and Knuckey, 1969; Saayman et al., 1972; Würsig and Würsig, 1979; Hui, 1987; Tanaka, 1987; Williams et al., 1992; Ridoux et al., 1997; Wood, 1998; Fish and Rohr, 1999; Yazdi et al., 1999). Given the

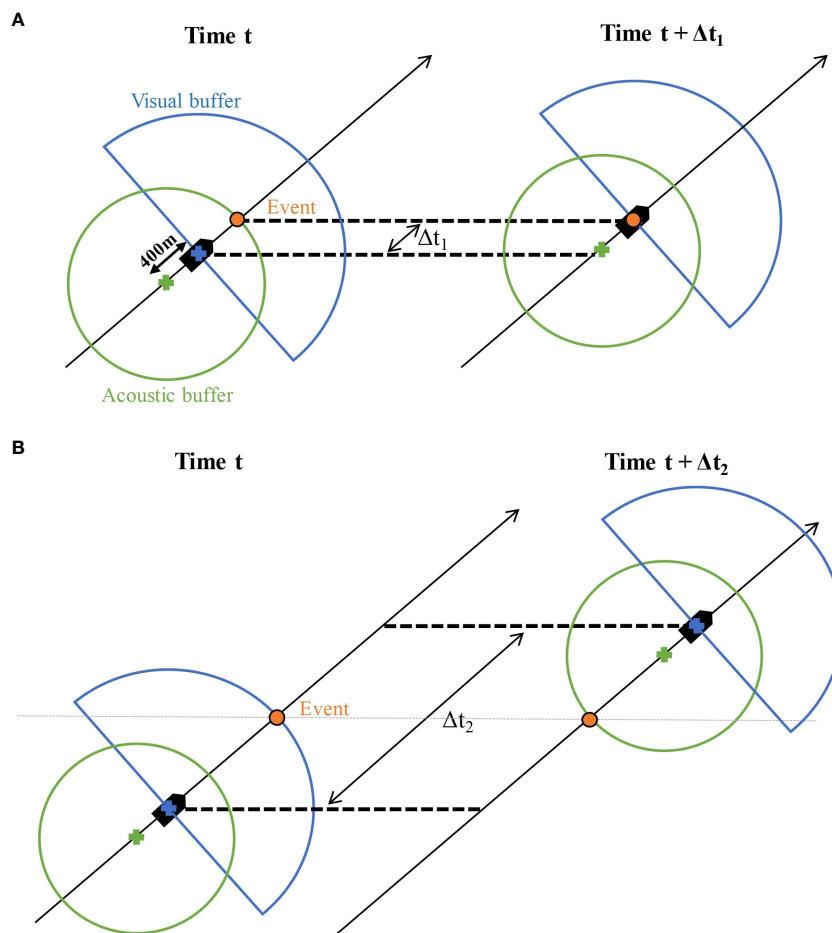


FIGURE 3

First step of the decision tree: the platform-related time lag or dual. The visual semi-buffer (blue) was centred on the vessel (blue cross) and the acoustic buffer (green) was centred on the hydrophone (green cross). A potential duplicate event was considered if a visual and an acoustic event were close in time (between Δt_1 and Δt_2). **(A)** The minimum time lag Δt_1 would correspond to the same group of small cetaceans being acoustically detected as early as possible by the hydrophone array and visually sighted as late as possible by the onboard observers. **(B)** The maximum time lag Δt_2 would correspond to the same group of small cetaceans being visually sighted as early as possible by the onboard observers and acoustically detected as late as possible by the hydrophone array. All intermediate situations between A and B would be accepted as potential duplicates.

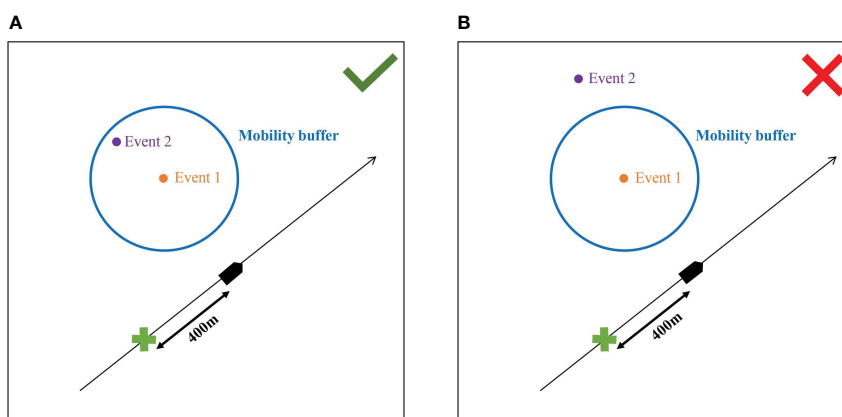


FIGURE 4

Second step of the decision tree: the animal-movement-related spatial lag or mobility buffer. The black line is the surveyed transect. The hydrophone array (green cross) was located 400 m behind the vessel (black pentagon). The mobility buffer is centred on the first event by either platform (blue circle). The status of confirmed duplicate was accepted when the 2nd event was within the mobility buffer **(A)**. The status of confirmed duplicate was rejected when the 2nd event was outside of the mobility buffer **(B)**.

potential left/right ambiguity of the localised acoustic event, we assumed that the acoustic event of a potential duplicate was on the same side as the corresponding visual event.

After passing the two steps of the decision tree, multiple replicate events could be confirmed (e.g. one visual event could correspond to up to three different acoustic events). Among these replicate events, we selected the one with the shortest distance difference to limit the responsive movement of the animal(s) (e.g. if the visual event's distance was 200 m, and the distances for the three acoustic events were 10 m, 100 m and 1000 m, the acoustic event with a distance of 100 m is chosen). The rest of the replicate events were deleted. In the end, a confirmed duplicate event was finally composed of one visual and one acoustic event. For each duplicate event, we selected the highest "best" group size estimate and the larger distance value between the visual and acoustic event.

2.7 Detection function and effective strip width

The detection function and $g(0)$ were calculated using data from both visual and acoustic platforms using the MRDS method (Laake and Borchers, 2004). Events from each platform were set as trials for the other. If events of the same group of animals were made by both platforms (confirmed duplicate, see above), they were considered successful, if not, they were considered failed. There are two possible assumptions in MRDS (Burt et al., 2014): full independence (FI) or point independence (PI). The FI assumption considers the two platforms to be independent at any distance and thus a mark-recapture (MR) model is applied at all distances (including distance zero) to estimate the overall detection probability p . It appears this assumption generates negative biases in abundance estimates in case of failure of the independence assumption (Laake et al., 2011; Burt et al., 2014). The failure can be identified if the abundance estimate is lower than the abundance estimates from the CDS, resulting in the presence of heterogeneity in detection probabilities which generates biases in abundance estimates (Buckland et al., 2010). Attempts have been made to minimise the unmodelled heterogeneity for example by including the effect of covariates in the detection function (Borchers et al., 1998; Laake and Borchers, 2004). To provide a solution to the problem of unmodelled heterogeneity, the concept of PI assumption was introduced by Laake (1999). The PI assumption considers the two platforms to be independent only at distance zero and reduces the impact of unmodelled heterogeneity on detection probability estimates (Buckland et al., 2010). The PI assumption uses a combination of MR and DS submodels. The MR submodel is used to estimate $g(0)$, while the DS submodel is used to estimate the decrease in detectability with distance, and these two are combined to get the overall detection probability p (Burt et al., 2014). In our study, the visual and acoustic platforms were beforehand considered independent but we did not know if this independency was valid for all distances or only at distance zero, so we tested MRDS models with both FI and PI assumptions. Factors affecting the detectability for both platforms were investigated and included in the model to improve precision (Marques and Buckland, 2003; Buckland et al.,

2004). We wanted to assess the effect of the platform on the detectability, so the platform was included as a covariate in all tested models. We also tested the effect of the sea state (0, 1, 2, 3, 4 Beaufort scale) as well as wave and swell height (values in metres grouped into classes: 0 to 0.5 m, 0.6 to 1 m, 1.1 to 1.5 m and 1.6 to 2 m). Single covariates and combinations of two covariates were tested. For the DS model, we tested models with a hazard-rate (HR) and a half-normal (HN) key functions and with or without covariates. The right truncation distance was set at 1,500 m, based on the inspection of the histogram of detection frequencies plotted against distances from the transect line (Buckland et al., 2001). Only segments conducted with good conditions (i.e. Beaufort sea state ≤ 4) were considered in the analysis. The decision was made to exclusively focus on Beaufort sea state due to the fact that visibility, swell and wave height are highly subjective metrics. We tested all models with FI and PI assumptions, with HR and HN key functions for the DS submodel, and combinations of covariates. The Akaike Information Criterion (AIC, Akaike, 1998) and the goodness of fit were used to select the best model fit for each key function. The MRDS analyses were performed in R 4.0.3 using the *mrds* package (Laake et al., 2013). Finally, to estimate the ESW, the overall detection probability was multiplied by the truncation distance (Buckland et al., 2004).

2.8 Sensitivity analysis of the decision tree

Correctly classifying events as unique or duplicate is a critical step in MRDS analysis (Hamilton et al., 2018). We investigated the effect of the thresholds considered in the two-step decision tree on the number of duplicates and on the detection probability. We tested different values of the distance distribution used to set the visual and acoustic buffers in the first step of the decision tree: 70%, 80%, 90%, and 100% based on a fixed value of the routine swimming speed, which was 3.6 m/s (7 knots). For the second step of the decision tree, different routine speeds were found in the literature, ranging from 1.6 to 4.2 m/s (3.1 and 8.2 knots). We analysed the effect of the routine speed by testing different values: 1.60, 2.25, 2.90, 3.55 and 4.20 m/s (3.11, 4.37, 5.64, 6.90, 7.00, 8.16 knots) with a fixed value of the distance distribution of 95%. For each value of the distance distribution and the routine speed, the number of duplicate events and $g(0)$ were estimated, as well as the overall detection probability using half-normal and hazard-rate key functions. This sensitivity analysis allowed comparison of the number of duplicate events and detection probability estimates obtained to assess the effect of using of the values in the decision tree.

3 Results

3.1 Summary of survey data

Transects where acoustic and visual data were simultaneously collected in good conditions (when Beaufort sea state ≤ 4) totalled 6,679 km of effort (Figure 1). The lengths and average speed of surveyed transects for each survey block are given in Supplementary

Table 2. A total of 108 visual and 122 acoustic events of small cetaceans were identified. Species identification based on the visual survey component is shown in Table 2. The striped dolphin was the most frequently observed species and represented 52.8% of the total visual events. The second most observed species was the short-beaked common dolphin (11.1%) followed by the bottlenose dolphin (4.6%). The Risso's dolphin (2.8%), the long-finned pilot whale (0.9%), and the rough-toothed dolphin (0.9%) were occasionally observed during the survey. About a quarter of the visual events could not be identified to the level of species (26.9%). The estimated “best” group size was higher in visual events 9.9 ± 14.0 individuals than in acoustic events 3.8 ± 1.5 individuals.

3.2 Matching visual and acoustic events

A total of 87 potential duplicates were identified after the first temporal threshold was applied, reducing to 44 confirmed duplicates after applying the second spatial threshold. By selecting a single visual and acoustic event for each match, we finally obtained 30 unique duplicate events, which represent 16% of the total events. The visual platform recorded 77 events that the acoustic platform did not. Conversely, 79 events were identified by the acoustic platform only. Among the duplicate events, the species most observed by the visual platform was the striped dolphin (56.7%) followed by the common dolphin (16.7%) and unidentified dolphins (13.3%). Not surprisingly, bottlenose (6.7%), Risso's (3.3%) and rough-toothed (3.3%) dolphins were rarely seen in the duplicate events. Under the assumption that unidentified dolphins have the same species composition as the identified dolphins, about 63% of the duplicate events would be striped dolphins.

3.3 Estimation of the detection probability

A truncation distance was set at 1,500 m, which removed 10 unique visual, 2 unique acoustic and 2 duplicate events,

TABLE 2 Number of visual events for each studied species.

| Species | Number of visual events | Part of the total visual events (%) |
|-------------------------|-------------------------|-------------------------------------|
| Bottlenose dolphin | 5 | 4.6 |
| Long-finned pilot whale | 1 | 0.9 |
| Risso's dolphin | 3 | 2.8 |
| Rough-toothed dolphin | 1 | 0.9 |
| Common dolphin | 12 | 11.1 |
| Striped dolphin | 57 | 52.8 |
| Unidentified dolphin | 29 | 26.9 |

representing 7.5% of the total events (Figure 5). Thus, in total, 67 unique visual, 77 unique acoustic and 28 duplicate events were used to fit the detection function in the MRDS method.

Based on the AIC and the goodness of fit, the PI model with a HR key function was the best model (Supplementary Figure 1 and Supplementary Table 3). The MR submodel included perpendicular distance, swell height and platform as covariates. The DS submodel with the HR key function included sea state only. However, the model did not appear to fit the data well and overestimated detectability close to the transect line (Figure 6). Although the fit of the PI model with a HN key function was not optimal, it had a better fit to the data (Figure 6) and could therefore be considered as a more conservative model for estimating detection probabilities.

For both key functions, all parameters of the detection function were negative (Table 3), such that the detection probability decreased with increasing perpendicular distance from the transect, swell height and sea state (the further away from the vessel and the worse the conditions, the more difficult it is to detect the animals). However, $g(0)$ was fixed in all conditions. The detection probability in the MR submodel was slightly higher with the acoustic platform than with the visual platform (parameter estimate for the visual platform equal to -0.14), but the standard error (SE) was high relative to the parameter estimate, so the effect of the platform was marginal (Table 3) which means their effect on the detectability of small cetaceans was negligible. In contrast, the SE was low for the distance and swell height covariate in the MR submodel and for the sea state in the DS submodel (Table 3). These results highlighted the strong effect these covariates have on the detectability of small cetaceans on the transect line.

The number of events identified by the visual and acoustic platforms did not differ greatly and duplicate events occurred mainly within 500 m of the transect line. However, the acoustic platform detected more events on the transect line and at a greater distance (Figure 7). Indeed, the $g(0)$ was slightly higher for the acoustic platform from 0.32 (CV = 25.1%) to 0.33 (CV = 23.2%) depending of the key function (Table 4). The $g(0)$ of the visual platform was estimated between 0.29 (CV = 25.6%) and 0.30 (CV = 23.8%). Finally, by using combined platforms, we obtained a $g(0)$ of 0.52 (CV = 19.8%) with the HR key function and 0.51 (CV = 21.7%) with a HN key function. The use of the key function had a large effect on the overall detection probability estimations and therefore on the ESW. It was estimated to 0.07 (CV = 28.9%) and 105 m for the HR key function and 0.21 (CV = 20.3%) and 315 m for the HN key function respectively.

If detection biases were not accounted for, i.e. assuming $g(0) = 1$, the estimated overall detection probability and ESW would be 0.14 and 210 m respectively for the HR key function and 0.40 and 600 m for the HN key function.

The sensitivity analysis explored the effect of using different values of the distance distribution and routine swimming speed on the number of duplicate events and the detection probability estimates (Figure 8 and Supplementary Tables 4, 5). With a distance distribution ranging from 70 to 100% and a routine speed ranging from 1.6 to 4.2 m/s (3.1 to 8.2 knots), the number of duplicate events increases from 14 to 35 and 3 to 37 respectively. Both $g(0)$ and the overall detection probability became stable for

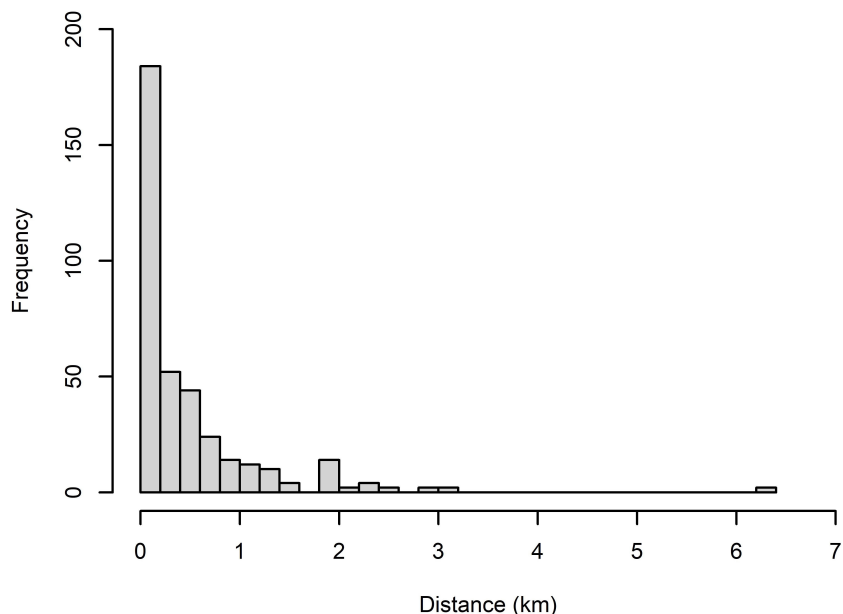


FIGURE 5
Perpendicular distance (km) frequency distributions for small cetaceans identified by the *R/V Song of the Whale* either with the visual or acoustic platforms.

both models from 70% of the distance distribution. On the contrary, $g(0)$ continuously increased as the routine speed increased, and overall probability detection increased more slowly for both models.

4 Discussion

The objectives of our study were to develop a method to match visual and acoustic events and to estimate the detection probability

of small cetaceans accounting for detection biases. Visual and acoustic data were collected simultaneously using a visual-acoustic dual platform in a distance sampling framework. Most studies estimate the detection probability by assuming $g(0)$ is equal to 1 with a single platform (Barlow, 2006; Øien, 2009; Dick and Hines, 2011; Hildebrand et al., 2015). To account for detection biases in abundance estimates, $g(0)$ needs to be estimated. The benefit of using a dual visual-acoustic platform is to quantify the proportion of missed events to estimate $g(0)$ and thus to correctly

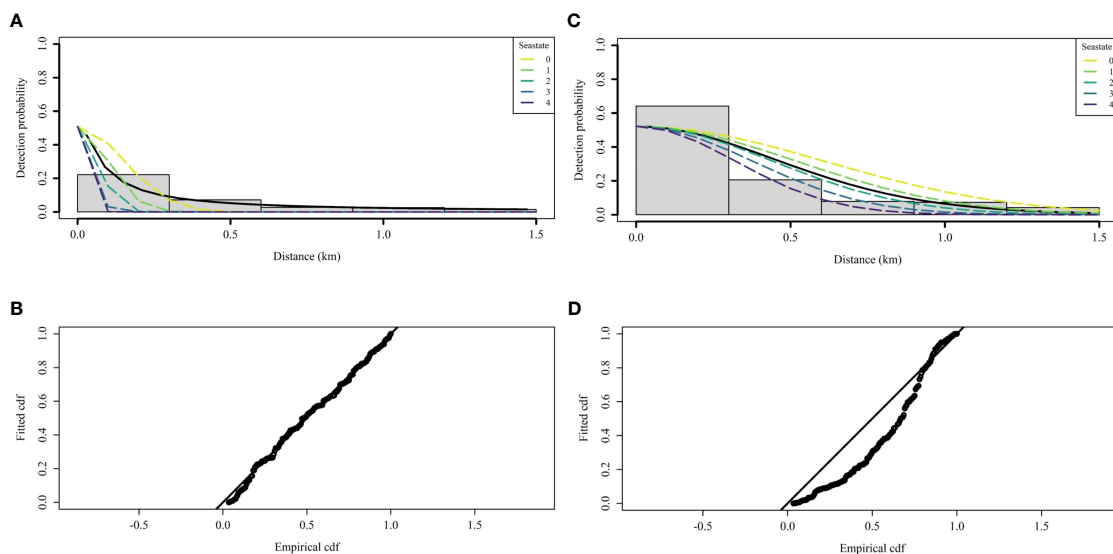


FIGURE 6
Fitted detection function of the best model with a hazard-rate key function (A) with the associated goodness of fit (B) and with a half-normal key function (C) with the associated goodness of fit (D). The selected model is a point-independence model with an MR submodel including the covariate platform and a DS submodel including the covariate sea state. Each line represents the fitted detection function for each class of the sea state covariate.

TABLE 3 Coefficients and standard errors estimated in the PI model with a hazard-rate key function (HR) and a half-normal key function (HN).

| | Coefficients (HR) | SE (HR) | Coefficients (HN) | SE (HN) |
|------------------------|-------------------|---------|-------------------|---------|
| MR submodel | | | | |
| Intercept | -0.34 | 0.32 | -0.34 | 0.32 |
| Perpendicular distance | -1.11 | 0.72 | -1.11 | 0.72 |
| Swell Height | -0.49 | 0.30 | -0.45 | 0.30 |
| Visual platform | -0.14 | 0.17 | -0.14 | 0.17 |
| DS submodel | | | | |
| Intercept | -1.47 | 0.44 | -0.34 | 0.12 |
| Sea state | -0.42 | 0.16 | -0.16 | 0.04 |

A PI model includes an MR submodel which estimates the $g(0)$ and a DS submodel which estimates the shape of the detection function. SE: standard error.

calculate the detection probability. To do so, we first developed a method to identify duplicate events by taking the movements of the vessel and of the animal(s) into account. Then, we estimated the detection probability through an MRDS analysis by including covariates that can affect the detection.

4.1 Methodological considerations

4.1.1 Responsive movement

Performing distance sampling analysis assumes that animals are moving slower than the speed of the survey platform and are detected before any responsive movement related to the presence of the vessel, which requires detecting animals ahead of the vessel (Buckland et al., 2001). The effect of responsive movement on the detection function can be corrected by using two independent visual teams on the same vessel where one searches further ahead to detect animals before they respond (Borchers et al., 1998). When the second platform is an acoustic platform, it is more complex to account for responsive

movement since small cetaceans are less easy to track with acoustic methods. For example, when they move away, they no longer face the hydrophone and may be less available for detection. Among the species studied, the three most commonly seen species were striped, common and bottlenose dolphin. These species are known to be attracted to the bow of vessels (Würsig, 2018). To reduce the bias due to responsive movement, we first assumed a minimal attraction or avoidance effect from the boat because the *R/V Song of the Whale* is a quiet research vessel designed for this purpose. Second, the responsive movement was partially taken into account in the identification of the duplicate events by setting a mobility buffer based on an average cetacean routine swimming speed. Field observations during the ASI surveys suggested the use of routine speed was appropriate for assessing responsive movement as animals were rarely observed ‘racing’ towards the research vessel. Additionally, a single distance was required for each duplicate event. The distance selected between the matching visual and acoustic events was chosen according to the first event that was detected. In general, animals were first detected visually in front of the

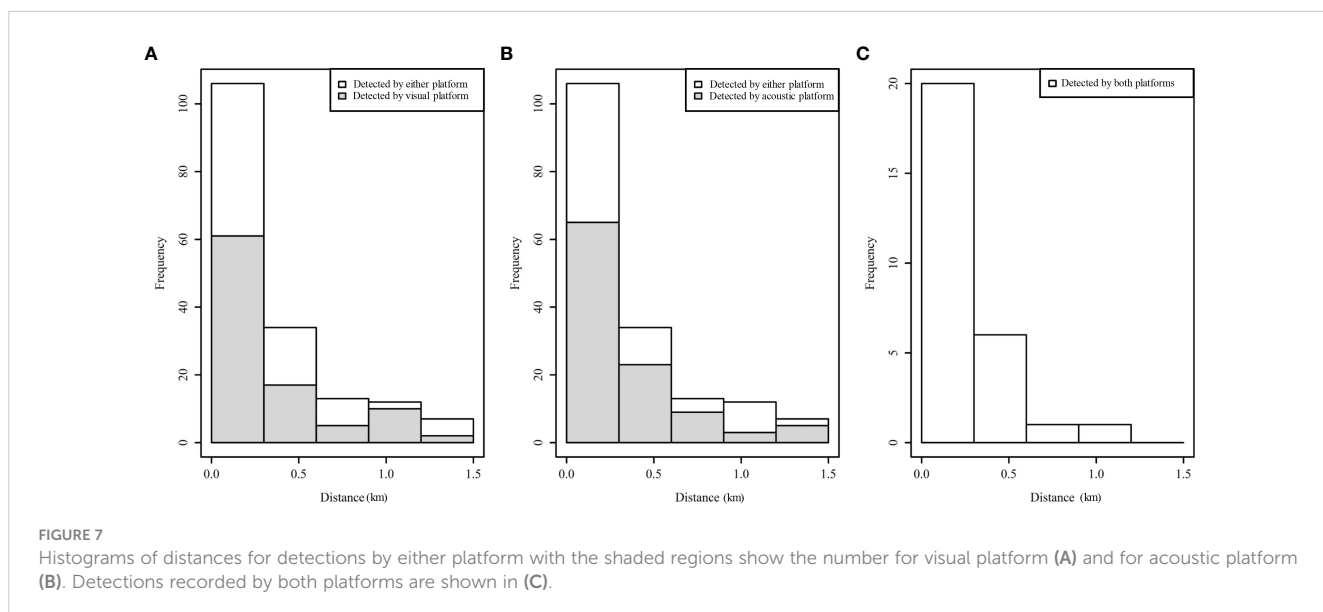


FIGURE 7 Histograms of distances for detections by either platform with the shaded regions show the number for visual platform (A) and for acoustic platform (B). Detections recorded by both platforms are shown in (C).

TABLE 4 Detection probabilities obtained from the MRDS model with a hazard-rate key function (HR) and a half-normal key function (HN).

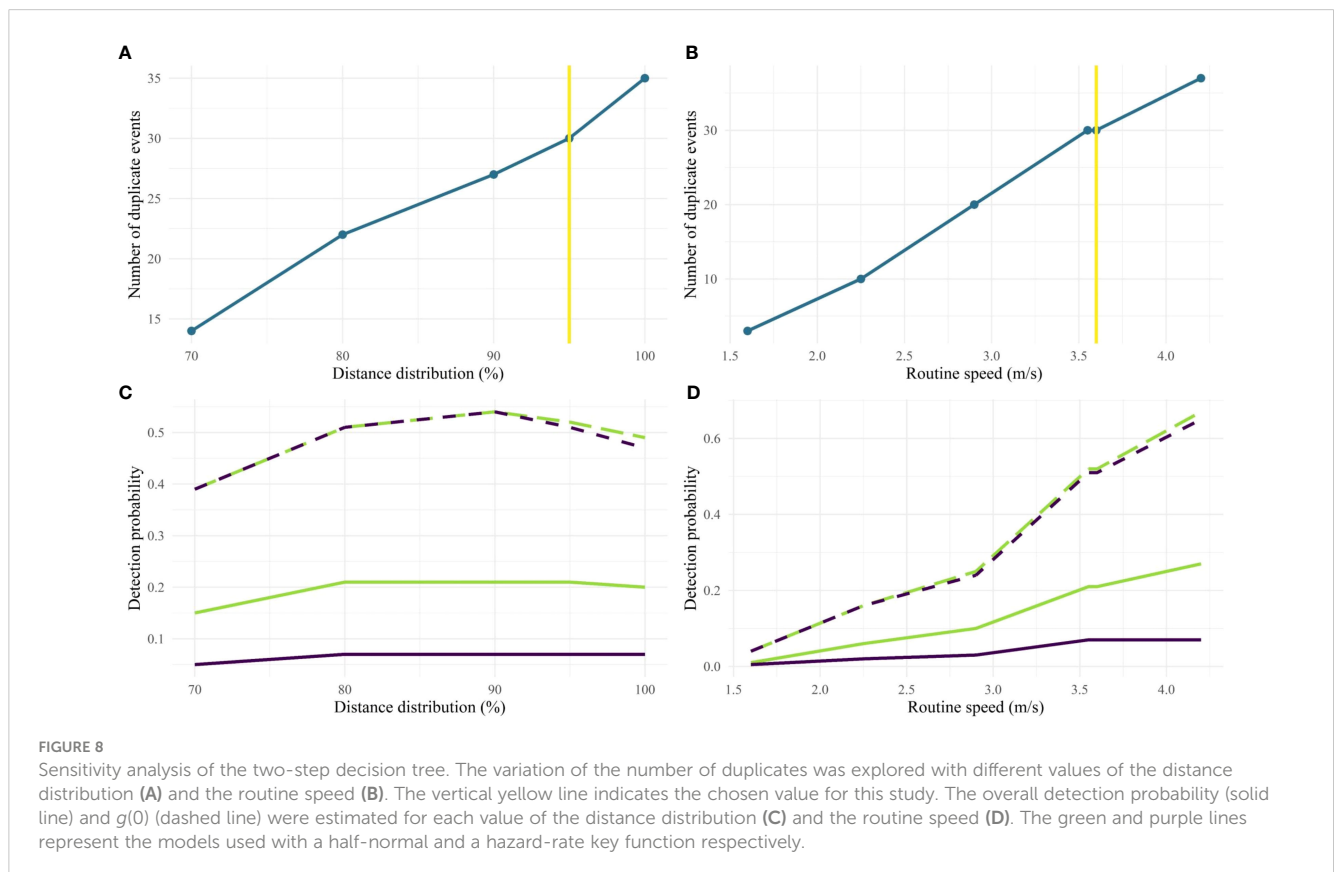
| Probability | Model used | Estimate (HR) | SE (HR) | CV (HR) | Estimate (HN) | SE (HN) | CV (HN) |
|--|-------------|---------------|---------|---------|---------------|---------|---------|
| Probability of detection assuming $g(0) = 1$ | DS submodel | 0.14 | 0.03 | 18.2% | 0.40 | 0.02 | 4.2% |
| $g(0)$ of the visual platform | MR submodel | 0.29 | 0.07 | 25.6% | 0.30 | 0.07 | 23.8% |
| $g(0)$ of the acoustic platform | MR submodel | 0.32 | 0.08 | 25.1% | 0.33 | 0.08 | 23.2% |
| $g(0)$ of combined platforms | MR submodel | 0.51 | 0.11 | 21.7% | 0.52 | 0.10 | 19.8% |
| Overall probability of detection | MRDS model | 0.07 | 0.02 | 28.9% | 0.21 | 0.04 | 20.3% |

The overall detection probability of the MRDS model was obtained by combining the DS submodel and the $g(0)$ of combined platforms from the MR submodel.

boat and then later by the hydrophone towed 400 m behind the boat. By choosing the distance of the first detected event, we minimised the influence of any reactive motion and this partially addressed the responsive movement problem. Martin et al. (2020) assessed responsive movement based on animal orientation and behaviour information based on visual data. They also set the trial configuration (one platform is informed about detections of the other platform) and chose the FI assumption in their model to partially address the responsive movement issue (Laake and Borchers, 2004; Burt et al., 2014). They recommended that responsive movement be properly considered in future vessel-based surveys for abundance assessments. Although responsive movement is difficult to assess and avoid, we believe that taking a mobility buffer into account partially addressed the issue of responsive movement in the MRDS analysis with two independent platforms.

4.1.2 Duplicate events

The number of duplicate events plays an important role in the MRDS analysis when estimating detection probability (Evans and Hammond, 2004; Hamilton et al., 2018). Classifying unique events as duplicates will lead to an underestimation of the detection probability. In the opposite way, classifying duplicate events as unique events would result in an overestimation of the detection probability (Evans and Hammond, 2004). In the present study, only 16% of the total events were confirmed duplicates, while in other studies, they represent more than 30% of total events (35%, Dalpaz et al., 2021; 30%, Rankin et al., 2020; 48%, Richman et al., 2014). We tested the decision tree with different values of the distance distribution in the first step and the routine speed in the second step. The distance distribution was based on the data and was not an arbitrary threshold. Changing the value of the distribution did not



have a great impact on detection probabilities, particularly from 80% to 100%, and this can be explained by the truncation distance value set at 1,500 m. As for the routine speed chosen from values between 1.6 and 4.2 m/s (3.1 and 8.2 knots) found in the literature, it was an arbitrary threshold. The effect of varying this speed on detection probabilities was not negligible: the higher the routine speed, the higher the number of duplicate events and detection probabilities. By choosing the 95% quantile of the swimming speed distribution, i.e. 3.6 m/s (7 knots), we lost 7 duplicate events, which was not insignificant. The choice of a higher speed would probably correspond to an attraction or repulsion movement relative to the vessel, but we were unable to determine whether the animals detected were being attracted or repelled or not. It seemed more appropriate to consider a routine swimming speed, with the aim of including all motivational states, including travelling, socialising, resting and foraging. Our number of duplicate events seemed low compared to other studies, but the approach used to identify duplicates was different from that of other studies. Dalpaz et al. (2021) used a decision tree based on three criteria: (1) less than 30 min between events, (2) less than 6 km between events and (3) taxonomic compatibility between detections of Delphinidae and Ziphiidae. Rankin et al. (2020) identified visual and acoustic detections of rough-toothed dolphins as duplicates when both detections occurred in a close range. However, the authors did not explain in detail how they matched the detections and how “close” was defined. Richman et al. (2014) studied detectability of Ganges River dolphins and used a distance threshold between a visual and an acoustic detection to identify duplicates. They found the value of the distance threshold based on visual inspection of the frequency distribution of number of matched detections over distance; which was 249 m for a single animal and 349 m for a group of more than one animal. In open ocean habitats, such as in our study, hydrophones are towed as far back as possible to avoid self-boat noise. The delay between a visual sighting from in front of the vessel and the subsequent detection of the animal by the hydrophone to the rear of the vessel can be relatively long. As small cetaceans are highly mobile species, it is necessary to take their movement into account during this time. Although routine speed remains a sensitive parameter for the decision tree, the application of the mobility buffer still reduced the number of duplicate events identified by the time buffer by half, which can be considered very restrictive. However, it allowed to identify with more certainty the potentially true duplicate events, reducing the risk of false duplicates.

4.2 Detectability of small cetaceans

4.2.1 Detection process

During the survey and the analytical stage, a consistent protocol was implemented to define distinct events. However, the performance of the models tested was not perfect, as either the goodness of fit was good but the model did not seem to fit the data, or the opposite was observed. The detection function using the HR key function was unable to accurately describe the data observed close to the transect line due to a poor fit at low perpendicular distances. This indicates a possible problem associated with the

detection process. Accurate distance estimation can be an issue in visual surveys (Marques et al., 2006). In this study, radial distances were estimated by naked eyes without tools, which may bias perpendicular distance estimates. For a small vessel with a low platform like the *R/V Song of the Whale*, the use of reticule binoculars or photogrammetry is complex (Leaper et al., 2023). Observers during the ASI survey had varying levels of field experience and identification skills. Thus, using the photogrammetry or reticules might have been counter-productive if being used by novice observers. Laser rangefinders can be a useful tool but only under optimal sea state conditions to avoid waves interfering with the laser and/or the motion of the vessel making reliable range-finding challenging. All of these methods would also result in a biased distance estimate. With distance estimation training conducted prior to the survey, naked eye measurements appeared to be the best approach in these conditions.

4.2.2 Group size estimation

During a survey, detectability between individuals may vary for multiple reasons; some animals may surface/vocalize more than others, or some may be more detectable in specific habitats such as shallow or deep waters. Due to this variability, each individual, species or population should have its own detection probability. However, some variables that influence the detection probability cannot be observed, which corresponds to unmodelled heterogeneity and therefore does not allow a reliable estimation of detection probability and abundance (Buckland et al., 2004; Buckland et al., 2015). The first source of unmodelled heterogeneity could be related to group size estimation. Estimating group size is complex in visual and even more so in acoustic studies because animals are moving and an unknown fraction of the group might be underwater or silent at any given time (Gerrodette et al., 2019). In visual surveys, estimating the group size of a large school of active dolphins is a difficult task and the estimates can vary considerably between observers (Gerrodette et al., 2002). The average group size was estimated to be 10 individuals in this study, which was consistent with other studies averaging between 4 and 30 individuals (Notarbartolo di Sciarra et al., 1993; Bearzi et al., 2003; Cañadas and Hammond, 2008; Boisseau et al., 2010; Notarbartolo di Sciarra and Tonay, 2021) in the Mediterranean, although larger aggregations are known (Watkins et al., 1987; Boisseau et al., 2010; Notarbartolo di Sciarra and Tonay, 2021). In acoustic surveys, group size cannot be estimated directly during surveys and most studies use visual events to determine group size of the acoustic events (Barlow & Taylor, 2005; Pirota et al., 2015). Another approach is to use cue counting to estimate the density of cues that animals produce, such as calls, that can be converted into animal density using the cue production rate of the species (Marques et al., 2009). In our study, we used overlapping clicks trains as an indicator of the number of acoustically active individuals in the group and to estimate the acoustic group size for each event, following Thomas and Marques (2012). With our methodology, the estimated visual group size was approximately three times higher than the acoustic group size. Such a discrepancy between the visual and acoustic group size suggests that the latter was underestimated. The first assumption suggests that our recordings may have captured only a subset of the group, namely those animals

that were echolocating. The second assumption is that we counted individuals moving from the front of the boat to the back, and that all the animals in a group were probably not moving in the same way toward the hydrophone, so that only part of the group was detected and counted, the others having moved away or not in the direction of the hydrophone. The third assumption is a mixture of the two, implying that disentangling availability bias and perception bias from the acoustic method is difficult. Due to probably incorrect estimates of the acoustic group size, we did not include this covariate in the model and the remaining unmodelled heterogeneity can lead to a potential overestimation of the detection probability (Borchers et al., 2006; Burt et al., 2014). With further studies of vocalization rates, it may be possible to scale up the underestimation of acoustic group size, but currently we do not have enough meaningful data on vocal rates for small odontocetes in the Mediterranean Sea.

4.2.3 Pooling species

Pooling species with different behaviours may be another source of unmodelled heterogeneity in detection probability. Indeed, small cetaceans show different group sizes, dive durations, vocalization rates or preferred habitats. For example, the three most observed species in the Mediterranean Sea are distributed differently. The bottlenose dolphin mostly lives on the continental shelf (Bearzi et al., 2009; Cañadas et al., in review), while the striped dolphin is an oceanic species that is usually found in open waters (Cañadas et al., in review; Notarbartolo di Sciara and Tonay, 2021). The common dolphin can be observed in both inshore and offshore waters (Bearzi et al., 2003). By grouping species together, the variation in species occurrence and distribution within a study area would not be significant if the detectability across species were equal. In acoustic studies, the common spectral features of the studied species and the characteristics of clicks (i.e. directionality, high-frequency) contribute to click variability and complexity in classification. Although ongoing research opens avenues for improved classification (Oswald et al., 2003; Soldevilla et al., 2008; Bittle and Duncan, 2013; Pedersen et al., 2021), species identification from echolocation clicks remains limited and we had to pool the different species. By grouping all species together, a single detection function was fitted for species. However, the striped dolphin is a dominant species in the Mediterranean, where our study detected over 63% and Panigada et al., (in review) detected over 85% in an aerial line-transect survey. Pooling species is a common practice in aerial line-transect survey where some species were merged (striped dolphin/common dolphin; ACCOBAMS, 2021). As striped dolphins were highly dominant in the study area, the problem of pooling species would be reduced.

4.3 Comparison of $g(0)$ estimation with other studies

Despite the main limitations of this study, our results were statistically accurate, as shown by reasonably low CVs (20–27%),

and were consistent with other studies, especially for the visual platform. Rankin et al. (2020) estimated $g(0)$ at 0.37 and 0.77 for the visual and acoustic platforms respectively and 0.84 with the combined platforms for rough-toothed dolphins. The $g(0)$ for the visual platform was similar to our results (0.29, CV = 25.7% and 0.30, CV = 23.8%). For acoustics, our results were lower (0.32, CV = 25.1% and 0.33, CV = 23.2%) but Rankin et al. (2020) also included other vocalizations such as whistles and burst-pulses (Rankin et al., 2020), which resulted in a higher number of acoustic events and thus a higher estimate of $g(0)$. Additionally, echolocation clicks are highly directional and therefore if the animals are too far away or off-axis of the hydrophone, the detection probability decreases sharply (Au et al., 2012; Finneran et al., 2014), which could partly explain the low estimate of $g(0)$ from the acoustic platform in our study. Although the appropriate data are lacking for the Mediterranean, it is possible that small odontocetes are more vocal when submerged, as is typically the case for larger odontocete species including sperm whale and Cuvier's beaked whale (Akamatsu et al., 2001). This situation would preclude exact duplicates to occur. However, since dolphins can switch between the two conditions in a matter of a few seconds, and the time window for potential duplicates was within 271 s before and 1,179 s after the visual event, this left ample time for duplicates to be recorded if the individual was acoustically active during this time interval. Therefore, these methods appeared to be complementary and, as expected, we obtained a higher detection probability by combining both platforms (Laake et al., 2011; Rankin et al., 2020).

4.4 Implication for cetacean conservation

In this study, we highlight the importance of using a visual-acoustic dual platform in multispecies line transect surveys to estimate the detection probabilities of small cetaceans with consideration of detection biases, which have a major effect on the detection probability estimates. While recognising that most cetacean conservation programs use minimal abundance estimates (Evans and Hammond, 2004), we emphasise an unbiased abundance estimate to provide a better approach to assessing the sustainability of cetaceans in the face of anthropogenic mortalities. Based on our estimates of $g(0)$ and p , if we were to estimate cetacean abundance in the Mediterranean Sea without correcting for detection biases, this would be underestimated by a factor of two when using both acoustic and visual data for either model (HR and HN key functions). In order to estimate the abundance of small cetaceans from the ASI vessel survey, it would be necessary to consider all transects, i.e. acoustic, visual and combined transects to ensure uniform coverage. A homogeneous distribution of dual platform effort over the study area would be recommended to avoid spatial bias (over-representation of a habitat or species) which could then affect the $g(0)$ estimate. Further research is needed to estimate small cetacean abundance from a visual-acoustic dual platform in the Mediterranean Basin.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary Material](#). Further inquiries can be directed to the corresponding author.

Author contributions

The present work was designed by CO, AV and VR. OB provided the data. CO and IS developed the decision tree and conducted the analyses. CO wrote the manuscript. All revisions were done by OB, VR and AV. All authors contributed to the article and approved the submitted version.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2023.1244474/full#supplementary-material>

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B

Double-platform survey effort

Table B.1: Simultaneous visual and acoustic survey effort of the *R/V Song of the Whale* during the ASI survey.

| Survey block | Number of transects surveyed | Total length of surveyed transects in km | Mean survey speed in m/s (knots) |
|--------------|------------------------------|--|----------------------------------|
| 01 | 3 | 362 | 3.2 (6.2) |
| 02 | 3 | 189 | 3.3 (6.4) |
| 03 | 11 | 906 | 2.7 (5.2) |
| 04 | 5 | 307 | 3.4 (6.6) |
| 05 | 4 | 295 | 2.9 (5.6) |
| 06 | 3 | 302 | 3.9 (7.6) |
| 07 | 5 | 524 | 3.2 (6.2) |
| 08a | 1 | 42 | 3.9 (7.6) |
| 08b | 2 | 131 | 2.4 (4.7) |
| 09 | 3 | 82 | 3.2 (6.2) |
| 10 | 2 | 160 | 3.2 (6.2) |
| 11 | 3 | 232 | 3.1 (6.0) |
| 12 | 2 | 183 | 3.7 (7.2) |
| 13 | 4 | 341 | 3.0 (5.8) |
| 14 | 6 | 391 | 3.2 (6.2) |
| 15 | 4 | 350 | 3.3 (6.4) |
| 22c | 6 | 453 | 3.0 (5.8) |
| 22e | 4 | 137 | 2.9 (5.6) |
| 22w | 3 | 80 | 3.6 (7.0) |
| 25 | 4 | 251 | 2.8 (5.4) |
| 26 | 11 | 961 | 2.7 (5.2) |
| Total | 88 | 6679 | 3.2 (6.2) |

C

Sensitivity analysis of the decision tree for duplicate events identification

C. Sensitivity analysis of the decision tree for duplicate events identification

Table C.1: Sensitivity analysis of the first step of the decision tree with the effect on the overall detection probability p and $g(0)$ estimates. The value chosen was 95%.

| Distance distribution (%) | Number of duplicate events | $g(0)$ (HN) | p (HN) | $g(0)$ combined (HR) | p (HR) | Covariates |
|---------------------------|----------------------------|----------------------|----------------------|----------------------|----------------------|---|
| 70 | 14 | 0.39 (CV = 24.4%) | 0.15 (CV = 24.7%) | 0.3 (CV = 24.4%) | 0.05 (CV = 29.2%) | MR submodel: Perpendicular distance + Observer DS submodel: Sea State |
| 80 | 22 | 0.51 (CV = 16.9%) | 0.20 (CV = 17.4%) | 0.51 (CV = 16.9%) | 0.07 (CV = 24.4%) | MR submodel: Perpendicular distance e + Observer DS submodel: Sea State |
| 90 | 27 | 0.54 (CV = 15.2%) | 0.21 (CV = 15.8%) | 0.54 (CV = 15.2%) | 0.07 (CV = 23.2%) | MR submodel: Perpendicular distance + Observer DS submodel: Sea State |
| 95 | 30 | 0.52 (CV = 19.8%) | 0.21 (CV = 20.3%) | 0.51 (CV = 21.7%) | 0.07 (CV = 28.9%) | MR submodel: Perpendicular distance + Observer + Swell Height DS submodel: Sea State |
| 100 | 35 | 0.49 (CV = 29.8%) | 0.20 (CV = 30.2%) | 0.47 (CV = 34.8%) | 0.07 (CV = 40.5%) | MR submodel: Perpendicular distance + Observer + Wave Height DS submodel: Sea State |

Table C.2: Sensitivity analysis of the second step of the decision tree with the effect on the overall detection probability p and $g(0)$ estimates. The value chosen was 3.60 m/S

| Routine Speed in m/s (knots) | Number of duplicate events | $g(0)$ combined (HN) | p (HN) | $g(0)$ combined (HR) | p (HR) | Covariates |
|---------------------------------|-------------------------------|-------------------------|----------------------|-------------------------|-----------------------|---|
| 1.60 (3.11) | 3 | 0.04 (CV = 69.0%) | 0.01 (CV = 69.1%) | 0.04 (CV = 69.0%) | 0.005 (CV = 70.6%) | MR submodel: Observer DS submodel: Sea State |
| 2.25 (4.37) | 10 | 0.16 (CV = 29.8%) | 0.06 (CV = 30.0%) | 0.16 (CV = 29.8%) | 0.02 (CV = 33.3%) | MR submodel: Observer DS submodel: Sea State |
| 2.90 (5.64) | 20 | 0.25 (CV = 63.6%) | 0.10 (CV = 62.8%) | 0.24 (CV = 66.4%) | 0.03 (CV = 69.0%) | MR submodel: Perpendicular distance + Observer + Swell Height DS submodel: Sea State |
| 3.55 (6.90) | 30 | 0.52 (CV = 20.0%) | 0.21 (CV = 20.2%) | 0.51 (CV = 21.5%) | 0.07 (CV = 29.0%) | MR submodel: Perpendicular distance + Observer + Swell Height DS submodel: Sea State |
| 3.60 (7.00) | 30 | 0.52 (CV = 19.8%) | 0.21 (CV = 20.3%) | 0.51 (CV = 21.7%) | 0.07 (CV = 28.9%) | MR submodel: Perpendicular distance + Observer + Swell Height DS submodel: Sea State |
| 4.20 (8.16) | 37 | 0.67 (CV = 14.0%) | 0.67 (CV = 14.0%) | 0.65 (CV = 16.3%) | 0.07 (CV = 29.3%) | MR submodel: Perpendicular distance + Observer + Swell Height DS submodel: Sea State |

D

Article - Temporal patterns in dolphin foraging activity in the Mediterranean Sea: insights from vocalisations recorded duringt the ACCOBAMS Survey Initiative



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Temporal patterns in dolphin foraging activity in the Mediterranean Sea: insights from vocalisations recorded during the ACCOBAMS Survey Initiative

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Marine organisms continually adapt their physiology and behaviour to temporal variations in their environment, resulting in diurnal rhythmic behaviour, particularly when foraging. In delphinids, these rhythms can be studied by recording echolocation clicks, which can provide indicators of foraging activity. The foraging rhythms of delphinids and their relationship to temporal parameters are poorly documented and most studies so far have used moored passive acoustic systems. The present study provides, for the first time, information on the activity rhythms of delphinids investigated in relation with temporal variables at a basin scale from a moving platform, in the western and central Mediterranean Sea. We used passive acoustic recordings collected by hydrophones towed along transect lines during the ACCOBAMS Survey Initiative in the summer 2018. We extracted variables that may influence daily and monthly rhythms, including time of day, lunar cycle, lunar illumination and sea state and fitted generalised additive models. The nycthemeral and lunar cycles were the two main factors influencing dolphin activity rhythms. Echolocation activity was predominant at night, with a maximum of 0.026 acoustic events per minute at 21:00/22:00 compared to as few as 0.0007 events per minute at 11:00. These events were also more frequent during the third quarter of the moon; 0.033 acoustic events on day 22 of the lunar cycle as opposed to 0.0008 on day 8 of the lunar cycle, corresponding to the first quarter of the moon. Variations in the echolocation activity of delphinids in the Mediterranean Sea could reflect variation in their foraging effort and be related to prey density, composition, accessibility and catchability within dolphin foraging depth range. These results should also improve interpretation of passive acoustic monitoring data.

KEYWORDS

foraging activity rhythms, Generalised Additive Models (GAMs), delphinids, echolocation clicks, Mediterranean Sea

1 Introduction

Marine animals live in habitats that are subject to temporal variations that can be seasonal, lunar or daily and that shape the adaptive strategies of each species (Häfker et al., 2023). Species adapt their physiology and behaviour to these environmental fluctuations and associated rhythms (Pirota et al., 2020). These adaptations result in biological activity being in phase with the main natural cycles, which are governed by the Earth's orbit around the Sun (seasons), the Moon's orbit around the Earth (tides) and the Earth's rotation (nycthemeron). Biological rhythms are controlled by endogenous systems, some of which are light sensitive. Changes in light levels can trigger physiological or behavioural responses (Simonis et al., 2017). Therefore, the nycthemeral cycle can be the source of daily changes and adaptations, although the exact nature of these rhythms also depends on other factors such as habitat type, coordinates, and physicochemical properties (Häfker et al., 2023). The aggregation of marine predators for feeding has been shown to be associated with primary production, bathymetry, and sea surface temperature (Hastie et al., 2004; Prieto et al., 2017; Scales et al., 2016).

The best known example of a biological rhythm in the pelagic environment is the Diel Vertical Migration (DVM) of the Deep Scattering Layer (DSL), composed mainly of planktonic and micronectonic organisms such as a variety of crustaceans (euphausiids, mysids, copepods), fish (e.g., myctophids) or cephalopods (e.g., histioteuthids) which generally migrate towards the surface layer at dusk and return to the depths at dawn (Wang et al., 2019). According to Marohn et al. (2021), this phenomenon would reflect a balance between meeting food requirements and avoiding predators. The most plausible hypothesis is that the vertical migrations of marine organisms at the base of the food web lead to similar rhythms in their mesopelagic and epipelagic predators, such as number of fish, squid and sharks (Häfker et al., 2023) which forage when their prey is most efficiently exploited. Similarly, air-breathing diving top predators such as cetaceans, that feed on these meso- and epipelagic species, would develop a strategy in which the optimal decision about where and when to feed would allow them to maximise their energy intake, especially as these predators must hold their breath during dives to access resources (Miller et al., 2010). The challenge for these marine mammals is to find the best compromise between breathing at the surface and feeding at depth. To achieve this, they are likely to adapt their feeding rhythms to the dynamics, availability, or catchability of their prey (Giorli et al., 2016).

In pelagic ecosystems, cetacean activity tends to be nocturnal, with an increase in activity in the evening, followed by a peak at night and a decrease in the early morning (Linnenschmidt et al., 2013). This pattern likely occurs due to the greater availability of prey closer to the sea surface at night. Furthermore, in demersal ecosystems, cetaceans that prey on bottom-dwelling fish, many of which are not particularly active at night, may exhibit different diel activity patterns (Brandt et al., 2014). In the Mediterranean Sea, where neritic habitats are quite limited, Giorli et al. (2016) highlighted that several typically offshore dwelling cetaceans (Risso's dolphin *Grampus griseus*, long-finned pilot whale

Globicephala melas, Cuvier's beaked whale *Ziphius cavirostris*, and sperm whale *Physeter macrocephalus*) exhibited mostly nocturnal foraging activity. Similarly, Caruso et al. (2017) studied several delphinids (striped dolphin *Stenella coeruleoalba*, bottlenose dolphin *Tursiops truncatus*, common dolphin *Delphinus delphis*, Risso's dolphin and long-finned pilot whale) in the Ionian Sea and found a daily pattern in foraging activity, with greater activity at night. The explanatory hypothesis put forward in these two studies is that the foraging behaviour of odontocetes would be dictated by the presence and dynamics of their prey, which are more active and putatively easier to capture at night.

There are several approaches to study cetacean activity rhythms. Longitudinal approaches (e.g., biologging techniques and focal tracking) have the advantage of following the activity of known individuals over time (Brauer et al., 2022), although they can be very time-consuming to implement and, in the case of visual tracking, are typically dependent on good weather and daylight conditions. Cross-sectional approaches sample activity data across a population as a function of time, for example during acoustic or visual surveys. They provide rapid results that reflect the general characteristics of a population. However, individual variability is not measurable (Brauer et al., 2022). The distribution, dynamics and activity rhythms of vocalising cetaceans can be studied using this second method, thanks to acoustic surveys (Barlow et al., 2021). Here we used a cross-sectional approach to investigate delphinid foraging activity using a large-scale acoustic line-transect survey.

Sound emission is common to all cetaceans, which have developed highly sophisticated sound production systems. Sound plays an important role in their daily lives, being used for communication, socialisation, navigation, and predation (Hildebrand, 2009). Vocalisations are also used to compensate for poor visibility conditions such as night, depth and turbidity, and are a critical component of the evolutionary success of odontocetes in general (Au, 1993). Odontocetes emit different types of acoustic signals, sometimes near the surface, sometimes at depth (Gillespie et al., 2009), which can travel long distances (probably tens of kilometres in some whale species, Bittle and Duncan, 2013). Acoustic signals emitted by odontocetes can be classified into three categories: tonal signals (or whistles), pulsed calls and echolocation clicks (Azzolin et al., 2014). Whistles and certain pulsed calls are long and complex sounds with intermediate frequencies (often below 10 kHz, González-Hernández et al., 2017), modulated and with a narrow bandwidth. They mainly provide information about the identity of a species, population or individual, as well as on the physiological and behavioural state of the emitter. These signals are essential for maintaining organisation and cohesion within social groups (Azzolin et al., 2014). Clicks, emitted in series (known as click trains), and certain pulsed calls, are short, repetitive sounds that cover a wide range of frequencies (from 20 kHz to over 100 kHz, González-Hernández et al., 2017). They are used for foraging, navigating and detection of predators (Au, 2018). Foraging involves all the activities required to reach, locate, detect and capture prey, with searching generally being the most time-consuming activity and this includes echolocation, which is becoming more important for both navigation and prey detection (Madsen and Wahlberg, 2007; Giorli et al., 2016). As clicks allow the

detection of prey in the environment, they are considered to be the most relevant acoustic indicator of foraging activity (Caruso et al., 2017). In this context, we assumed that temporal pattern in foraging activity would strongly affect click production rate. In addition, clicks are the most abundant type of sound emitted, and therefore would provide a larger sample size than the other types of vocalisations. Studying them can therefore help our understanding of how cetacean foraging activity changes over time.

The Mediterranean Sea is home to 7% of the world's marine biodiversity, of which around a fifth is considered endemic (Pace et al., 2015). Eleven cetacean species are known to permanently occur in the Mediterranean Sea and are regularly observed in the basin: the bottlenose dolphin, the striped dolphin, the common dolphin, the Risso's dolphin, the rough-toothed dolphin *Steno bredanensis*, the long-finned pilot whale, the Cuvier's beaked whale, the sperm whale, the fin whale *Balaenoptera physalus*, the orca, *Orcinus orca* and the Black Sea harbour porpoise *Phocoena phocoena relicta*, which is present in the northern Aegean Sea (Cucknell et al., 2016; Notarbartolo di Sciara and Tonay, 2021). The false killer whale *Pseudorca crassidens*, the minke whale *Balaenoptera acutorostrata*, and the humpback whale *Megaptera novaeangliae* are occasional visitors (Notarbartolo di Sciara and Tonay, 2021).

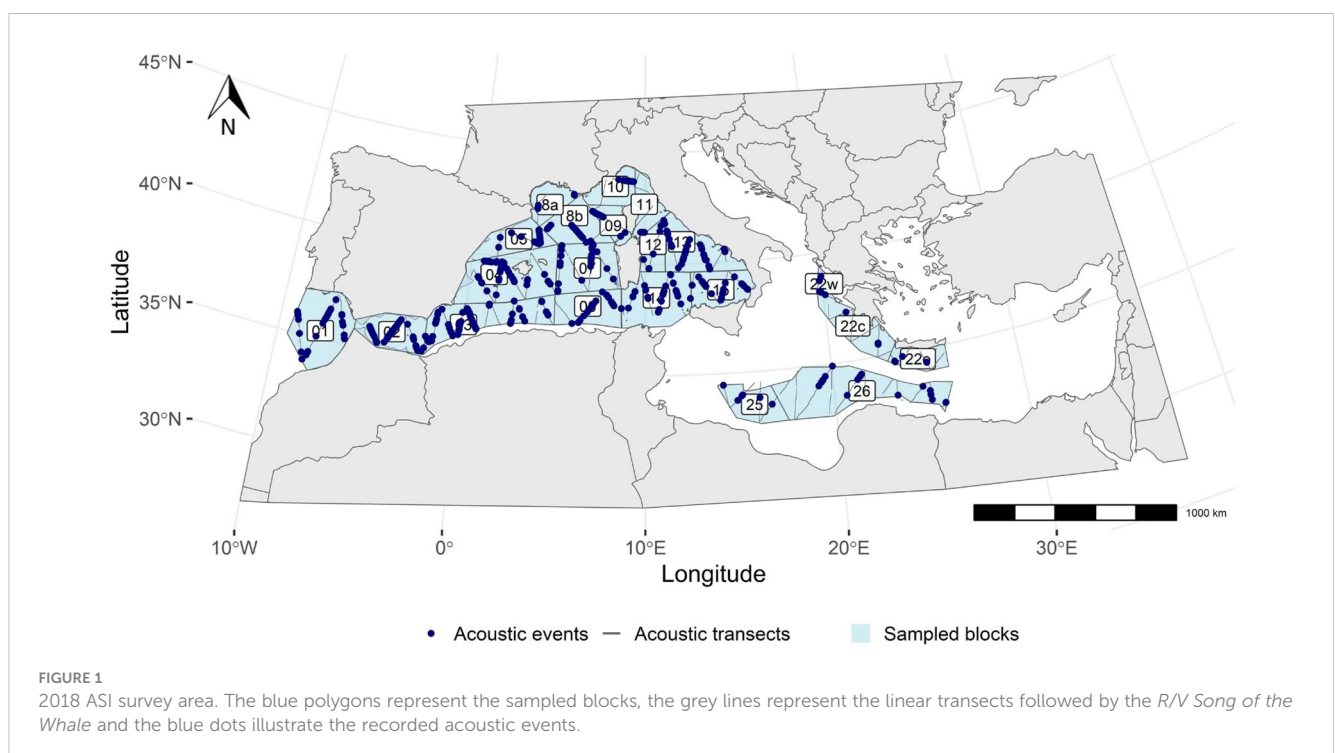
The main objective of this study was to analyse the rhythm of foraging activity of Mediterranean pelagic delphinids of which the striped, common and bottlenose dolphins are the most abundant (Panigada et al., 2024). Most previous studies of delphinid foraging rhythms in the Mediterranean Sea have used fixed acoustic devices within limited geographic areas (Giorli et al., 2016; Cascão et al., 2020). Here we used acoustic recordings provided by the Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and contiguous Atlantic area (ACCOBAMS) and collected during the vessel component of the basin-wide 2018 ACCOBAMS Survey Initiative

(ASI), which aimed to assess cetacean abundance and distribution in the Mediterranean Sea. Acoustic recordings were collected day and night using towed hydrophones along predetermined transect lines. Only echolocation clicks were analysed, as they are the most relevant signals to study the foraging activity. Diel rhythms in the number of acoustic events were investigated, as well as their relationship with a selection of temporal parameters. We hypothesised that a strong diel pattern would prevail, with more acoustic events during the night. We first extracted click emissions from acoustic recordings. The number of acoustic events per unit of time was then modelled in a generalised additive model (GAM) framework using a selection of temporal variables thought to be involved in the foraging strategies of delphinids.

2 Materials and methods

2.1 Study area

The study area covered the entire Mediterranean basin, from 34°S to 45°N and from 6°W to 17°E (Figure 1). The Mediterranean Sea is a semi-enclosed mid-latitude sea virtually isolated from the main oceanic systems, stretching east-west over about 3,800 kilometres. The general circulation of the Mediterranean Sea is cyclonic, with Atlantic surface waters flowing along the southern shores of the basin and returning along the northern shores, whose complexity generates many eddies. Winter cooling of the surface waters in the north of the basin is responsible for the formation of rich, deep waters that flow towards the Atlantic Ocean (Robinson et al., 2001; Millot and Taupier-Letage, 2005). Although the Mediterranean Sea is generally considered to range from oligotrophic to ultra-oligotrophic, it is characterised by significant spatial variability in primary productivity, with decreasing



productivity observed from west to east (Lazzari et al., 2012). Geomorphological features such as canyons, seamounts and deep trenches also provide a variety of unique habitats (Aissi et al., 2015) resulting in highly diverse and rich ecosystems.

2.2 Data collection

The acoustic data used in this study were collected from May to September 2018 during the ASI survey, during which two types of platforms were used to collect cetacean data; aircraft conducted visual detection only, and vessels supplemented the visual observations collected by the aerial component with acoustic data, particularly for deep-diving sperm whales and Cuvier's beaked whales (Boisseau et al., 2024; Panigada et al., 2024). In this study, we focused only on acoustic data from delphinids collected aboard the *R/V Song of the Whale*. Overall, the visual data collected from the boat indicated that delphinids were represented by three main species: the striped, the common and the bottlenose dolphins. Risso's dolphin, long-finned pilot whale and rough-toothed dolphin were also present, although less frequently.

The acoustic survey was conducted continuously (24 hours per day) wherever permitted by the riparian states, except where weather conditions, water depth (minimum 50 m) or technical constraints did not allow it. It focused on the Atlantic region near the Strait of Gibraltar, the western Mediterranean basin from the Alborán Sea to the Tyrrhenian Sea, and parts of the central Mediterranean basin (the Ionian waters and the Hellenic Trench; Figure 1). No survey effort was allocated in the Aegean Sea. The study area was divided into 21 blocks, designed to estimate cetacean abundance (ACCOBAMS, 2021).

Sampling was carried out along linear transects, and the hydrophone array was towed 400 m behind the vessel. This sampling method was used to maximise the coverage of the study area and to provide a robust estimate of species density and abundance (Buckland et al., 2004). Transects were defined using the Distance software (version 7.3, ACCOBAMS, 2021) and a zig-zag pattern was used to achieve equal probability coverage. A total of 17,271 km of transects were travelled, representing approximately 74,000 minutes of effort. This total sampling effort was divided into one-minute duration segments. The vessel speed was maintained between 5 and 8 knots to minimise bias due to species movement. The hydrophone array was housed in an oil-filled tube and consisted of two pairs of hydrophones in a linear configuration. The pair of broadband hydrophones, spaced 0.25 m apart, recorded sounds from 1 to 100 kHz with a sensitivity of -204 dB re 1V/μPa, in the frequency band in which most odontocete vocalisations are produced. The outputs of the broadband hydrophones were digitised at a sampling rate of 192 kHz. The audio recordings were stored in 16-bit wav files.

2.3 Acoustic data analysis

Field recordings were compressed into binary storage files using PAMGuard (version 2.2.7.0, Gillespie et al., 2008). These files were manually analysed using the 'click detector' module, which allows

the user to identify acoustic events, following the methodology of Ollier et al. (2023). Only click series, defined as sequences of clicks produced by the same animal or group of animals that exhibited a consistent change in bearing (*i.e.*, from the bow to the stern of the vessel) were examined. Sequences of clicks that did not show a consistent bearing trajectory or did not cross the 90° line were not considered as acoustic events. To ensure that the series of echolocation clicks identified were indeed from delphinids, the characteristics of the clicks making up the series were examined. The waveform of a click had to cross the horizontal axis several times (known as "zero crossing"). The spectrum of each click should ideally have a frequency peak between 20 kHz and 40 kHz. If this frequency peak was below 10 kHz, it could be a sound signal emitted by a boat (ACCOBAMS, 2021).

2.4 Statistical analysis

2.4.1 Variables

We selected variables relevant to temporal scales ranging from hourly to monthly time resolution such as time of day, lunar cycle, lunar illumination and sea state (Table 1). The time of day of the acoustic events was considered as a circular variable to account for the temporal cyclicity (so that the statistical models considered that 00:00 = 24:00). This improved the accuracy of the model and captured the large cyclical variations in the data. As the study area was relatively large, and to avoid any time zone bias, the times at which these acoustic events were detected, given in Coordinated Universal Time (UTC), were converted to solar time (Waugh, 1973) by using the equation:

$$\text{Solar Time} = 4(\text{longitude}) + \text{Coordinated Universal Time}$$

The longitude in the equation is expressed in decimal degrees. The value 4 represents minutes and comes from the fact that the Earth rotates in 24 hours (= 1440 minutes), *i.e.* one degree of rotation every 4 minutes. Depending on whether the longitude is positive or negative (whether the acoustic event was detected east or west of the Greenwich meridian), the duration in minutes obtained is added to or subtracted from Coordinated Universal Time to obtain Solar Time (Waugh, 1973).

Sea state is expected to affect foraging efficiency on epipelagic prey. It was recorded during the ASI survey according to the Beaufort scale. The lunar cycle and lunar illumination are expected to modulate the extent and intensity of the diel vertical migration of planktonic and micronectonic organisms. The lunar cycle lasts 29.53 days, and during this cycle the moon goes through different phases (Wang et al., 2015): new moon (day 1 of the lunar cycle), first quarter (day 8 of the lunar cycle), full moon (day 15 of the lunar cycle), and last quarter (day 22 of the lunar cycle). The lunar cycle is also a circular variable as the lunar phases change from day to day, completing a cycle at the end of a lunation. The phase of the lunar cycle and the lunar illumination of each day were obtained using the 'lunar' R-package (Lazaridis 2022). To obtain the day of the lunar cycle, the lunar phase was divided by 0.212769 (the lunar phase increases by this value per day for a complete cycle).

TABLE 1 Temporal and spatial variables used in the GAMs that potentially influence the cetacean rhythm activity.

| Variable | Description/ Relevance to the topic | Source | Variable type | Range of values/Units | Resolution |
|--|---|-----------------------------------|---------------|--|----------------------|
| Time of day | Time of acoustic events | PAMGuard analysis | Circular | Hour [0-23] | Temporal |
| Geographical coordinates (Longitude, Latitude) | Environmental parameter - indicator of habitat use | ASI survey | Continue | Degrees | Spatial |
| Sea state | Environmental parameter - indicator of habitat use | ASI survey | Category | Beaufort scale [0-6] | Temporal and spatial |
| Lunar cycle | Influences the vertical migration of organisms (Simonis et al., 2017) | Lunar R-package (Lazaridis, 2022) | Circular | Days [1-29] 1: New moon 15 th : Full moon | Temporal |
| Lunar illumination | Influences the vertical migration of organisms (Simonis et al., 2017) | Lunar R-package (Lazaridis, 2022) | Continue | [0-1] 0: New moon 15 th : Full moon | Temporal |

Beside nocturnal illumination, the lunar cycle also determines tidal range. Although the tide is limited in the Mediterranean Sea it does exist with an amplitude from 0 around the Balearic Islands to 60 cm in the Gulf of Gabès, Tunisia. Tidal range is greater at full and new moon and is minimal at first and last quarters, following a cyclical pattern with a period of approximately 15 days. Recognising the importance of spatial distribution of delphinids in the Mediterranean Sea (Cañadas et al., 2023), we included longitude and latitude as spatial factors rather than as explanatory variables to focus on temporal patterns.

2.4.2 Generalised additive models

GAMs (Wood, 2006) were fitted to determine how the number of acoustic events could be explained by these different variables. GAMs were chosen because unlike linear models, they offer great flexibility in describing non-linear relationships between predictors and a response variable. They have the advantage that the data

dictate how the shape of the response variable is affected by each covariate by fitting non-parametric models (Marian et al., 2021). The explained variable was the number of acoustic events per minute. Correlations between variables were assessed using a correlation matrix. If the Pearson coefficient between two variables was greater than 0.5, then the variables could not be included together in any model selection. Due to the very large number of null values and the overdispersion of the data, a Tweedie distribution was used for the analysis (Foster and Bravington, 2013). For the time of day and lunar cycle variables, the degrees of freedom (k) were set to a maximum of 15 and 7 respectively, to allow the relationships to have multiple inflection points (non-linear responses expected for these two variables). To account for the circularity of these two variables, we have included circular smoothing terms (splines, bs = 'cc'). This approach allowed the model to better capture temporal variations and effectively model the cyclicity of the data. For the other variables, we set the degrees

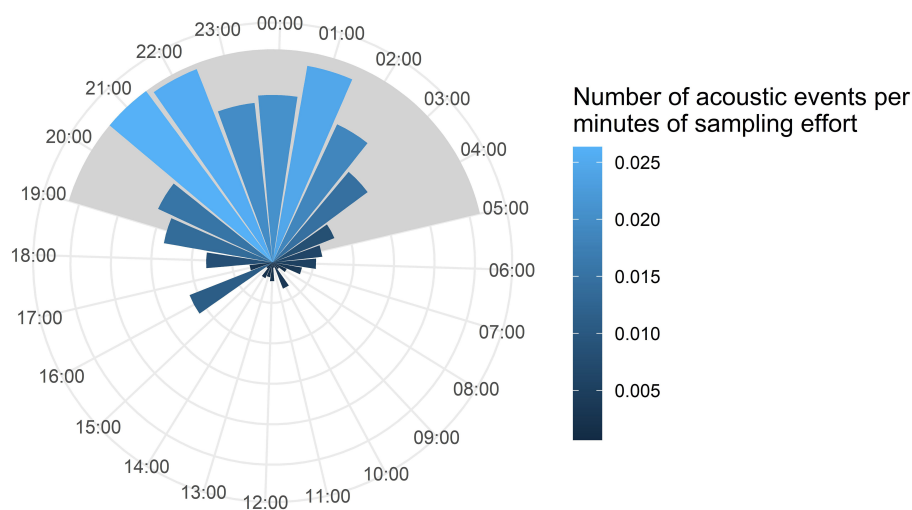


FIGURE 2

Temporal distribution of acoustic events corrected by sampling effort over the nycthemeral cycle. The shaded area represents the nocturnal phase. The largest radius has a value of 0.026 acoustic events per minute of effort at 21:00.

of freedom to a maximum of 4, as the expected relationships were less complex, and used thin plate regression splines ($bs = 'tp'$) as these are considered optimal (Wood, 2017). GAMs were fitted using the 'gam' function in the 'mgcv' R-package (Wood, 2017). Model selection was performed to determine the best model from all the models tested (combinations of 1 to 6 variables). The best model was selected based on the Akaike information criterion (AIC; Akaike, 1998), the AIC weight ('akaike.weight' function in the 'qpcR' R-package, Spiess, 2018), and the explained deviance. The importance of each variable was determined by summing the Akaike weights of the models in which the variable was selected (Symonds and Moussalli, 2011). The variables were then ranked according to their individual contribution to the models. All analyses were performed using the R software (version 4.1.2, R Core Team, 2022).

3 Results

Approximately 12,000 km were covered by the *R/V Song of the Whale* between May and September 2018, which represents a total of 74,000 minutes of sampling effort. Almost 40,000 minutes were sampled during the day while 34,000 were sampled at night. We identified a total of 741 acoustic events in PAMGuard during this sampling period. 41 events were recorded in May, 288 in June, 290 in July, 64 in August and 58 in September. Acoustic events were detected in all blocks sampled (Figure 1). More acoustic events were recorded at night (shaded area, Figure 2) with two peaks, reaching around 0.026 acoustic events per minute at 21:00/22:00 (solar time) and then around 01:00. After 01:00, the number of events decreased considerably; down to 0.0007 events per minute at 11:00 (Figure 2).

No correlations were found between the variables in the correlation matrix (Figure 3). Therefore, all the variables could be selected simultaneously in the models tested (Supplementary Table 1). The variables that contributed most to explaining the number of events were the time of day and the sea state, with Akaike weights of 99-100% (Table 2). They were followed by the lunar cycle

with an AIC weight of 80%. In contrast, lunar illumination, had a relatively low AIC weight of 60% (Table 2). The best model explained 14.3% of the deviance and included all the variables tested, although lunar illumination was not significant ($p = 0.39$, Supplementary Table 1). The second model also explained 14.3% of the deviance and did not include lunar illumination. As the top two models were very similar ($\Delta AIC < 2$), the second model was selected as the final model because lunar illumination was not significant (Supplementary Table 1). The final model included the spatial effect and the variables time of day, lunar cycle and sea state.

The number of acoustic events increased as night approached, peaking around 21:00/22:00 and at 01:00, with only a slight decrease between these two periods (Figure 4A). The number of acoustic events then decreased to a diurnal minimum around 11:00 (Figure 4A). For the lunar cycle variable, the number of events decreased from day 0, corresponding to the new moon, to a minimum on day 8, corresponding to the first quarter of the moon (Figure 4B). The response variable then increased, reaching a maximum during the third quarter of the moon (day 22 of the lunar cycle) and decreasing again until the end of the lunar cycle (day 29, Figure 4B). The relationship with sea state was unimodal from 1 to 4 and became positive at higher sea states (above 4, Figure 4C). Longitudinal and latitudinal gradients were observed, with more frequent acoustic events in the northern part of the western and central Mediterranean sub-regions (Figure 4D).

4 Discussion

4.1 General considerations

To date, knowledge of the dynamics of delphinid foraging activity throughout the Mediterranean basin has been relatively patchy. Most studies analysing delphinid foraging rhythms have been carried out using fixed passive acoustics and have focused on specific Mediterranean subregions or even local sites (e.g. Sicily, Caruso et al., 2017; Ligurian Sea, Giorli et al., 2016). These studies

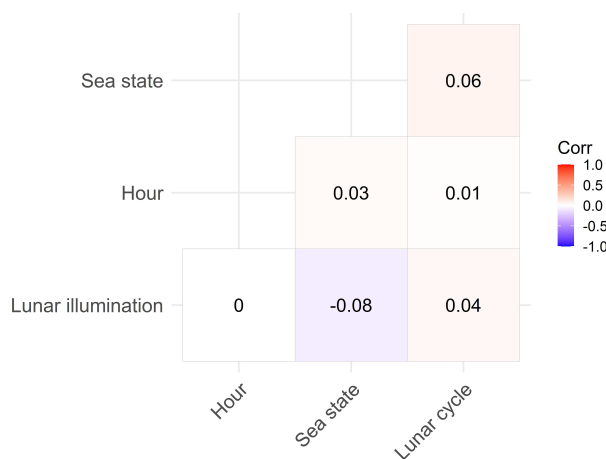


FIGURE 3

Correlation matrix including all variables tested in model selection. The numbers represent the coefficients of Pearson.

showed a diel foraging activity pattern with a peak at night. However, in these settings, it can be challenging to discriminate true patterns in echolocation activity around the recording stations from local movements in and out of the detection radius of these stations. The present study provides, for the first time, information on the activity rhythms of delphinids investigated at a basin scale from a moving platform, in the western and central Mediterranean Sea. At such a large scale, we can assume that the abundance of dolphins in the study area does not change during a diel cycle. Therefore, any change in the detection rate of acoustic events on the hydrophone array is assumed to be primarily due to changes in the dolphin vocal behaviour in relation to their foraging activity rather than changes in their occurrence. This is an inherent benefit of using large spatial datasets to identify activity rhythms. The GAM results suggested that delphinids in the Mediterranean Sea exhibit a strong diel foraging pattern, as evidenced by a nocturnal predominance of acoustic events. The distribution of effort between day and night condition was fairly well balanced and cannot be a source of bias in the number of acoustic events per unit time. The lunar cycle and also had a clear influence on the number of acoustic events, with more events being detected during the third quarter of the moon.

Carrying out this study at the scale of the western and central Mediterranean provided an overall picture of delphinid activity in the area but required spatial variability and time zone to be considered. To do this, we transformed all UTC times into solar time so that the time zone did not bias the results (Carlucci et al., 2016) and we included a spatial effect in the model to smooth out the effect of the distribution of animals in the model. A very clear signal of the influence of selected temporal variables on the number of acoustic events was found as the uncertainties associated with the relationships obtained were very low (narrow confidence intervals, Figure 4), suggesting that the highlighted patterns were quite reliable.

However, the selected model only explained 14.3% of the deviance suggesting that processes other than those considered in this study could also contribute to explain the variation in the number of acoustic events. For example, tidal height or sea surface temperature were considered by Gauger et al. (2022) and found to influence the number of acoustic events. Benoit-Bird and Au (2003) analysed and compared the relative abundance and density of spinner dolphins (*Stenella longirostris*) and the mesopelagic community off three Hawaiian islands using a modified echo-

sounder and showed that the dolphins followed the vertical dynamics of their prey. In this study, we were limited to using temporal variables that were available at all locations in a large study area, *i.e.* through available remote sensing datasets or oceanographic model outputs. This lack of direct data on prey behaviour throughout the study area necessitated the use of other parameters such as time of day or lunar cycle, thought to influence prey density and catchability at dolphin foraging depths. More detailed information on local delphinid prey activity and their catchability may have allowed for a more precise explanation of delphinid activity rhythms.

Grouping species which have distinct ecological and behavioural requirements (Cipriano et al., 2022) may also contribute to the relatively low deviance explained by the model. The exclusive use of echolocation clicks provides a solid description of delphinids foraging activity but clicks do not allow the precise identification of the species recorded. Here, delphinids were mainly represented by three species, the striped, bottlenose and common dolphins, which may have different diel activity patterns, with other species like the long-finned pilot whale, the Risso's dolphin and the rough-toothed dolphin being extremely marginal in the data set (ACCOBAMS, 2021; Ollier et al., 2023). Striped dolphins, for example, typically live in productive waters deeper than 350 m off the continental shelf (Carlucci et al., 2016). They exploit mesopelagic fish, cephalopods, and planktonic crustaceans (Würtz and Marrale, 1993) and follow their vertical distribution and dynamic movements. The bottlenose dolphin is quite flexible in its requirements, with populations living in extreme coastal, estuarine or even lagoon habitats, while others live offshore in oceanic waters (Wursig and Wursig, 1979). Its diet is quite eclectic, with combinations of benthic, demersal and pelagic shelf species versus oceanic assemblages according to the habitats where it is found (e.g., Bearzi et al., 2009; Blanco et al., 2001; Neri et al., 2023; Queiros et al., 2018). The common dolphin occurs in both pelagic and neritic environments, often sharing the former with striped dolphins and the latter with bottlenose dolphins (Notarbartolo di Sciara and Tonay, 2021). The temporal patterns presented here result from a combination of the foraging strategies of these three species in approximate proportions of 80% striped dolphins, 10% bottlenose dolphins and 10% common dolphins (proportions derived from table 4 in Panigada et al., 2024). Hence, the present results might be considered as a fair image of striped dolphin behaviour, slightly blurred by limited inputs from the other two species. However, as we were not able to distinguish species from the click trains alone in this study, any assumptions regarding species identity should be treated with caution.

4.2 Activity rhythms of delphinids in the Mediterranean Sea

The results of this study, showing that Mediterranean delphinids have a very distinct diel rhythm of acoustic event production, mainly displayed processes related to the striped dolphins in offshore habitats (Panigada et al., 2024). The other species present did not contribute much to the overall picture and

TABLE 2 Ranking of variables according to their AIC weight.

| Variable | Count | Percent | Akaike weight |
|--------------------|-------|---------|---------------|
| Time of day | 8 | 50 | 100 |
| Sea state | 8 | 50 | 99 |
| Lunar cycle | 8 | 50 | 80 |
| Lunar illumination | 8 | 50 | 60 |

The Count column corresponds to the number of times the variable appears in all the models tested, the Percent column expresses the associated percentage, and the Akaike weight corresponds to the relative contribution of the variable in the model.

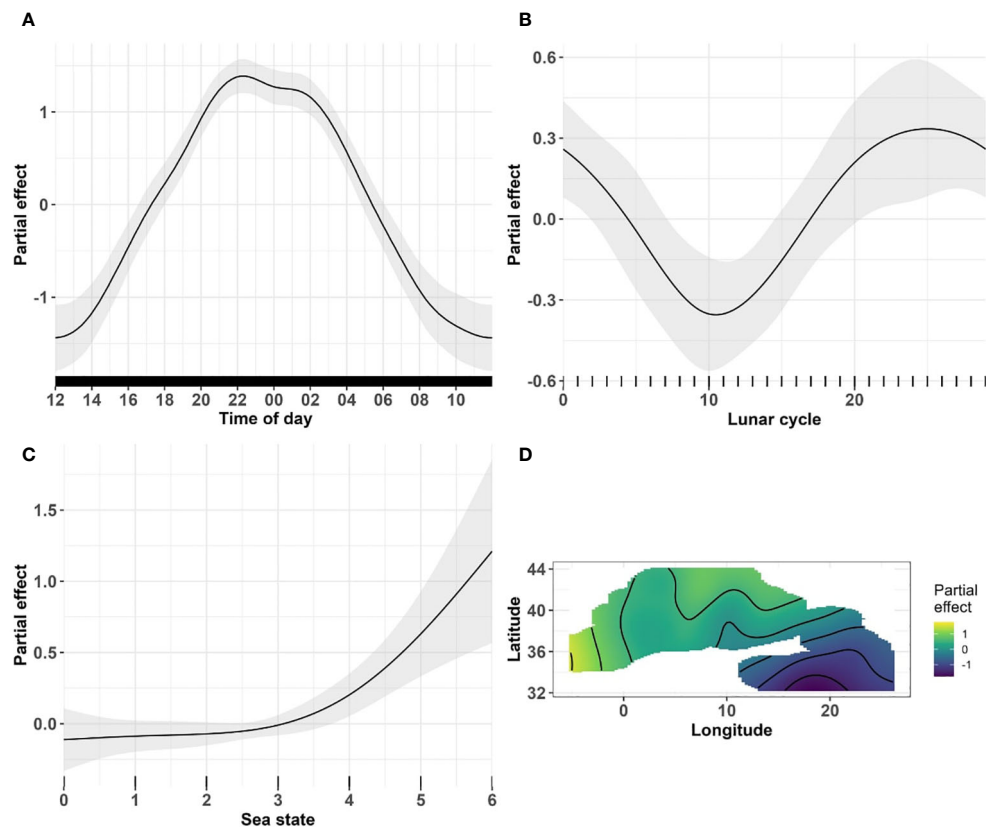


FIGURE 4

Results of the selected GAM model with a Tweedie distribution for the variables (A) time of day (B) lunar cycle, (C) sea state and (D) for the joint smoothing of longitude and latitude (yellow represent the highest predictions and blue the lowest) and. The black lines on the x-axis represent the distribution of the data. (A) time of day is a continuous variable with a resolution in minutes and labels in hours. (B) lunar cycle and (C) sea state are categorical variables. The shaded area illustrates the confidence interval associated with the curve estimate.

were likely merely contributing to the uncertainty around the observed general patterns. These variations in the number of acoustic events illustrated the activity or foraging strategy of the dolphins, which would vary according to the availability and type of prey (Benoit-Bird and Au, 2003).

The variable that contributed most to our model was the time of day of the nycthemeral cycle. Here, the variation in the number of acoustic events expresses a change in foraging activity, based on the availability of prey. The latter is shaped by depth distribution and density of prey. Dolphins assess the accessibility of prey, the potential encounter rate during foraging dives, and the associated costs in order to maximise their foraging success (MacArthur and Pianka, 1966). When prey is scarce or too deep, dolphins would stop foraging because it would not be profitable (Cascão et al., 2020), hence few acoustic events would be recorded. When prey is more abundant and accessible, dolphins would forage actively (MacArthur and Pianka, 1966). In the latter situation, it is also possible to imagine that when prey is most abundant less foraging effort would be necessary to meet calorific requirements, whereas when there is slightly less prey but still enough for foraging to be profitable, then foraging would be greater, hence acoustic events more numerous.

In our study, dolphins exhibited a higher number of acoustic events emitted during the night, suggesting a nocturnal peak in foraging activity. This is thought to occur in response to nocturnal changes in the dynamics and vertical distribution of cetacean prey (Thompson and Miller, 1990). The latter migrate vertically between the surface to feed at night and deeper layers to escape from predators during the day (Marohn et al., 2021). During the ascent of the DSL to the surface, the defence mechanisms of organisms, particularly small pelagic fish, are thought to be reduced; they would be present in less aggregated schools and would have a reduced individual swimming speeds (Zein et al., 2019). Furthermore, as night-time can lead to a loss of visual information and an increase in backscatter (Mass and Supin, 2018), the nocturnal increase in prey concentration near the surface would be advantageous for nocturnal air-breathing predators; this is the case for odontocetes, whose highly developed sonar allows them to detect prey regardless of light conditions.

To maximise foraging success while minimising dive duration, pelagic delphinids might be expected to concentrate their foraging activity at night, when the DSL get closer to the surface (Giorli et al., 2016). Maximum amounts of prey would then be available, easy to capture and accessible near the surface. Dolphins consume more

oxygen per unit time than deep diving odontocetes which may consume less oxygen due to evolutionary adaptations (Tyack et al., 2006). As a result, delphinids deplete their oxygen reserves more quickly before reaching their aerobic diving limit. To maximise hunting time relative to vertical transit time, they would ideally limit their foraging depth and thus foraging at night may be more favourable to them. Simonis et al. (2017) have highlighted a similar diurnal pattern in certain delphinids, stating that foraging activity was mainly nocturnal, and that social behaviours tended to take place during the day.

The number of acoustic events were found to be higher in the north and west of the western and central Mediterranean subregions. According to Goffredo and Dubinsky (2013), the different Mediterranean subregions are characterised by different micro phytoplanktonic compositions, with diatoms dominating in the west, and coccolithophorids and dinoflagellates in the east. The Mediterranean basin would then be characterised by significant spatial variability in terms of primary production, with decreasing levels of primary productivity from west to east, and to a lesser extent from north to south. This gradient could be a cause for a lower availability of cetacean prey, resulting in a lower densities of cetaceans (see Cañadas et al., 2023 for an analysis of gradient in cetacean distribution observed during the ASI) and therefore fewer acoustic events in the eastern and southern parts of the basin.

Other parameters may influence the increase in acoustic events, but more indirectly, as they could affect the migration dynamics of the DSL. This is the case for the lunar cycle. The number of acoustic events was minimal on day 8, corresponding to the first quarter of the moon, and maximal during the third quarter (22st day of the lunar cycle). According to Ochoa and collaborators (2013), the extent of these vertical migrations would depend on the intensity of nocturnal versus diurnal illumination and would only be possible if light intensity fluctuates sufficiently during the diel cycle. During full moon nights, when nocturnal illumination is the highest, vertical migrations would be delayed or attenuated (Ochoa et al., 2013) and fish would therefore be less available near the surface. As a result, small cetaceans may reduce their use of acoustic foraging behaviour or switch to visual predation, resulting in fewer acoustic events. However, the results of this study are inconsistent with previous research that have observed minimal acoustic foraging activity during the full moon. Simonis et al. (2017) found that common dolphin echolocation activity in the Southern California Bight was the lowest during the full moon and the highest during the third quarter phase. They suggested that the brightness of the full moon delayed or shortened vertical migrations to avoid predators, causing predators to reduce foraging or switch to visual predation. During the third quarter, a prolonged period of darkness after sunset allows mesopelagic prey to migrate to the surface before the moon rises, making them more vulnerable and available to predators. In the Mediterranean Sea, Caruso et al. (2017) found no evidence of a relationship between echolocation activity and the lunar cycle in a pelagic area. These mixed results

suggest that the response of small cetaceans to the lunar cycle is more complex than previously thought (Benoit-Bird et al., 2009; Caruso et al., 2017; Simonis et al., 2017; Shaff and Baird, 2021; Cohen et al., 2023). Therefore, in our study, lunar illumination alone cannot explain the variation in the rhythm of delphinid activity as maximum acoustic activity was found close to the third quarter of the moon and not at full moon. The mesopelagic community would be affected by the lunar cycle in a more complex way than just a direct effect of nocturnal light that would limit the DSL vertical migration and in cascade reduce nocturnal prey density in the surface layer at full moon. Indeed, detailed analyses of the DSL composition at night suggest that the main phyla constituting the DSL, i.e. fish, squids and crustaceans, and probably the main taxa constituting those, might display more complex variation in relation to the lunar cycle, drastically affecting prey availability for top predators (e.g. Battaglia et al., 2020). For example, blue-finned tuna (*Thunnus thynnus*) in the Strait of Messina show extensive changes to their prey composition during the lunar cycle, with mesopelagic fish being predominant during first quarter and full moon, mesopelagic squid after first and third quarters and other invertebrates at third quarter and new moon. If different prey types are available at different times of the lunar cycle, dolphins may use different foraging strategies, including variable echolocation rates.

Sea state was also selected in the best model. This variable may have an influence on cetacean sound activity. The number of acoustic events increased from Beaufort 4. However, it is difficult to interpret this trend due to the limited data coverage in these conditions. Changes could appear with significant ambient noise, whether natural or anthropogenic, as an adaptation strategy (Isojunno et al., 2022). For example, cetaceans may compensate for higher ambient noise by increasing the amplitude or shifting the frequency or temporal pattern of their acoustic signals (Isojunno et al., 2022). Elevated ambient noise may also affect the detection range of a hydrophone array. An independent measure of ambient noise may be useful in future surveys to explore whether dolphins adjust their sound activity to ambient noise.

4.3 Monitoring and conservation implications

Our results have important implications for the monitoring of small delphinid populations using passive towed acoustics. Highlighting the strong signal in the intensity of delphinid acoustic activity as a function of time may have implications for cetacean abundance estimation programmes. A uniform acoustic detection probability over the nycthemeral cycle cannot be used because the relationship between the number of acoustic events and the number of individuals would change with the activity of those individuals. Therefore, a variable cue rate should be included when estimating dolphin abundance in order to duly consider variation in acoustic detection probability with the time of day. This would apply to the analysis of data from towed passive acoustic surveys

following a linear transect strategy. In contrast to stationary passive acoustic surveys using moored hydrophones, changes in dolphin activity on the one hand and small scale movements affecting local dolphin density within the detection range of the hydrophone on the other hand, determine together the number of acoustic detection per unit time and are hard to disentangle.

The existence of these activity rhythms may also have conservation implications. While fishing may occur day or night (Levy et al., 2015), depending on the diversity of fishing practices, increased foraging activity at night could make dolphins more vulnerable to fisheries bycatch as they would be more focused on foraging and less alert to environmental hazard (Todd et al., 2020). Anthropogenic sound sources in the same frequency bands as dolphins can have a masking effect on these signals (Marian et al., 2021) which can affect foraging success and, indirectly, the survival of the species.

5 Conclusion

This study is the first of its kind to be carried out across a large part of the Mediterranean Sea. It was conducted to explore the activity rhythms of Mediterranean delphinids, mostly represented by the striped dolphin in offshore habitats. A nycthemeral rhythm of echolocation activity was demonstrated. These dolphins showed a predominantly nocturnal foraging pattern, illustrated by much higher echolocation clicks at night. This rhythmicity of foraging activity was shown to be linked to temporal variables such as time of day, sea state and lunar cycle. This result is consistent with available knowledge on the DSL vertical migration. In the context of foraging ecology, the use of echolocation clicks by towed passive acoustics has proved to be highly relevant for identifying diel patterns in delphinid foraging activity.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

MS: Data curation, Methodology, Formal analysis, Writing – original draft. CO: Data curation, Methodology, Formal analysis, Conceptualization, Writing – review & editing. OB: Writing, review & editing. VR: Conceptualization, Methodology, Writing – review & editing. AV: Conceptualization, Methodology, Formal analysis, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2024.1378524/full#supplementary-material>

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E

GAMs models - Relationship between the
number of acoustic events and temporal
variables

Table E.1: Selection of the five best GAM models. The "nb_events" variable is the response variable, the argument s(Longitude, Latitude) is the spatial factor represented by the interaction between longitude and latitude variables, while the others are the explanatory variables. The arguments k and bs are used to define the degrees of freedom and function types respectively.

| | Model | AIC | Deviance explained | AIC weight |
|---|---|---------|--------------------|------------|
| 1 | nb_events~1 + s(Longitude, Latitude) +s(Time of day, k = 15, bs = 'cc') + s(Lunar_cycle, k = 7, bs = 'cc') + s(Lunar_illumination, k = 4, bs = 'tp') + s(Sea state, k = 4, bs = 'tp') | 5066.84 | 14.3 | 0.4066 |
| 2 | nb_events~1 + s(Longitude, Latitude) +s(Time of day, k = 15, bs = 'cc') + s(Lunar_cycle, k = 7, bs = 'cc') + s(Sea state, k = 4, bs = 'tp') | 5066.92 | 14.3 | 0.3892 |
| 3 | nb_events~1 + s(Longitude, Latitude) +s(Time of day, k = 15, bs = 'cc') + s(Lunar_illumination, k = 4, bs = 'tp') + s(Sea state, k = 4, bs = 'tp') | 5068.30 | 14.3 | 0.1955 |
| 4 | nb_events~1 + s(Longitude, Latitude) +s(Time of day, k = 15, bs = 'cc') + s(Sea state, k = 4, bs = 'tp') | 5074.71 | 14.2 | 0.0079 |
| 5 | nb_events~1 + s(Longitude, Latitude) +s(Time of day, k = 15, bs = 'cc') + s(Lunar_cycle, k = 7, bs = 'cc') + s(Lunar_illumination, k = 4, bs = 'tp') | 5080.83 | 14.0 | 0.0004 |

F

Small cetaceans acoustic and visual group size estimates

This appendix is based on a short communication that is currently in preparation.

As shown in chapter 4, the mean acoustic group size of all acoustic events was three times smaller than that of mean visual events during acoustic-visual transects. We hypothesised that the acoustic group size was underestimated in this study. To test this, we examined the group sizes of 30 duplicate events identified in chapter 4 from both platforms. A linear regression was fitted to determine if there was a correlation between the acoustic and visual group sizes for these duplicate events.

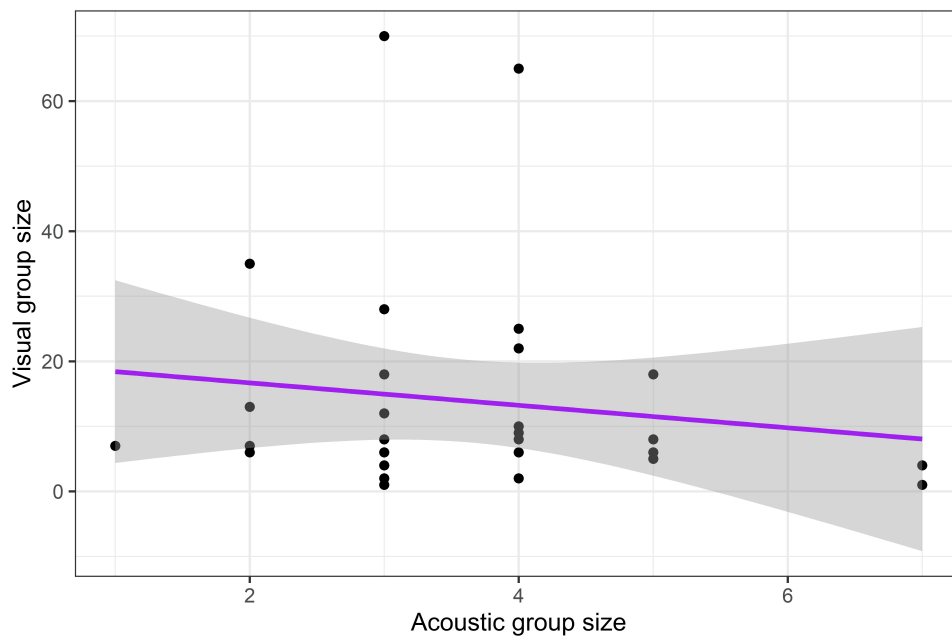


Figure. F.1: Regression linear of group size of duplicate events

Acoustic group sizes ranged from 1 to 7 individuals, while visual group sizes ranged from 1 to 70 individuals. The adjusted R-squared was -0.01569 . The regression analysis showed that the relationship between acoustic and visual group sizes was not linear. The result indicate a lack of correlation between acoustic and visual group sizes, which does not support the hypothesis that acoustic group size was underestimated in this study. Acoustic group size does not provide the same information and does not directly measure group size in the same way as visual group size. Therefore, acoustic group size was not used in this study.

The lack of correlation can lead to a number of tentative explanatory hypotheses: (1) The first explanatory hypothesse suggests that the recordings may have captured only a subset of the group, namely those animals that were echolocating. This may due to the effect of eavesdropping, where individuals in a group may improve foraging efficiency and reduce the energetic costs by listening to and interpreting acoustic signals produced by conspecifics (Barrett-lennard et al., 1996; Krause & Ruxton, 2002; Jones & Sayigh, 2002). (2) The second explanatory hypothesse is that individuals moving from the front of the boat to

F. Small cetaceans acoustic and visual group size estimates

the back were counted, and that all the animals in a group were probably not moving in the same way toward the hydrophone, so that only part of the group was detected and counted, the others having moved away from the hydrophone. (3) The third assumption is a mixture of the two, implying that disentangling availability bias and perception bias from the acoustic method is difficult.

Table F.1: Visual mean group size assigned to acoustic events per block in the Mediterranean sea. The mean group size of visual events from each block was assigned to the corresponding acoustic events. If no visual events occurred in a block, the mean group size of visual events from all blocks was used

| Block | Acoustic mean group size |
|-------|--------------------------|
| 1 | 4 |
| 10 | 12 |
| 12 | 17 |
| 13 | 2 |
| 14 | 8 |
| 15 | 5 |
| 2 | 12 |
| 22c | 6 |
| 22w | 8 |
| 26 | 7 |
| 3 | 11 |
| 4 | 5 |
| 5 | 8 |
| 6 | 7 |
| 7 | 22 |
| 8a | 10 |
| 8b | 35 |
| 9 | 26 |

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G

Correction factor for aerial-based abundance
estimates

Table G.1: $g(0)$ values obtained from the literature based on aerial surveys. Each $g(0)$ value is accompanied by a description of the study including references, species studied, survey conditions and the method used to estimate $g(0)$.

| Reference | $g(0)$ value | Studied species | Survey conditions | Method for estimating $g(0)$ |
|-------------------------------|---|---|---|--|
| Hammond et al. (2021b) | 0.805 (good conditions) 0.414 (moderate) | Bothnose dolphin White-beaked dolphin White-sided dolphin Common dolphin Striped dolphin Unidentified dolphin | Target altitude: 183 m Target speed: 90 knots Bubble windows: yes | Circle back (Hiby, 1999) |
| Forcada et al. (2004) | 0.7784 | Bottlenose dolphin | Target altitude: 150 m Target speed: 81 knots Bubble window: no | Based on dive data (Laake et al., 1997) |
| Gómez De Segura et al. (2006) | 0.676 (Striped dolphin ≤ 15 ind) 1 (Striped dolphin > 15 ind) 0.778 (Bottlenose dolphin) | Bottlenose dolphin Striped dolphin | Target altitude: 152 m Target speed: 90 knots Bubble windows: no | Based on dive data (Laake et al., 1997) |
| Carretta et al. (2000) | 0.960 (1-25 ind) 0.994 (> 25 ind) | Bottlenose dolphin Striped dolphin | Target altitude: 152 m Target speed: 110 knots Bubble windows: no | Based on surfacing behavior (Laake et al., 1997) |
| Palka (2005) | 0.58 | White-sided dolphin bottlenose dolphin common dolphin Risso's dolphin Unidentified dolphin | Target altitude: 183 m Target speed: 110 knots Bubble windows: yes | Direct duplicate method (Palka, 2005) |
| Palka (2005) | 0.77 | White-sided dolphin bottlenose dolphin common dolphin Risso's dolphin Unidentified dolphin | Target altitude: 183 m Target speed: 110 knots Bubble windows: yes | Circle back (Hiby, 1999) |
| Forney et al. (1995) | 0.67 (1-10 ind) 0.85 (>15 ind) | Harbor porpoise Dall's porpoise White sided dolphin Risso's dolphin Bottlenose dolphin Common dolphin Right whale dolphin | Target altitude: 213 m Target speed: 90-100 knots Bubble windows: yes | Double observers (Forney and Barlow, 1993) |

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H

Small cetaceans vessel-based abundance
estimates

Table H.1: Corrected abundance of small cetaceans in the Western Mediterranean Sea with associated Coefficients of variation (CV) and Confidence intervals at 95% (95% CI). Abundance estimates were derived from data collected in the Western Mediterranean study area, which included blocks 2 to 15, covering a total area of 875,295km². Abundance was estimated for each dataset and scenario. The three different datasets were: visual dataset (visual effort only), double-platform dataset (visual and acoustic effort during the day), and full dataset (visual and acoustic effort during both day and night). The four scenarios were as follows: scenario 1 ($g(0) = 1$), scenario 2 (flat platform-specific $g(0)$), scenario 3 (day-phase-specific $g(0)$ for acoustic effort and flat $g(0)$ for visual effort), and scenario 4 (hour-specific $g(0)$ for acoustic effort and flat $g(0)$ for visual effort).

| Scenario | dataset | Abundance | CV (%) | 95% CI Abundance |
|----------|-----------------|-----------|--------|----------------------|
| 1 | visual | 181,292 | 19 | 125,946 - 260,959 |
| | double-platfrom | 202,956 | 13 | 158,063 - 260,599 |
| | full | 518,920 | 8 | 440,735 - 610,975 |
| 2 | visual | 590,990 | 30 | 330,637 - 1,056,353 |
| | double-platfrom | 643,125 | 5 | 583,915 - 708,340 |
| | full | 1,496,031 | 43 | 13,913 - 160,865,677 |
| 3 | visual | 590,990 | 30 | 330,637 - 1,056,353 |
| | double-platfrom | 643,125 | 5 | 583,915 - 708,340 |
| | full | 862,551 | 20 | 549,807 - 1,353,192 |
| 4 | visual | 590,990 | 30 | 330,637 - 1,056,353 |
| | double-platfrom | 677,799 | 10 | 551,459 - 833,084 |
| | full | 847,298 | 10 | 702,862 - 1,021,415 |

Table H.2: Corrected abundance of small cetaceans in the Mediterranean Sea based on common blocks with the aerial component, with associated Coefficients of Variation (CV) and 95% Confidence Intervals (95% CI). Abundance estimates were derived from data collected in the Mediterranean study area, which included blocks 3 to 5 and 7 to 15 and blocks 22c, 22e, 22w, covering a total area of 846,975km². Abundance was estimated for each scenario (using full dataset). The four scenarios were as follows: scenario 1 ($g(0) = 1$), scenario 2 (flat platform-specific $g(0)$), scenario 3 (day-phase-specific $g(0)$ for acoustic effort and flat $g(0)$ for visual effort), and scenario 4 (hour-specific $g(0)$ for acoustic effort and flat $g(0)$ for visual effort).

| Scenario | Abundance | CV (%) | 95% CI Abundance |
|----------|-----------|--------|---------------------|
| 1 | 429,093 | 9 | 358,732 - 513,255 |
| 2 | 1,226,736 | 40 | 18,959 - 79,375,592 |
| 3 | 726,617 | 16 | 519,188 - 1,016,921 |
| 4 | 699,436 | 10 | 577,598 - 846,975 |

Suivi de population des cétacés : les mérites et les défis de la combinaison des données acoustiques et visuelles

Résumé :

Les petits cétacés sont vulnérables aux pressions anthropiques et leur abondance absolue est nécessaire pour les efforts de conservation. La méthode de distance sampling par transects linéaires fournit une estimation fiable de l'abondance en déterminant la probabilité de détection des animaux à différentes distances du transect. Les détections sur la ligne de transect sont supposées certaines, *i.e.* $g(0) = 1$, ce qui n'est généralement pas le cas en raison des biais de détection. Pour cela, des campagnes acoustiques passives et visuelles sont utilisées pour fournir des données complémentaires, bien qu'elles soient rarement combinées. Cette thèse vise à exploiter les forces des deux méthodes pour améliorer la détectabilité et les estimations d'abondance. Le navire de l'ACCOBAMS Survey Initiative a navigué en continu en utilisant les plateformes acoustiques et visuelles, ensemble ou séparément. Dans le cadre de la double plateforme, les probabilités de détection ont été estimées avec un $g(0)$ de 0,52 pour les plateformes combinées, à 0,33 et 0,30 pour l'acoustique et le visuel séparément. Un rythme diurne des détections acoustiques a été observé avec une forte augmentation la nuit. Cette variabilité a été intégrée dans les estimations d'abondance et a permis d'estimer 847 298 de petits cétacés en Méditerranée occidentale, contre 518 920 sans prise en compte des biais de détection. Cette étude a montré que la combinaison des données visuelles et acoustiques est efficace lorsque les biais de détection propres à chaque méthode sont pris en compte. Des recommandations ont été formulées pour améliorer l'utilisation de ces plateformes dans la surveillance des populations de cétacés.

Mots clés : **Abondance, probabilité de détection, petits cétacés, campagne acoustique passive, campagne visuelle, biais de détection**

Cetacean population monitoring: the merits and challenges of combining acoustic and visual data

Summary:

Small cetaceans are vulnerable to anthropogenic pressures and their absolute abundance is needed to manage conservation efforts. The line-transect distance sampling method provides a reliable abundance estimate by determining the detection probability of animals at different distances from the transects. Detections on the transect line are assumed to be certain, *i.e.* $g(0) = 1$, but this is generally not the case due to detection biases. To address this, passive acoustic and visual surveys are used to provide complementary data although they are rarely combined. This thesis aims to exploit the strengths of both methods to improve detectability and abundance estimates. The vessel of the ACCOBAMS Survey Initiative operated continuously using acoustic and visual platforms either together or separately. Detection probabilities for each platform were estimated using the double platform framework. The $g(0)$ was estimated to be 0.52 for combined platforms, 0.33 for acoustic and 0.30 for visual platforms. A significant diel pattern in acoustic events was observed with higher number of events at night. This variability was incorporated into abundance estimates, resulting in an estimated 847,298 small cetaceans in the Western Mediterranean, compared to 518,920 without detection biases correction. This study showed that combining visual and acoustic data is mostly effective when detection biases inherent to each method are properly taken into account. Recommendations were made to improve the use of these platforms in cetacean population monitoring.

Keywords: **Abundance, detection probability, small cetaceans, passive acoustic survey, visual survey, detection biases**



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Abstract

Small cetaceans are vulnerable to anthropogenic pressures and their absolute abundance is needed to manage conservation efforts. The line-transect distance sampling method provides a reliable abundance estimate by determining the detection probability of animals at different distances from the transects. Detections on the transect line are assumed to be certain, i.e. $g(0) = 1$, but this is generally not the case due to detection biases. To address this, passive acoustic and visual surveys are used to provide complementary data although they are rarely combined. This thesis aims to exploit the strengths of both methods to improve detectability and abundance estimates. The vessel of the ACCOBAMS Survey Initiative operated continuously using acoustic and visual platforms either together or separately. Detection probabilities for each platform were estimated using the double platform framework. The $g(0)$ was estimated to be 0.52 for combined platforms, 0.33 for acoustic and 0.30 for visual platforms. A significant diel pattern in acoustic events was observed with higher number of events at night. This variability was incorporated into abundance estimates, resulting in an estimated 847,298 small cetaceans in the Western Mediterranean, compared to 518,920 without detection biases correction. This study showed that combining visual and acoustic data is mostly effective when detection biases inherent to each method are properly taken into account. Recommendations were made to improve the use of these platforms in cetacean population monitoring.

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