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Mapping the exposure of the common bottlenose dolphin to environmental and anthropogenic stressors in Maltese waters

By

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Dedication

This work is dedicated to my brother, Fabio, whose curiosity and intelligence have been the driving force behind my passion for science.

Abstract

The common bottlenose dolphin (*Tursiops truncatus*) is one of the cetacean species regularly found in Malta. However, knowledge on its distribution and on its exposure to the threats caused by human activities remains limited, thus explaining the lack of conservation measures for the species in the region. The identification of areas where human activities are concentrated, and the creation of risk maps contribute to the generation of knowledge that can be used to develop appropriate conservation strategies. To examine the distribution of the common bottlenose dolphin in relation to oceanographic and anthropogenic variables a habitat suitability map was generated using MaxEnt. Subsequently, the map was used to identify areas of high-risk exposure through an overlap analysis with the spatial distribution of vessel traffic and the potential distribution of Fish Aggregating Devices. The study revealed a significant impact of depth and chlorophyll-a concentrations on the distribution of the common bottlenose dolphin, highlighting a strong preference for productive and shallow coastal waters. Furthermore, the overlap analysis indicated that all suitable areas for common bottlenose dolphins are affected by either vessel traffic, fishing, or both. This research establishes a baseline assessment of the common bottlenose dolphin's suitable habitat and provides insights into its vulnerability to anthropogenic stressors, identifying specific regions where impacts are most pronounced. The results are intended to guide management practices in reducing the species' exposure to the mentioned stressors.

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List of Frequently Used Abbreviations

ACCOBAMS	Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic Area
AICc	Akaike Information Criterion corrected for small sample sizes
AUC	Area Under the Curve
CDO	Climate Data Operators
ERA	Environment and Resources Authority
FAD	Fish Aggregating Devices
FMZ	Fisheries Management Zone
GFCM	General Fisheries Commission for the Mediterranean
HD	Habitats Directive
MSFD	Marine Strategy Framework Directive
ROC	Receiver Operating Characteristic
SAC	Special Areas of Conservation
SDM	Species Distribution Model
SSS	Sea Surface Salinity
SST	Sea Surface Temperature

1. Introduction

1.1. Definitions

Stressors: external factors, whether environmental or anthropogenic, that induce stress on organisms and cause them to operate outside of their normal range. Stressors are alternatively referred to as “pressures” (Pirootta et al., 2022).

Threats: actions, processes, or events that may directly or indirectly cause damage, degradation, or harm to species or habitats (Geary et al., 2019; Salafsky et al., 2008).

Risk: likelihood of negative consequences as a result of being exposed to a threat factor (EPA, 1998).

Species Distribution Models: computational tools that integrate environmental variables with species occurrence to forecast species distributions across landscapes (Elith & Leathwick, 2009; Miller, 2010).

Habitat Suitability Models: another term used for SDM; they are used to forecast the likelihood of occurrence based on specific environmental factors (Hirzel & Le Lay, 2008; Miller, 2010).

Predictors: ecogeographical independent variables, also known as covariates, are used to model and predict the spatial distribution of a species. They include environmental and anthropogenic factors (Hirzel & Le Lay, 2008; Zimmermann et al., 2007).

1.2. Background

The common bottlenose dolphin occupies a position of utmost ecological significance within marine ecosystems. Being an apex predator, it stands atop the marine food chain, playing a crucial role in maintaining the balance and dynamics of the marine environment (Bowen, 1997). However, global environmental changes and direct and indirect human impacts are causing the deterioration of their habitat and posing significant threats to this species (IUCN, 2023). Accurate mapping of distribution and preferred habitats based on the relationship between the species' presence and physiographic and oceanographic data, along with identifying where they overlap with the spatial distribution of human disturbances, is crucial for effective protection and guides targeted conservation efforts (Hoyt, 2012).

The common bottlenose dolphin (*Tursiops truncatus*), hereafter only “bottlenose dolphin,” is a charismatic cetacean species that has been subject to fascination, admiration, and cultural significance for centuries, becoming a symbol that interconnects with human societies and receiving important political and public attention (Parsons et al., 2015). However, its ecological significance extends beyond its charismatic nature. The abundance and distribution of the bottlenose dolphin have important implications for the functioning of marine ecosystems (Bowen, 1997), while its occurrence and behaviour actively influence the abundance and behaviour of other species, thereby contributing significantly to the overall balance and biodiversity of these ecosystems (Kiszka et al., 2022).

Recognised as a sentinel species, the bottlenose dolphin serves as an indicator of changes and potential degradation in oceanic ecosystems, reflecting the health of these environments (Katona & Whitehead, 1988; Moore, 2008). In other words, changes or disturbances in

cetacean behaviour and populations can reflect broader environmental issues (Pace, Tizzi, & Mussi, 2015). Owing to their significance, bottlenose dolphin conservation and protection are relevant issues that underscore the necessity of evaluating and maintaining the health and status of their populations (Katona & Whitehead, 1988). Moreover, being a keystone species, the conservation efforts directed towards the bottlenose dolphin extend protection to a broad spectrum of marine life that shares their habitat (Giovos et al., 2016).

The bottlenose dolphin is protected globally under several regulations and agreements. At a Mediterranean level, the conservation status of the bottlenose dolphin has recently been listed as “Least Concern” in the Red List of Threatened Species by the International Union for the Conservation of Nature (IUCN), suggesting an overall stable population, with the exception of populations from particular sub-regions such as the Gulf of Ambracia (IUCN, 2023).

Despite the fascination surrounding the bottlenose dolphin and despite its conservation status, this species is exposed to multiple threats directly or indirectly linked to human activities, as preferred habitats for the species frequently overlap with significant anthropogenic stressors. These threats, encompassing vessel traffic, fishing practices, pollution-induced chemical contamination, and the overarching impact of global climate change, are recognised for introducing significant disruptions to the species, affecting its population dynamics and distribution patterns (Pace, Tizzi, & Mussi, 2015). The consequences of such disturbances reach beyond immediate impacts, causing substantial degradation to the habitat and, consequently, imposing far-reaching effects on the overall health of bottlenose dolphin populations (Pirodda et al., 2018). Environmental shifts, coupled with the above-mentioned threats, create a complex web of threats that necessitates continuous monitoring and the implementation of mitigation measures for the conservation of bottlenose dolphin populations (Pirodda, Bearzi, Gonzalvo, et al., 2011).

The distribution of bottlenose dolphins is influenced by a combination of natural oceanographic processes, environmental characteristics, and topography. Several oceanographic phenomena and environmental factors play a crucial role in determining where they are found (Fiedler, 2018). Seasonal variations are mainly attributable to shifts in hydrological variables, responsible for changes in prey distribution and availability throughout the year (Bearzi et al., 2008; Wilson et al., 1997). Nevertheless, shifts in distributions have also been observed in response to alterations in environmental conditions generated by the impact of human activities on environmental variables, particularly primary productivity (Azzellino et al., 2017). Therefore, by understanding the distribution and preferences of a species for its habitat, one can observe and articulate how environmental changes or human-induced stressors affect the region where the species resides (Azzellino et al., 2017).

The waters surrounding Malta make no exception to posing evident threats to the marine environment, due to the intense use and the interactions between various sectors that have shaped the country’s complex maritime landscape (Said et al., 2017). Maltese waters are vital to many industries, including fishing, aquaculture, shipping, tourism, and recreation (Galdies & Refalo, 2015). In particular, shipping emerges as a crucial economic sector in this region, thanks to the strategic location of the archipelago within the Strait of Sicily, in close proximity to vital shipping routes. Furthermore, the fishing industry is well-established in the country and primarily relies on artisanal practices concentrated along the coast. Concurrently, aquaculture is on the rise (Said et al., 2017). However, the impact of these industries on the population of local bottlenose dolphins is poorly understood (LIFE+ MIGRATE, 2016b).

The interaction between environmental changes, anthropogenic activities, and the ecological significance of the bottlenose dolphin sets the stage for the present study to explore how these dynamics overlap in the maritime landscape surrounding Malta.

1.3. Rationale of the Study

The identification of risk hotspots, or areas where specific stressors are particularly concentrated, and the creation of risk maps contribute to the generation of knowledge that can be used to develop appropriate conservation strategies. Moreover, studies on bottlenose dolphin distribution are fundamental to enhancing our understanding of the basic ecology of these marine mammals and key aspects of their habitat preferences (Giovos et al., 2016). The combination of these elements allows for the formulation of targeted measures to address specific threats in key areas, thereby contributing to the overall protection and well-being of cetacean populations (Avila et al., 2018).

While a limited number of studies have explored the occurrence of the bottlenose dolphin in Maltese waters (LIFE+ MIGRATE, 2016a; Patti & Mifsud, 2019; Vella, 2004, as cited in UNEP, 2017), they provide conflicting and scattered information, resulting in a notable gap in understanding its habitat preference, distribution, and spatial exposure to the aforementioned anthropogenic and environmental stressors. Notably, prior research has not mapped the risks posed by such stressors on the species.

The absence of risk exposure assessments for the bottlenose dolphin in Maltese waters is primarily due to the challenge of identifying the distribution and preferred habitats for this species. These factors, crucial for understanding the species' ecological needs and vulnerability to stressors, have not been clearly identified in previous research.

In order to formulate effective conservation measures, it is essential to have a comprehensive understanding of where the stressors have been documented and the specific ways in which the species is affected. This involves a comprehensive understanding of where the species is found and an evaluation of whether the areas affected by threats overlap with the key habitats of the species. This comprehensive knowledge is essential for developing targeted and effective conservation strategies that consider the spatial dynamics and ecological context of the species.

1.4. Aims and Objectives

The present study aims to investigate the exposure of bottlenose dolphins to environmental and anthropogenic stressors to offer a preliminary understanding of the species' vulnerability to such stressors in Maltese waters and to identify the areas where they are most likely to be affected.

To achieve this, the relationship between the distribution of bottlenose dolphins and the spatial extent of stressors will be investigated by employing a two-step approach. Firstly, the bottlenose dolphin distribution will be predicted using a Species Distribution Model (SDM) based on Maximum Entropy which will provide a predicted occurrence map based on habitat suitability in Malta. Presence-only data on the species, obtained from previous survey initiatives, will be used as input for the model. Environmental and anthropogenic variables, namely hydrographic, topographic, and vessel traffic density, referred to as predictors, will be considered to better understand the factors influencing the spatial distribution. The selection of these predictors will be informed by prior research examining the relationship between cetacean distribution and the surrounding environmental factors. Subsequently, the bottlenose dolphin habitat suitability map will be overlapped with spatial data representing vessel traffic and the potential distribution of Fish Aggregating Devices (FADs). By integrating these spatial datasets, the potential interactions between dolphin distribution and anthropogenic stressors, as well as the effects of the environmental variables, will be assessed. This comprehensive assessment will facilitate the identification and characterization of potential threats.

This approach will help answer the following questions:

- i. What is the geographic distribution of the bottlenose dolphin in Maltese waters?
- ii. How do environmental and anthropogenic stressors influence the distribution patterns of bottlenose dolphins?
- iii. What are the specific regions where bottlenose dolphins face the highest risk of exposure to vessel traffic and FADs?

1.5. Significance of the Study and Potential Limitations

The present study will establish the groundwork for comprehending the distribution patterns and evaluating the impact of various threats on bottlenose dolphins in Maltese waters. The research will provide a fundamental preliminary perspective on the coexistence of dolphins and human activities in a region characterised by various environmental and anthropogenic stressors. Furthermore, by examining the spatial exposure of bottlenose dolphins to anthropogenic stressors, specifically vessel traffic and FADs, this study takes an important first step towards identifying high-risk areas for these cetaceans.

Furthermore, the study's findings are expected to provide significant insights that can support the development of conservation strategies and management protocols tailored to the context of bottlenose dolphins in the region. Understanding the interactions between distribution patterns, preferred habitats, and concurrent threats provides a solid foundation for developing precise and effective conservation measures.

The study will encompass a wide scope, involving the consideration of numerous variables. However, some limitations are expected due to the reliance on fragmented information sources. These limitations may constrain the distribution analysis and the overlap analysis to spatial considerations, offering a snapshot of the environmental state without accounting for temporal changes. Consequently, the limitations identified by the end of this study will be discussed in the concluding chapter.

1.6. Dissertation Structure Outline

The present dissertation consists of six chapters, described as follows:

- **Chapter 1. Introduction:** Introduced the study's context, research problem, and questions. The significance of this research was made clear, and the expected limitations were also discussed.
- **Chapter 2. Literature Review:** Will summarise and critically evaluate existing research on bottlenose dolphins, their ecology, and the impact of anthropogenic activities, identifying gaps to justify the study.
- **Chapter 3. Methodology:** Will describe the research design, data collection methods, and analysis techniques employed to investigate the distribution and risk exposure of bottlenose dolphins to anthropogenic and environmental stressors in Maltese waters.
- **Chapter 4. Results:** Will present the findings of the study, including the distribution patterns of bottlenose dolphins, the influence of stressors, and identified risk exposure areas.
- **Chapter 5. Discussion:** Will analyse and interpret the results in the context of existing literature, evaluating and discussing the significance and implications of the research findings.
- **Chapter 6. Conclusion:** Will summarise the main findings, address the limitations, highlights the contributions of the study, and suggest practical applications and recommendations for conservation efforts.

2. Literature Review

2.1. Diversity and Distribution of Cetaceans in the Mediterranean Sea

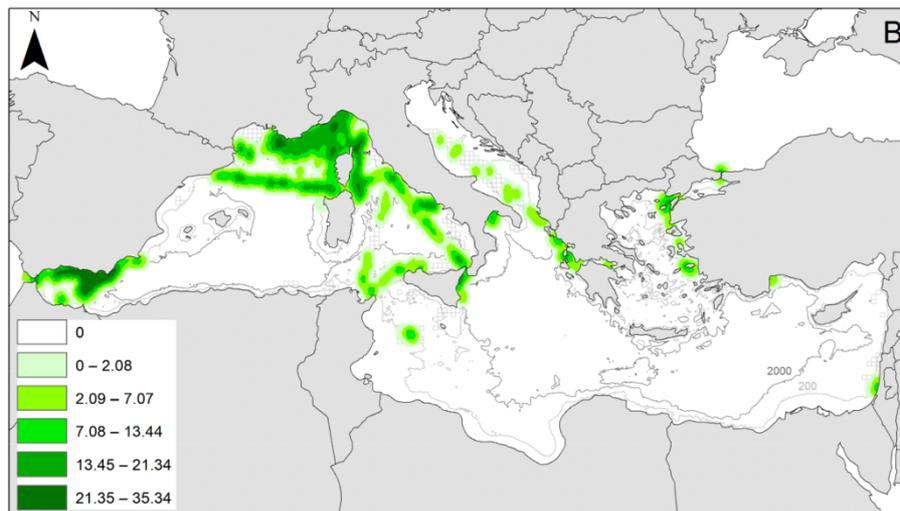
The Mediterranean Sea hosts a significant diversity of marine species with over 17,000 catalogued so far. This accounts for approximately 7% of global marine biodiversity, establishing it as a renowned hotspot for biological diversity (Coll et al., 2010). The Mediterranean, although classified as a single Large Marine Ecosystem (LME), exhibits distinct distributions of invertebrate and vertebrate species. It is in fact characterised by a pronounced biodiversity gradient from the Strait of Gibraltar to the Levantine Sea, with decreasing diversity from West to East. These patterns are influenced by unique oceanographic dynamics, ecosystem components, and significant anthropogenic activities, such as fishing and pollution (Bas, 2009).

The Mediterranean Sea stands out as an important habitat for cetaceans – whales, dolphins, and porpoises. These marine mammals, as predators occupying upper trophic levels, play a critical role in the balance, dynamics, and overall health of the marine ecosystems within the basin (Kiszka et al., 2022). Their extensive vertical and horizontal movements allow large cetaceans to act as important vectors of material transport across the sea. Meanwhile, delphinids have the capacity to control prey populations, exemplifying their ecological influence (Estes et al., 2016).

The spatial distribution of cetaceans, on the other hand, is shaped by various factors such as demographics, ecology, evolution, and human activities, which collectively affect the distribution patterns of cetaceans across diverse spatial and temporal scales. Additionally, individual cetacean species exhibit preferences influenced by specific physical, chemical, and biological characteristics of water masses (Forcada, 2018). Within the Mediterranean Sea, densities and abundance estimates show a wide yet uneven distribution of cetacean species (ACCOBAMS, 2021b). This disparity aligns with the overall biodiversity gradient observed in the basin (Coll et al., 2010), but presents considerable exceptions resulting in hot spots distinguished by higher species diversity and population densities (**Figure 1**). Notably, regions like the Alboran Sea and the North-western Mediterranean, including the Pelagos Sanctuary, a Special Area of Mediterranean Importance (SPAMI), stand out as major examples of these high-density areas. On the other hand, certain areas within the basin exhibit lower population densities of cetaceans, including the Levantine Sea (Gnone et al., 2023).

Figure 1

Spatial Patterns of Cetacean Diversity based on the Shannon Diversity Index (Gnone et al., 2023, p. 20)



Note: The figure represents the distribution of cetacean diversity calculated by Gnone et al. (2022) using the Shannon Index. The dark green area represents the maximum diversity index which is found in the Alboran Sea. The index decreases moving eastwards across the basin.

Despite the availability of basin-wide estimates for cetaceans, it is crucial to recognise the existing variations in past systematic survey efforts across the area. These variations can potentially impact the accuracy and reliability of the distribution analyses, especially for specific regions, such as those along which the countries to the south and east of the Mediterranean are situated, which have received limited monitoring and require additional research and dedicated efforts. Furthermore, a substantial data gap persists in terms of survey effort and abundance estimations, particularly in non-summer months, emphasising the significant need for further data collection and analysis (Mannocci et al., 2018).

In terms of species diversity, the Mediterranean Sea hosts 25 cetacean species (**Table 1**), accounting for approximately 27% of the total global species count of 94 (ACCOBAMS, 2021a). Out of these 25 species, nine are considered regular residents, displaying varying degrees of genetic distinction from their conspecifics in the Atlantic region (Bérubé et al., 1998; Drouot et al., 2023; Garcia-martinez et al., 1999; Gaspari et al., 2007, 2015; Natoli et al., 2005, 2008). Additionally, five species are classified as visitors, making repeated but irregular appearances, while 11 species are categorised as vagrants, appearing rarely in the Mediterranean Sea. Among the regular species found in this region are six members of the Delphinidae family: the striped dolphin (*Stenella coeruleoalba*), the common bottlenose dolphin (*Tursiops truncatus*), the common dolphin (*Delphinus delphis*), the Risso's dolphin (*Grampus griseus*), the long-finned pilot whale (*Globicephala melas*), the rough-toothed dolphin (*Steno bredanensis*). Additionally, two odontocetes, the Cuvier's beaked whale (*Ziphius cavirostris*), the sperm whale (*Physeter macrocephalus*), as well as the fin whale (*Balaenoptera physalus*), the sole mysticete, are also regular inhabitants of the Mediterranean (ACCOBAMS, 2021a).

Table 1

List of Regular, Vagrant and Visitor Species Present in the Mediterranean Sea (ACCOBAMS, 2021a)

Species	English Name	Presence
<i>Balaenoptera acutorostrata</i>	Common minke whale	Visitor
<i>Balaenoptera borealis</i>	Sei whale	Vagrant
<i>Balaenoptera physalus</i>	Fin whale	Regular
<i>Delphinus d. ponticus</i>	Black Sea common dolphin	Visitor
<i>Delphinus delphis delphis</i>	Short-beaked common dolphin	Regular
<i>Eschrichtius robustus</i>	Grey whale	Vagrant
<i>Eubalaena glacialis</i>	North Atlantic right whale	Vagrant
<i>Globicephala macrorhynchus</i>	Short-finned pilot whale	Vagrant
<i>Globicephala melas</i>	Long-finned pilot whale	Regular
<i>Grampus griseus</i>	Risso's dolphin	Regular
<i>Hyperoodon ampullatus</i>	Northern bottlenose whale	Vagrant
<i>Kogia sima</i>	Dwarf sperm whale	Vagrant
<i>Megaptera n. novaeangliae</i>	Humpback whale	Visitor
<i>Mesoplodon bidens</i>	Sowerby's beaked whale	Vagrant
<i>Mesoplodon densirostris</i>	Blainville's beaked whale	Vagrant
<i>Mesoplodon europaeus</i>	Gervais' beaked whale	Vagrant
<i>Orcinus orca</i>	Killer whale	Visitor
<i>Phocoena p. phocoena</i>	North Atlantic harbour porpoise	Vagrant
<i>Physeter macrocephalus</i>	Sperm whale	Regular
<i>Pseudorca crassidens</i>	False killer whale	Visitor
<i>Sousa plumbea</i>	Indo-Pacific humpback dolphin	Vagrant
<i>Stenella coeruleoalba</i>	Striped dolphin	Regular
<i>Steno bredanensis</i>	Rough-toothed dolphin	Regular
<i>Tursiops truncatus</i>	Common bottlenose dolphin	Regular
<i>Ziphius cavirostris</i>	Cuvier's beaked whale	Regular

The presence of cetaceans across the basin is influenced by a range of factors, spanning from the underlying physiography to historical and contemporary threats that stem directly or indirectly from human activities. Furthermore, individual cetacean species distinctly exhibit preferences for specific habitats, each showcasing unique patterns of habitat use in response to oceanographic features (Cox et al., 2018).

In the context of environmental drivers (see section 2.3), the distribution patterns of Mediterranean cetaceans are shaped by some key factors, including higher levels of primary ocean productivity and a diverse seabed profile (Cañadas et al., 2002; Gannier, 2005), as well as the broader physiographic characteristics of a region (Azzellino et al., 2017). These key factors play a significant role in shaping the distribution patterns of Mediterranean cetaceans, emphasizing the correlation between their presence and the characteristics of the surrounding physical environment. The connection becomes clear when one considers how the distribution and abundance of food resources for cetaceans are influenced indirectly by the structure and shape of the ocean floor. This effect is due to the topography-induced nutrient upwelling, which increases primary production (Croll et al., 2005).

In contrast, it is important to recognise that historical whaling and culling campaigns have substantially affected the current spatial distribution of cetaceans, and that they have been the main driver of population decline worldwide for different species (Whitehead & Shin, 2022). In the present day, human activities still have a major impact, altering cetacean habitats in ways that make it unsuitable for their survival (Azzellino et al., 2017). In particular, overfishing and the related decline of fish stocks (Piroddi, Bearzi, Gonzalvo, et al., 2011), marine traffic and tourism-related activities (La Manna et al., 2013), habitat degradation due to unsustainable coastal development (Brandt et al., 2011), and climate change (Evans & Bjørge, 2013) pose significant threats leading to the redistribution of the species (see section 2.4).

2.2. The Common Bottlenose Dolphin

The common bottlenose dolphin is a widely studied and cosmopolitan odontocete (toothed cetacean), belonging to the Delphinidae family. It is found across almost the entire globe, in most of the temperate to tropical seas between the 45° parallels and as far north as the 60° parallel in the North Atlantic (Wells & Scott, 2018). In the Mediterranean Sea, it stands as one of the most frequently encountered cetaceans across the basin (ACCOBAMS, 2021b), where it is found in a wide range of habitats, including the continental shelf (Azzellino et al., 2012), inshore waters (Bearzi, Agazzi, et al., 2008), waters surrounding islands and archipelagos (Forcada et al., 2004), and deeper offshore waters over the edge of the continental shelf (Cañadas et al., 2002). While cetacean research in the Mediterranean Sea began relatively recently in the 1980s, there has been a notable increase in the amount of new information available on the species in recent years. However, despite these advancements, our understanding of bottlenose dolphins in the region still remains limited (Natoli et al., 2021).

The Aerial Survey Initiative, carried out across the entire Mediterranean Sea by the Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic Area (ACCOBAMS), estimates the population to exceed 60,000 individuals (ACCOBAMS, 2021b), though this number may be underestimated due to some portions of the region not being covered (Natoli et al., 2021). In the Mediterranean, the distribution of bottlenose dolphins appears fragmented, with higher abundances found in specific areas, including the Strait of Gibraltar, Alboran Sea, Balearic Sea, Gulf of Lion, waters surrounding Corsica, north of the Tyrrhenian Sea, northern Adriatic Sea, Strait of Sicily, and Aegean Sea (ACCOBAMS, 2021b). Causes of this variation can be related to habitat

characteristics, prey availability, and social behaviours. Past culling campaigns, which took place in the first half of the 1900s (Bavestrello et al., 2020), and ongoing threats may have also contributed to the current patchy distribution of bottlenose dolphins in the region (Bearzi et al., 2004).

Mediterranean bottlenose dolphins exhibit significant genetic differentiation, not only when compared to Eastern Atlantic populations but also within the Mediterranean basin itself. Natoli et al. (2005) provided evidence of a distinct genetic separation between eastern and western dolphin populations, which is linked to variations in the hydrographic characteristics of the respective basin areas. These differences have led to adaptations that suit the complexities of each region, characterised by different topography, salinity, productivity and temperature. It is interesting to note that the Italian peninsula and the Strait of Sicily could potentially serve as the geo-ecological demarcation between the two distinct Mediterranean populations (Gaspari et al., 2015; Natoli et al., 2005, 2021).

Furthermore, Gaspari et al. (2015) conducted a more in-depth investigation and revealed a fine-scale population structure in the Eastern Mediterranean. This concept involved the identification of smaller, distinct groups within the overall eastern population, each displaying specific characteristics. The researchers also observed a differentiation between an offshore population and a coastal population based on samples of stranded animals. However, the understanding of offshore populations of bottlenose dolphins remains limited (Bearzi et al., 2009; Dromby et al., 2023; Fahlman et al., 2023).

The findings of recent comprehensive research by Gnone et al. (2023), covering the entire basin and encompassing diverse Mediterranean regions, consistently indicate that the concentration of bottlenose dolphin sightings predominantly occurs along the continental shelf. In contrast, sightings in the deeper and more pelagic waters are notably less frequent (Gnone et al., 2023).

Within the Mediterranean, bottlenose dolphins exhibit different levels of both site fidelity and mobility. Site fidelity pertains to their tendency to either maintain a presence within specific zones or revisit them. Mobility, on the other hand, encompasses a spectrum of behaviours, ranging from individuals displaying a residential attitude to those being occasional visitors or transients (Ascheri et al., 2022; Gnone et al., 2011; Gonzalvo et al., 2014; Pace et al., 2021). Moreover, certain populations appear largely isolated (Bearzi, Agazzi, et al., 2008), while others form open groups, characterised by a broad home range and movements between different areas (Papale et al., 2017). Under different circumstances, the heterogeneity in site fidelity is associated with seasonal variations and with human activities, including aquaculture facilities along with the activities conducted within them (Díaz López, 2012).

As human activities tend to concentrate around coastal zones, dolphins that display pronounced site fidelity might become more susceptible to local anthropogenic impacts, such as habitat degradation, pollution, and vessel traffic, as they repeatedly use the same areas for feeding, breeding, and social interactions. This overlap increases their exposure to potential dangers and reduces their ability to adapt to changing environmental conditions (Gonzalvo et al., 2014).

Multiple agreements and conventions provide necessary protection to the species on global, regional and national scales. Notably, the bottlenose dolphin is listed under Appendix II of the Bern Convention on the Conservation of European Wildlife and Natural Habitats, which aims to protect and conserve European biodiversity, including species and their habitats. Additionally, the bottlenose dolphin is included in Annex II of the Barcelona Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean. This treaty, along with its Protocols, addresses various environmental concerns in the Mediterranean Sea region, including the protection of marine species and habitats. Furthermore, the bottlenose dolphin is protected under the Washington Convention, formally recognised as the Convention

on International Trade in Endangered Species of Wild Fauna and Flora (CITES). This international agreement serves to regulate the international trade of endangered species to ensure their survival and prevent unsustainable exploitation. At the Mediterranean level, the bottlenose dolphin is protected by the Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea, and contiguous Atlantic area (ACCOBAMS). ACCOBAMS, created under the Convention on Migratory Species (CMS), also known as the Bonn Convention, represents the first-ever agreement on cetacean conservation in the region.

Within the European legislation context, the bottlenose dolphin is protected under the Habitats Directive 92/43/EEC (HD), a major European initiative for conserving species of community interest, aimed at maintaining and restoring natural habitats and wildlife at a Favourable Conservation Status (FCS). Moreover, the bottlenose dolphin is listed in Annex II and IV of the HD, requiring specific conservation efforts and the designation of Special Areas of Conservation (SACs) forming part of the Natura 2000 network.

The Marine Strategy Framework Directive 2008/56/EC (MSFD) is another crucial legislative instrument that plays a significant role in the conservation and protection of the bottlenose dolphin and other marine species in European waters. Member States must therefore consider the conservation status of marine mammal species, including the bottlenose dolphin, when developing their marine strategies to achieve Good Environmental Status (GES). This involves assessing the population dynamics, habitat requirements, and potential threats to the bottlenose dolphin in their respective marine regions.

2.3. Impact of Environmental Variables on Cetacean Distribution and Habitat Preference

2.3.1. Overview on Oceanographic Processes

Cetaceans are highly adapted to the oceanic environment, and their habitat and distribution are intricately influenced by the physical and chemical attributes of their surroundings, along with the topography and the sea surface conditions (Fiedler, 2018). In response to these factors, cetaceans exhibit specific behaviours that vary with the seasons and locations, which can be attributed to their intentional selection of habitats with distinct and consistent oceanographic characteristics. (Tynan et al., 2005).

Oceanographic processes and topographic features play a vital role in delineating regions that are consistently utilised by cetaceans for feeding, breeding, calving, nursing and socialising, providing them with essential resources for their daily well-being and survival (Ballance et al., 2006; Cox et al., 2018). These important areas, known as critical habitats, are fundamental in sustaining healthy population growth rates for the species (Hoyt, 2012).

Cetacean distribution is significantly impacted by flow-topography interactions, where ocean currents interact with underwater topography. Therefore, by analysing the oceanographic data, researchers can account for the variation in cetacean distribution (Tynan et al., 2005). Oceanographic processes like upwelling and fronts support continuous productivity in the ocean, by enhancing a cascade of trophic dynamics and providing nutrient-rich environments that attract marine species, including cetaceans (Chavez & Messié, 2009; Thompson et al., 2012; Tynan et al., 2005).

The occurrence and distribution of the species are notably affected by seasonal variations in upwelling, which exert their impact through intermediate trophic levels in the marine food web, specifically phytoplankton, zooplankton, and forage fish biomass (Scales et al., 2014; Thompson et al., 2012). Upwelling events result in the upward movement of nutrient-rich cold water from deeper ocean layers to the surface, promoting phytoplankton growth and

proliferation. The increase in phytoplankton forms the basis of the marine food chain and supports the subsequent trophic levels (Ware & Thomson, 2005).

Scales et al. (2014) and Thompson et al. (2012) have demonstrated the indirect relationship between upwelling-driven trophic dynamics and cetacean occurrence. These investigations have highlighted that during periods of enhanced upwelling and elevated intermediate trophic biomass, cetaceans are more likely to be present and exhibit increased activity. Nevertheless, substantial variance exists among different delphinid species, each exhibiting distinct habitat preferences closely associated with specific water masses characterised by surface temperature, salinity, and chlorophyll-a concentration, rather than upwelling events (Ballance et al., 2006; Selzer & Payne, 1988). Moreover, the seasonal fluctuations in sea surface temperature and salinity, along with local nutrient upwelling in regions with significant sea floor depth variability, can influence the abundance of preferred prey, consequently impacting the distribution of dolphins (Selzer & Payne, 1988).

2.3.2. Topographic Features

Topographical features like seamounts and canyons enhance foraging opportunities by increasing food availability and attracting diverse marine life (Pace et al., 2018). Several studies have indicated the feasibility of delineating habitat suitability for various cetacean species by considering topographical attributes as key factors (Azzellino et al., 2008; Cañadas et al., 2002; De Boer et al., 2014; MacLeod & Zuur, 2005; Pace et al., 2018), influencing the aggregation of prey species (Selzer & Payne, 1988). In particular, depth, slope and type of substrate play a crucial role in the distribution of benthic and demersal prey species (Leitner et al., 2021; Priede et al., 2010), while pelagic fish and cephalopods' distribution is indirectly affected by upwelling induced by topography (Ward et al., 2006). This reflects onto the distribution of cetaceans, so that they show specific preference for particular topographic features (Cañadas et al., 2002).

In particular, bottlenose dolphins exhibit a strong correlation between their movements and foraging behaviour and environmental factors such as hydrography and topography. Specifically, the underwater landscape and small-scale fronts play a crucial role in concentrating and enhancing prey availability, creating favourable habitats for this species (Bailey & Thompson, 2010).

2.3.3. Hydrographic Variables

Previous studies have highlighted the significant role of hydrographic variables, particularly sea surface temperature (SST) and sea surface salinity (SSS), in determining the habitat suitability for cetacean species (Bearzi et al., 2008; Chavez-Rosales et al., 2019; Forney et al., 2012; Giralt Paradell et al., 2019; Mintzer & Fazioli, 2021; Thompson et al., 2012). SST and SSS are widely used as reliable predictors of cetacean occurrence and distribution due to their correlations with cetacean density, encounter rate, and group size (Cañadas & Vázquez, 2017; Selzer & Payne, 1988; Forney et al., 2012).

SST can influence the foraging behaviour of cetaceans, particularly for bottlenose dolphins as lower temperatures are associated with increased foraging activity, likely to meet the higher energy demand during such conditions (Methion & Díaz López, 2019). Moreover, SST has been shown to shape the ecological dynamics and reproductive patterns of cetaceans. Studies conducted by Bearzi et al. (1999) and Castro et al. (2020) demonstrate that warmer waters promote calving and favour birth rates among delphinids, which underscores the importance of SST in influencing cetacean population dynamics. However, in areas characterised by more

dynamic oceanic conditions, other factors such as topography and depth become more robust predictors of cetacean occurrence (Hastie et al., 2005).

The significance of Sea Surface Salinity (SSS) in assessing habitat suitability comes to the forefront in Mintzer & Fazioli's (2021) research. Their study, exploring the impact of SSS on the distribution of bottlenose dolphins in Galveston Bay, reveals a consistent pattern. Specifically, bottlenose dolphins exhibit a tendency to relocate from the estuary area during periods of low salinity resulting from river inflows in times of high precipitation. The authors attribute this behavioural shift to variations in prey availability. The authors attribute this displacement to variations in prey availability. This theory is rooted in the understanding that many species of estuary fish migrate to waters with higher salinities during freshwater events.

In addition to SST and SSS, a variety of environmental variables, including chlorophyll-a, and dissolved oxygen have been extensively utilised as reliable predictors of cetacean distribution (Chavez-Rosales et al., 2019; Forney et al., 2012; Giralt Paradell et al., 2019; La Manna et al., 2016). For example, dissolved oxygen and chlorophyll-a levels are particularly crucial for coastal fish dynamics, influencing fish distribution, abundance, and diversity (Methion, et al., 2019; Stevens et al., 2006). As proxies for photosynthetic activities and fish distribution, these two variables are widely used to predict the distribution of bottlenose dolphins (Bearzi et al., 2008). In particular, well oxygenated waters and primary productivity favour the presence of thriving fish populations which create abundant feeding grounds, making these areas optimal foraging locations for delphinids (Methion et al., 2023).

According to Smith et al. (1986), cetaceans are more likely to inhabit waters characterised by a higher primary productivity, suggesting a preference for this particular habitat. In particular, the study emphasizes that delphinids tend to exhibit distinct preferences based on chlorophyll-a concentration. In less productive waters the foraging behaviour of delphinids appears to be less specialised. In contrast, in more productive waters, they tend to display a greater degree of specialization in their foraging activities. However, such preference may be influenced by the local ecological conditions and trophic dynamics of a particular area.

Changes in chlorophyll-a levels can indeed influence the relationship between prey and predators, potentially leading to a decreased abundance of delphinids in areas with higher microalgae concentrations (Castro et al., 2020). This is further corroborated by Methion et al. (2023), who emphasize the significance of chlorophyll-a in shaping the group dynamics of bottlenose dolphins. In highly productive waters, smaller groups tend to form under conditions of low food availability, while larger groups are observed when environmental conditions are favourable, characterised by moderate chlorophyll-a concentrations and higher dissolved oxygen values.

Furthermore, it is essential to note that the impact of these predictors exhibits seasonal variability, with certain factors holding greater influence than others depending on the specific time of year (Bearzi et al., 2008).

Understanding the connections between species and their habitat remains challenging, given the complex interaction between biological seasonal patterns and oceanographic influences (Ballance et al., 2006). For cetaceans, their responses are shaped by the distribution of prey species, which, in turn, respond to the physical characteristics of their environment (Ballance et al., 2006). This highlights the strong link between cetacean distribution and the oceanographic characteristics of a region within the broader marine food web (Selzer & Payne, 1988).

2.3.5. Influence of Environmental Variables on Cetacean Distribution and Habitat Preference in the Mediterranean Sea

The Mediterranean Sea stands as a unique environment for cetaceans when compared to other oceanic regions. Despite its relatively smaller size, this sea hosts a diverse range of cetacean species, each exhibiting specific habitat preferences and distribution patterns. Understanding the influence of environmental variables on cetacean occurrence in this semi-enclosed sea is vital, and such influence may differ from that experienced in open-ocean environments.

Gnone et al. (2023) observed a significant link between greater bathymetric variability and increased cetacean diversity in the Mediterranean Sea, underlining the role that topographical features play in shaping their distribution. Additionally, specific cetacean species, such as bottlenose dolphins, Risso's dolphins, and Cuvier's beaked whales, demonstrate distinct depth and slope preferences, further emphasizing the significance of topography in defining their distribution (Azzellino et al., 2008). Interestingly, even in areas with lower chlorophyll-a concentrations, greater bathymetric variability in the Mediterranean Sea is associated with increased cetacean diversity (Gnone et al., 2023).

Cetacean species exhibit varying preferences for depth and slope within the Mediterranean Sea. Bottlenose dolphins are often found on the continental shelf, whereas Risso's dolphins and Cuvier's beaked whales prefer the upper and lower continental slopes, respectively. Sperm whales show a preference for both the upper and lower continental slopes (Azzellino et al., 2008, 2012). In contrast, fin whales, striped dolphins, and common dolphins tend to favour pelagic habitats (Azzellino et al., 2012; Gnone et al., 2022). The complex topography and unique hydrography of submarine canyons make them preferred habitats for species like sperm whales and Cuvier's beaked whales (Azzellino et al., 2012; Lanfredi et al., 2017). Additionally, the size and shape of the continental shelf appear to impact the home range of bottlenose dolphins, thereby affecting the size and structure of geographical units (Gnone et al., 2022).

The level of habitat preferences varies among cetacean species. Striped dolphins and Cuvier's beaked whales exhibit weaker preferences, while common bottlenose dolphins, fin whales, Risso's dolphins, and sperm whales have stronger preferences, with some species showing temporal variability in their habitat use (Azzellino et al., 2012). The distribution of these species is influenced by complex interactions between hydrological variables, with oxygen concentration potentially playing a significant role, suggesting a link between prey availability and oxygen saturation (Bearzi et al., 2008).

Additionally, La Manna et al. (2023) identified a link between SST and the clustering patterns of a Mediterranean common bottlenose dolphin population, which might be explained by the effect of water temperature on prey abundance and distribution.

Finally, in the Mediterranean Sea, chlorophyll-a emerges as an important predictor of the likelihood of bottlenose dolphin occurrence, operating as a main proxy for other bio-ecological factors linked to their feeding preferences (La Manna et al., 2016).

2.4. Human-Induced Threats

Bottlenose dolphins, along with other cetaceans, face a wide range of threats, most of which are directly or indirectly caused by human activities. The risks posed by these threats are particularly high for marine mammal populations living in enclosed seas, such as the Mediterranean. Avila et al. (2018) have indicated that the Mediterranean Sea is a hotspot for almost all threat categories, making the cetacean communities within them particularly vulnerable to the adverse effects of human activities. The Mediterranean Sea is known to be heavily exploited for various purposes like oil and gas extraction (Galdies, 2008), offshore renewable energy, fisheries, shipping, tourism, and recreation (Abdulla & Linden, 2008),

causing a critical environmental degradation of the marine habitat. Such activities are expected to grow significantly in the near future (Galdies & Refalo, 2015).

Micheli et al. (2013) assessed and mapped cumulative human impacts on 17 Mediterranean and Black Sea ecosystems. Their study considered 22 anthropogenic drivers and classified them under four categories:

- Climatic stressors, such as increased SST, increased ultraviolet (UV) radiation, and acidification.
- Land-based factors like nutrient input, organic pollution, urban runoff, risk of hypoxia and coastal population density.
- Sea-based activities, including commercial shipping, invasive species introduction, the risks associated with oil spills and oil rigs.
- Fishing, encompassing all gears and types.

Impact scores were determined by combining spatial data for anthropogenic drivers and ecosystems, transforming the data into a standardized scale, and calculating cumulative impact scores for each geographical pixel using impact weights estimated through expert judgment. The findings revealed that climatic drivers, including acidification, SST and UV increase, demersal fishing and shipping exerted most substantial average impact on the Mediterranean and Black Sea ecosystems (**Figure 2**). Approximately 20% of the entire Mediterranean and Black Sea experienced a high cumulative impact due to the major contributors mentioned above. Notably, these contributors, along with hypoxia generated by coastal runoff, resulted in a high cumulative impact on 60–99% of the territorial waters belonging to EU member states. The study further identified the most affected areas as the Alboran Sea, the Gulf of Lyons, the Sicily Channel and Tunisian Plateau, the Adriatic Sea, and the coasts of Egypt, Israel, and Turkey (**Figure 3**). These regions face the greatest combined human impacts, warranting special attention for conservation and management efforts.

Figure 2

Average Impact Scores of Anthropogenic Drivers on Mediterranean and Black Sea Ecosystems (Micheli et al., 2013, p. 6)

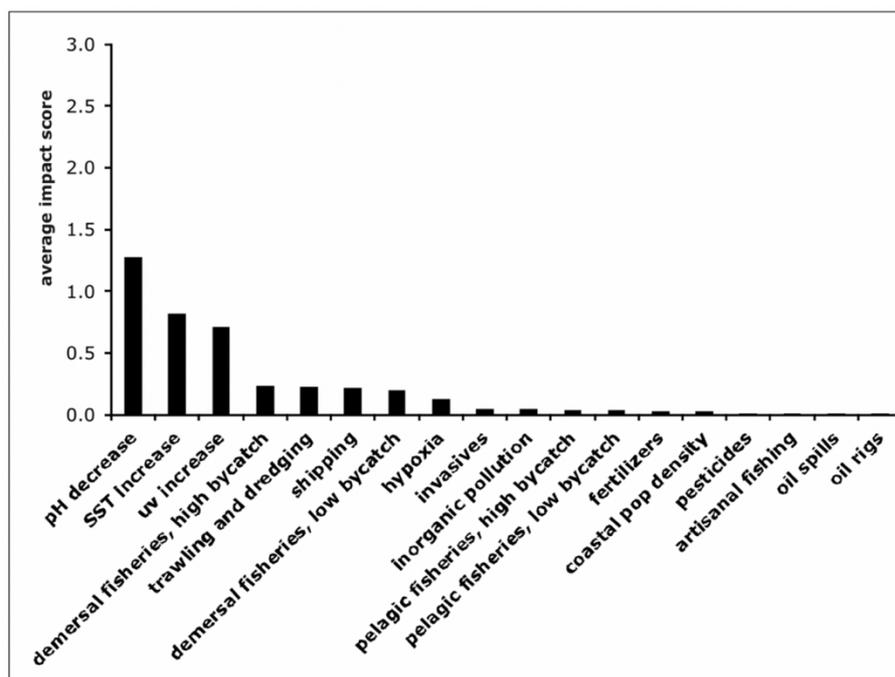
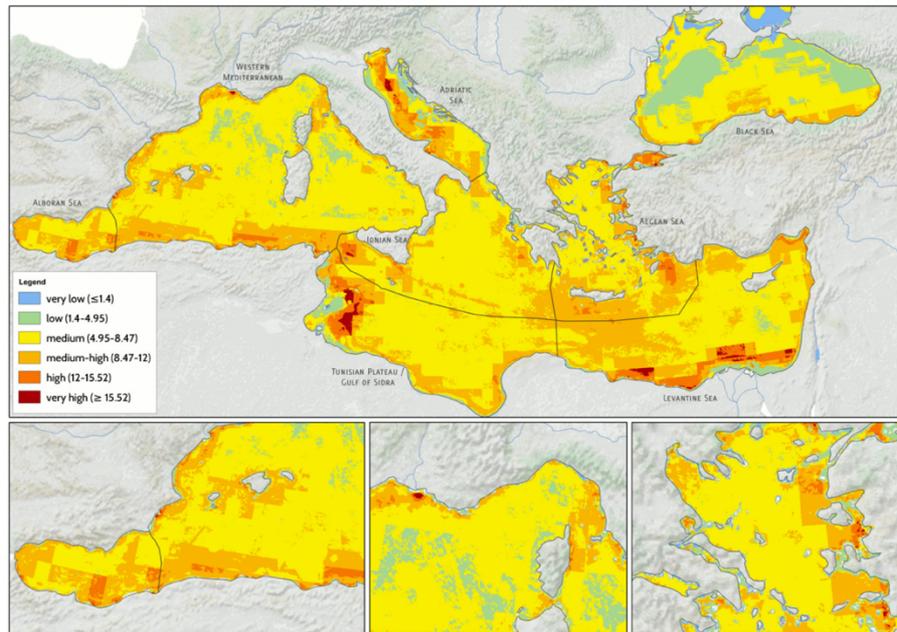


Figure 3

Spatial Distribution of Cumulative Impacts (Climatic, Land-based, Sea-based, and Fishing) to Marine Ecosystems of the Mediterranean and Black Sea (Micheli et al., 2013, p. 4)



Cetaceans like the bottlenose dolphin in the Mediterranean Sea face several significant anthropogenic threats, including incidental catch (bycatch) in fishing gear (FAO, 2020), prey depletion resulting from overfishing (Piroddi, Bearzi, Gonzalvo, et al., 2011), the consequences of climate change (Evans & Bjørge, 2013), habitat loss, and degradation of coastal and marine ecosystems (Gonzalvo et al., 2014; Pace, Tizzi, & Mussi, 2015), exposure to underwater noise (Simmonds et al., 2014), pollution, and chemical contamination in the marine environment (Bridge et al., 2023; Hall et al., 2018; Jepson et al., 2016), as well as disturbance caused by marine traffic (Papale, Azzolin, & Giacoma, 2011), vessel strikes (Panigada et al., 2006; Sèbe et al., 2023), and entanglement in fishing gear (Fossi et al., 2018a, 2018b). These multifaceted threats pose a serious risk to the survival and well-being of this and other cetacean species in the region (Oceancare, 2021).

The quantification of threats' impacts on cetacean populations mainly revolves around the study of trends in their distribution and population size, encompassing a range of consequences, from short-term to long-term displacements to potential direct mortality. The subsequent subsections are therefore dedicated to investigating the impacts of three primary threats on bottlenose dolphins, particularly affecting their distribution and habitat preference. These threats include disturbance caused by (1) vessel traffic, (2) habitat degradation resulting from climate change, and (3) the interactions with fishing gear.

2.4.1. Vessel Traffic

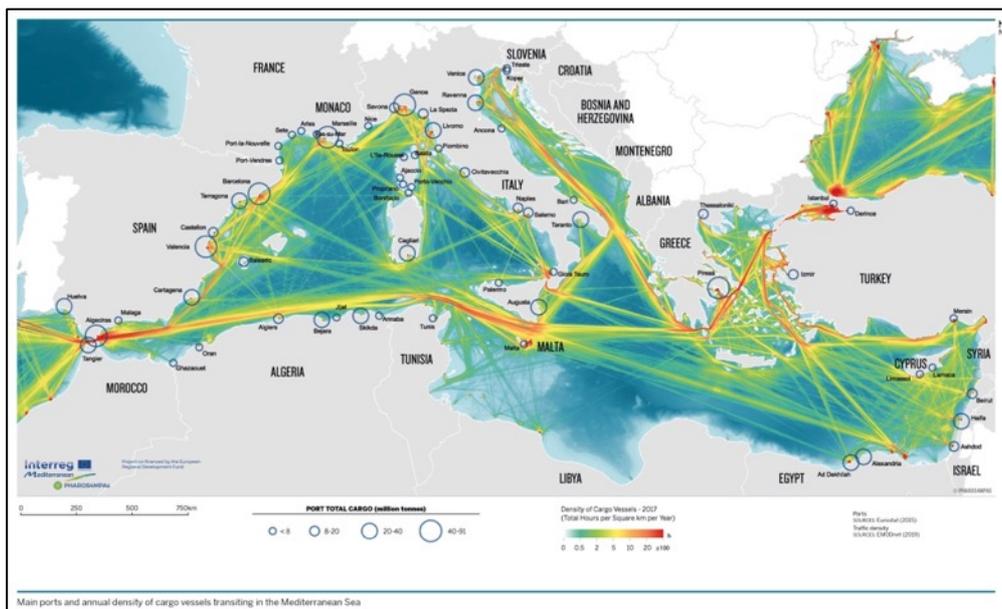
Vessel traffic poses a substantial source of disturbance to all cetacean species, resulting in a wide range of impacts. Firstly, it is recognised as a major contributor to underwater noise, which can have detrimental effects on cetacean communication, foraging, and navigation (Carlucci et al., 2021). Additionally, vessel traffic contributes to water quality degradation through sewage discharge and serves as a significant source of marine litter, further impacting

marine ecosystems (Fossi & Lauriano, 2008). Moreover, certain cetacean species, such as the fin whale, are particularly vulnerable to vessel strikes, leading to direct mortality (Panigada et al., 2006; Sèbe et al., 2023). Even the bottlenose dolphin is not exempt from this issue, often showing signs of collisions frequently documented through photo-identification (Van Waerebeek et al., 2007).

The Mediterranean Sea represents one of the most heavily trafficked waterways worldwide (**Figure 4**), encompassing approximately 27% of global maritime commercial traffic and hosting the largest cruise fleets (Union for the Mediterranean, 2021). Beside the overlap of the main shipping routes with critical cetacean habitats, vessel traffic tends to intensify during summer, due to tourism, fishing and recreational activities, involving an increased number of fishing vessels and pleasure boats (Campana et al., 2017; Coomber et al., 2016; Gannier et al., 2022; Rako et al., 2013; Saliba et al., 2021). Therefore, the expanding commercial shipping sector, coastal tourism, and the growing whale-watching industry, as well as episodes of harassment caused by recreational boaters, pose significant risks to cetacean species (Pace, Tizzi, & Mussi, 2015).

Figure 4

Vessel Traffic Density Map of the Mediterranean Sea (WWF, 2023)



In addition to its direct and immediate effects on cetaceans, such as injury, death and stress, disturbance from intense boat traffic can induce non-lethal negative effects, which have become a major source of concern in cetacean conservation (Bejder et al., 2022). While assessing long-term effects on cetacean populations is challenging due to their high mobility and the fact that they spend their lives in the ocean, frequent short-term behavioural disruptions have been observed to result in chronic consequences, potentially impacting population size. These effects may include reduced reproductive success (Lusseau et al., 2006) and increased exposure and vulnerability to pathogens (Collier et al., 2022).

A study by La Manna et al. (2019) illustrates the impact of the noise induced by boat engines on a small population of bottlenose dolphins, which appear to adjust their acoustic behaviour in response to the noise intensity. Specifically, dolphins were observed to increase their whistle frequencies in an effort to efficiently transfer information acoustically despite the loud environment, demonstrating their vulnerability to noise (La Manna et al., 2019).

According to Pirotta et al. (2015) the mere presence of a boat, intentionally or unintentionally approaching bottlenose dolphins, can cause short-term behavioural disruption, which is associated with a temporary reduction in foraging activity and more time spent for travelling. This study holds particular relevance as it quantitatively assesses the impact of boat interference on foraging behaviour, highlighting that physical presence, not only noise, significantly contributes to the disturbance. By combining acoustic and visual observations, researchers were able to quantify a 49% reduction in foraging activities in the presence of moving motorboats. This reduction was found to be proportional to the intensity of the disturbance, with boats actively following the animals causing more disruption than those following a predictable route.

The sizes and type of vessels have diverse impacts, with smaller vessels more likely to affect the surfacing intervals of the animals, because of the higher speed and unpredictability of their route, compared to larger vessels that do not modify speed and direction (Piwetz, 2019).

Changes in behavioural strategies in response to motorboats and trawlers were also investigated by La Manna et al. (2013), who revealed that the permanence of dolphin in an area decreases as the level of disturbance from motorboats increases. Moreover, the proximity of motorised boats significantly disrupts the behavioural budget of bottlenose dolphins, leading to a reduced repertoire of behaviours. This proximity often triggers avoidance, indicative of stress, replacing their usual activities such as feeding, resting, and socializing (Papale, Azzolin, & Giacoma, 2011).

These studies indicate that bottlenose dolphins may rely on diverse behavioural responses to mitigate the effects of human disturbance when their ability to modify their habitat preference by moving away from coastal areas is limited (Campana et al., 2015). On the other hand, studies on long-term avoidance in some populations have shown that this leads to the permanent displacement and abandonment of their preferred habitat (Rako et al., 2013). This variation in level of tolerance depends on population characteristics, with small, close populations being less able to avoid disturbances and, thus, more vulnerable compared to open populations (New et al., 2020).

2.4.2. Climate Change

2.4.2.1. Climate Change Impacts on Marine Biodiversity: A Global Perspective

The implications of increased atmospheric greenhouse gas emissions due to human activities, causing the Earth's climate to change, have significantly influenced marine biodiversity and ecosystem functions, culminating in considerable and progressively irreversible impacts (IPCC, 2019). Since around 1950, a significant number of marine species have undergone important range and behavioural shifts in response to ocean warming, changes in sea ice dynamics, and changes in biogeochemical conditions, including shifts in oxygen availability within their habitats (IPCC, 2019). These changes have also amplified the susceptibility of marine ecosystems to the stressors induced by human activities (IPCC, 2019).

The Sixth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2022) indicates that the impacts have surpassed prior assessments' estimations, inducing widespread degradation in ecosystem structure, function, resilience, and natural adaptive capacity, alongside modifications in seasonal timing. According to the report, a principal cause of concern is the rate at which the Arctic region is warming, which is more than twice as fast as the global average. The melting of ice in the Arctic is triggering significant transformations not only in ice-driven marine ecosystems but also extending beyond the region.

Climate change has emerged as a significant driver influencing the delicate balance of the Mediterranean marine biodiversity and ecosystems. Given its semi-enclosed nature, the region is particularly susceptible to cumulative threats, due to the substantial influence of the surrounding landscapes and further intensified by global and local climatic drivers as well as non-climatic drivers (IPCC, 2022).

Therefore, the Mediterranean Sea results in a climate change hotspot, with a variety of climatic stressors identified as the main drivers of ecosystem changes (IPCC, 2022). These stressors, as described in the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2022), include the following:

- The increase in the frequency of extreme weather events and marine heatwaves, causing mass mortalities throughout the basin.
- Acidification, impacting bivalves and coralligenous species.
- An east-west gradient in warming rate, potentially having implications for spatial variations in primary production, zooplankton, and fish abundance and diversity.
- Increasing presence of non-indigenous species, triggering biogeographic changes in fish diversity.
- The accelerated rise in sea levels, posing a significant threat to small pelagic fish.

Additionally, besides climatic factors, non-climatic stressors such as increased tourism and fishing activities are reducing ecosystems' ability to withstand the effects of climate change while also limiting organisms' migration options (IPCC, 2022).

Studies have shown that climate change can reduce cetacean abundance, change distribution and migratory patterns, deplete food availability, and negatively affect reproductive success and survival rates in many regions of the world (Learmonth et al., 2006.; Simmonds & Isaac, 2007). Direct effects of climate change on cetaceans include changes in ocean temperature, sea level rise, ocean acidification, and alterations in ocean currents and ecosystems, which can directly impact their health (Wilson et al., 1999) and their preferred habitats (Cañadas & Vázquez, 2017). Indirectly, climate change can have cascading effects on cetaceans through its impact on their ecosystems. Changes in temperature and ocean chemistry can lead to shifts in food webs and alter the abundance and distribution of prey species, potentially affecting the overall availability of food for cetaceans (Gambaiani et al., 2009; MacLeod, 2009).

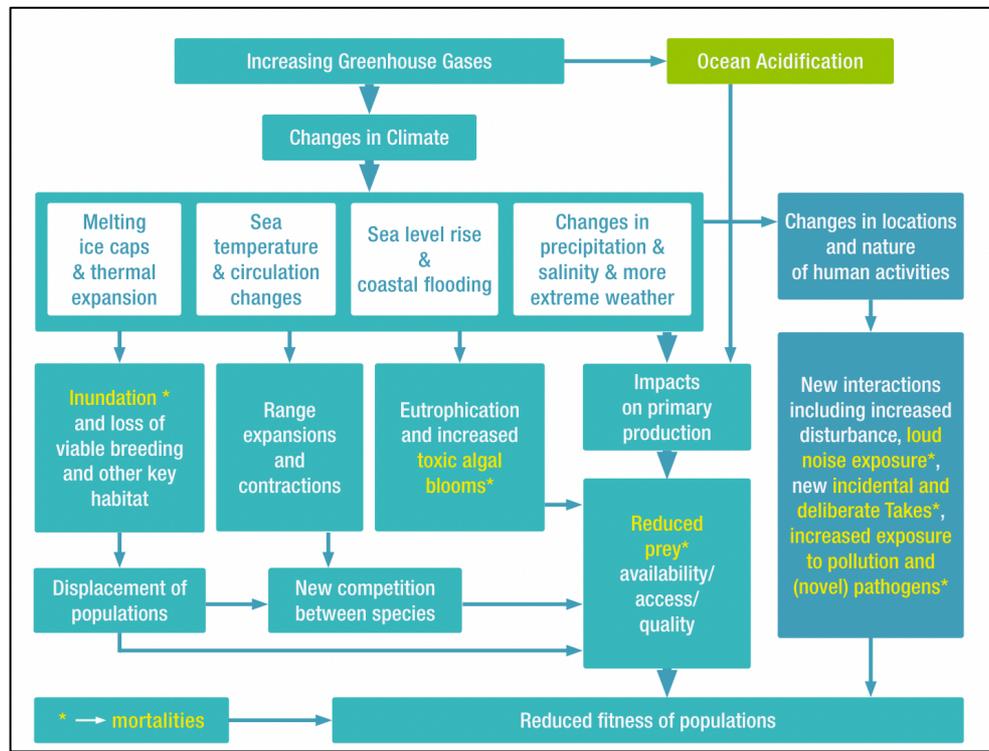
It is finally crucial to take into account the conservation status of the species, alongside the fact that those that are endangered or threatened with extinction may have their situation worsened by climate change (Simmonds, 2016).

2.4.2.2. Impacts of Global Warming on Marine Mammal Demography and Distribution: Case Studies from Diverse Ecosystems

The extensive and comprehensive body of literature on this subject presents a challenge in condensing and summarizing all the observed effects on marine mammals worldwide within the margins of a single chapter. Therefore, a summary of the impacts of climate change on marine mammals is represented in **Figure 5**. Additionally, some recent studies are described in detail to provide a more in-depth perspective on the current state of research and the critical issues.

Figure 5

Overview of the Potential Impacts of Climate Change on Marine Mammals (Simmonds, 2016, p. 316)



Note: Impacts on habitats are represented in white boxes, while areas indicated by yellow text and asterisks indicate potential mass mortalities. The blue boxes represent indirect consequences arising from shifts in human activities influenced by climate change.

Severe aftermath of global warming on the demography of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) have been recorded in Shark Bay (Australia), where a persistent marine heatwave occurred in 2011 (Wild et al., 2019). The damage to the seagrass meadows caused by this extreme weather event resulted in mass mortality of fish and invertebrates and in the consequent depletion of prey availability. Such changes affected the vital rates of the dolphin population living in the area, with a significant decrease in the survival rate, protracted over an extended period after the heatwave. Additionally, as a result of the prey reduction, females were observed spending more time foraging, which heightened the exposure of calves to predation, subsequently impacting calf survival rates. Moreover, an increase in abortion rates and a reduction in fertility were also observed.

A recent severe drought in Brazil has been associated with the deaths of over 100 pink river dolphins (*Inia geoffrensis*). While the exact causes of this mass mortality event are still under investigation, the most likely hypothesis is related to changes in water depth and temperature (WDC, 2023).

In terms of distribution, the warming temperatures in the North Atlantic have led to a northward shift presence of species that favour warmer waters, such as striped dolphins. Conversely, species that prefer colder waters, like the white-beaked dolphin (*Lagenorhynchus albirostris*) and the northern bottlenose whales (*Hyperoodon ampullatus*), have experienced a contraction in their ranges towards the North (Lambert et al., 2014).

Furthermore, Azzellino et al. (2008) investigated the relationship between SST and the distribution of fin whales, striped dolphins, and sperm whales in the North-Western Mediterranean Sea, concluding that SST is one of the key factors in these species' habitat selection and that the distribution of cetaceans in this area may change in response to climate change.

Cetacean habitat modifications in the Mediterranean Sea have also been described in relation to acidification induced by increased CO₂ concentrations (Pace, Tizzi, & Mussi, 2015). The ecological repercussions of acidification on the food web, in particular, are linked to changes in food availability for higher trophic levels. An example is provided by pilot whales that feed on squids, which are sensitive to the decrease in seawater pH (Nunny and Simmonds, 2020).

2.4.2.3. Climate Change Impacts on Bottlenose Dolphins: Varied Responses Across Biogeographical Contexts

The International Whaling Commission (IWC, 2010) has identified three primary responses of small odontocetes to climate change: thermal stress avoidance through redistribution, altered distribution driven by changes in ecosystem dynamics and food availability, and potential stress experienced by species restricted to specific habitats.

According to the Report of the Workshop on Small Cetaceans and Climate Change (IWC, 2010), climate change might impact bottlenose dolphins in two ways, including redistribution and restricted movement depending on the area. Some populations, in particular, exhibit a higher level of behavioural adaptation to variations in water temperature, as evidenced by short-term and long-term range shifts associated with changes in water temperature.

However, this adaptability is not uniform across all populations, and resident groups with restricted ranges may face limitations in their ability to shift to more suitable habitats. This could expose them to thermal stress, alterations in their food sources, and increased risks from diseases, biotoxins, and contaminants, potentially affecting their survival and reproductive success (IWC, 2010).

A comprehensive review conducted by Van Weelden et al. (2021) examined the impact of rising SST on bottlenose dolphins' distribution worldwide. In contrast with previous studies by Learmonth et al. (2006) and MacLeod et al. (2009), which observed range expansion in response to increased SST, Van Weelden et al.'s findings indicate that the species' high site fidelity results in limited distribution changes in relation to climatic shifts. This discrepancy in findings can be attributed to variations in their vulnerability to environmental factors, such as SST, salinity, pH, and primary productivity, which may vary depending on their habitat preferences (Sousa et al., 2021). For example, in the waters around Madeira Island, offshore populations of bottlenose dolphins display greater vulnerability compared to other cetaceans in the region, while coastal populations exhibit relatively lower susceptibility to the effects of climate change (Sousa et al., 2021).

Not many studies have been conducted to investigate the effects of climate change on bottlenose dolphins in the Mediterranean Sea. Nonetheless, Gambaiani et al. (2009) suggest that climatic stressors have reduced the availability of bottlenose dolphin prey in different areas of the basin. Increased SST in the Adriatic Sea, in particular, has resulted in a drop in key prey species populations due to increased competition with thermophilic species. This competition has led to changes in behaviour, such as an increase in the time spent foraging, among the affected populations of bottlenose dolphins (Gambaiani et al., 2009). Prey depletion has also had a significant impact on the health and abundance of bottlenose dolphin populations in the Ionian Sea (Politi & Bearzi., 2004, as cited by Gambaiani et al., 2009). To cope with the shifts in prey species availability, these populations have had to modify their feeding strategies,

resulting in increased time and energy expenditure during foraging activities, which, in turn, has contributed to increased vulnerability and a reduction in their reproductive success.

Furthermore, during the abnormally hot summer of 2003, coastal bottlenose dolphins demonstrated transitory migration to open sea waters off the coast of Corsica, as observed by Dhermain (2003) and cited by Gambaiani et al. (2009). This observation holds particular significance because it sheds light on dolphins' adaptive responses to the increasing occurrence of extreme events, as well as how their distribution may be affected.

In light of these findings, understanding the multifaceted impact of climate change on bottlenose dolphins requires a comprehensive examination of separate populations within different biogeographical contexts and dedicated long-term studies.

2.4.3. Fisheries Interactions

Cetacean populations are facing increasing threats due to human activities, and fishing is among the primary anthropogenic factors influencing their dynamics. Fishing activities can have both direct and indirect consequences on cetaceans (Northridge, 2018), leading to critical challenges in marine mammal conservation efforts.

The direct impacts of fishing activities involve physical interactions between cetaceans and fishing gear, such as entanglement and bycatch, which pose significant threats to these species. Additionally, interactions in the form of depredation, where cetaceans actively interact with fishing gear to access baits and catch, may result in economic losses and escalate conflicts between fishermen and marine mammal populations perceived as competitors (Bearzi et al., 2004; TUDAV, 2017). In numerous instances, both the mentioned problems of direct interaction between cetaceans and fishing activities are present within the same fisheries (Gonzalvo & Carpentieri, 2023).

Beyond the immediate consequences, the term “bycatch” encompasses the unintentional capture or entanglement of cetaceans in fishing gear intended for other species. This global issue spans various fishing activities, scales, and gear types, and given the demographic traits of cetaceans, it represents a severe danger to their populations due to the high risk of mortality (Reeves et al., 2013). In instances where direct mortality does not occur, the long-term survival and welfare of marine animals may still be impacted by entanglement-related implications. The entanglement process can subject the animals to elevated levels of stress and result in behavioural alterations that can have significant consequences on their overall well-being and survival (Dolman & Moore, 2017).

In response to the expanding fisheries sector, certain cetacean populations, notably odontocetes, have adapted their behaviour to capitalize on food resources provided by fishing activities, allowing them to reduce their energy utilisation while foraging (Bonizzoni et al., 2022). This behavioural change has led to interactions where cetaceans engage in foraging around fishing gear, impacting the availability of marketable organisms and bait. While the scientific community commonly uses the term “depredation” to describe this phenomenon, a more suitable term “foraging around fishing gear” has been proposed to accurately convey the nature of these interactions (Bearzi & Reeves, 2022).

Indirectly, overfishing driven by the fishing industry may contribute to prey depletion and habitat degradation, further impacting the marine ecosystem, influencing the distribution and abundance of cetacean prey species and increasing competition on food sources (Giralt Paradell et al., 2021). Additionally, anthropogenic food patches resulting from fishing activities and fish farming, have the potential to shape not only the distribution but also the behavioural repertoire and social structure of the species (Blasi et al., 2015; Díaz López, 2012; Pace et al., 2012).

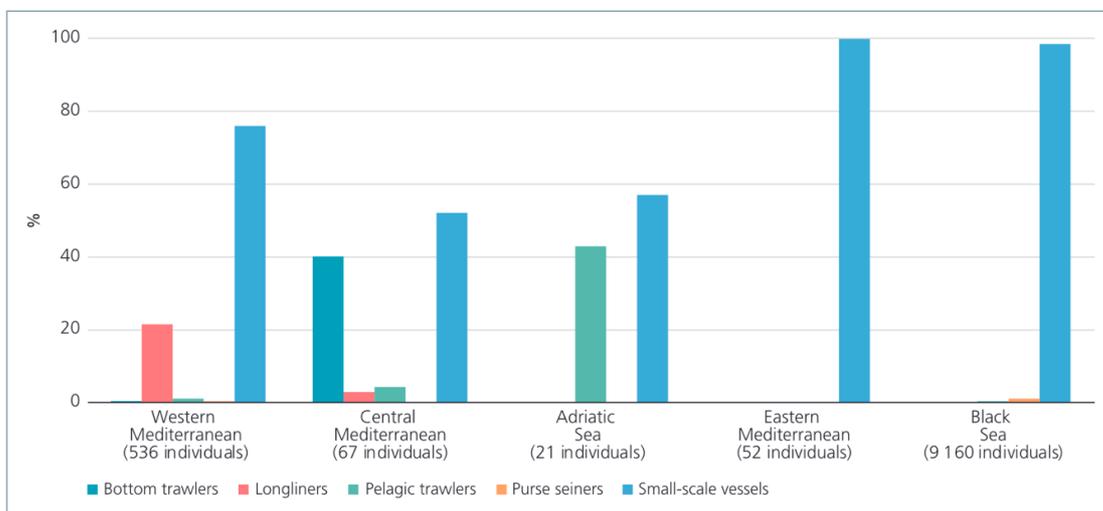
The illegal, unreported, and unregulated (IUU) fishing practices, including the use of pelagic driftnets despite being declared illegal in EU in 2002, continue to pose significant threats to

marine life, directly and indirectly affecting marine mammal populations, resulting in the bycatch of cetaceans such as common dolphins, striped dolphins and Risso's dolphins (OceanCare, 2021; ACCOBAMS, 2019).

In the Mediterranean region, interactions between fishing activities and cetaceans are primarily observed within the context of coastal small-scale fisheries. According to the Food and Agriculture Organisation (FAO, 2020), gillnets and trammel nets emerge as the predominant fishing gear types associated with reported incidents of unintentional marine mammal catch (**Figure 6**). Trammel nets are distinguished by their three-layered netting structure deployed in the water, specifically designed to capture fish through entanglement. Gillnets consist of single netting walls, vertically suspended by a float line and weighted at the bottom, strategically intended to entangle fish as they pass through the mesh.

Figure 6

Reported Incidental Catch of Marine Mammals by Vessel Group and GFCM Subregion, between 2000 and 2020 (FAO, 2020, p. 73)



Note: The chart illustrates the outcome of a subregional analysis conducted by FAO, emphasizing the significant level of interaction between marine mammals and small-scale fisheries.

The predominant cetacean species found in bycatch reports are the striped dolphin (47.7%), followed by the common dolphin (20.5%), and the bottlenose dolphin (13.8%). While the ban on large driftnets has led to a decrease in the number of cetaceans incidentally caught, the lack of standardised methods and data collection procedures, along with inadequate spatial and temporal coverage, hinders a comprehensive assessment of the complete extent of the issue (FAO, 2020). This results in significant knowledge gaps that persist across most of the General Fisheries Commission for the Mediterranean (GFCM) subregions. Further research and improved data collection are crucial to better understand and address the impact of bycatch on marine mammal populations in the Mediterranean (FAO, 2020).

Limited data are available regarding the impact of Fish Aggregating Devices (FADs) on cetaceans, and their interactions with these man-made fishing devices remain poorly understood. FADs typically consist of a floating component, often made of logs or palm leaves, anchored to the seafloor by plastic lines, and are designed to attract pelagic species that are subsequently captured using surrounding nets (Sechi et al., 2023), representing a source of

easily accessible prey for predators as well as a potential way of interaction between dolphins and fishing gear (Blasi et al., 2016).

However, a significant concern arises when many of these devices are not retrieved by fishermen (Blasi et al., 2016), leading to their abandonment and designation as Abandoned, Lost, and Discarded Fishing Gear (ALDFG; Gilman et al., 2021). The presence of FADs poses considerable risks, particularly regarding bycatch mortality, making them one of the highest-risk types of fishing gear with potential adverse effects on cetacean populations (Gilman et al., 2021).

The first case of a cetacean entangled in a FAD in the Mediterranean Sea has recently been published by (Manfrini et al., 2023), who documented the death of a striped dolphin in the Tyrrhenian Sea as a result of starvation caused by the entanglement. However, social media platforms offer the opportunity to gather information from videos and photos, revealing that in Malta at least two entanglement episodes have involved dolphin individuals of different species in recent years. In August 2020, a bottlenose dolphin was found entangled in a FAD off Dwejra, in the north of Gozo, and successfully released thanks to the prompt intervention of the authorities (Nature Trust - FEE Malta, 2020). Additionally, local fishermen came across an endangered common dolphin in distress and released it in the waters off Malta in November 2022 (Lovin Malta, 2022). As seen in the video, the dolphin was found entangled in a rope attached to a floating part and a palm leaf, which was most likely an abandoned component of a FAD (**Figure 7**).

Figure 7

Fishermen in Malta Release a Common Dolphin from Entanglement Caused by the Floating Part of an Abandoned FAD (Lovin Malta, 2022).

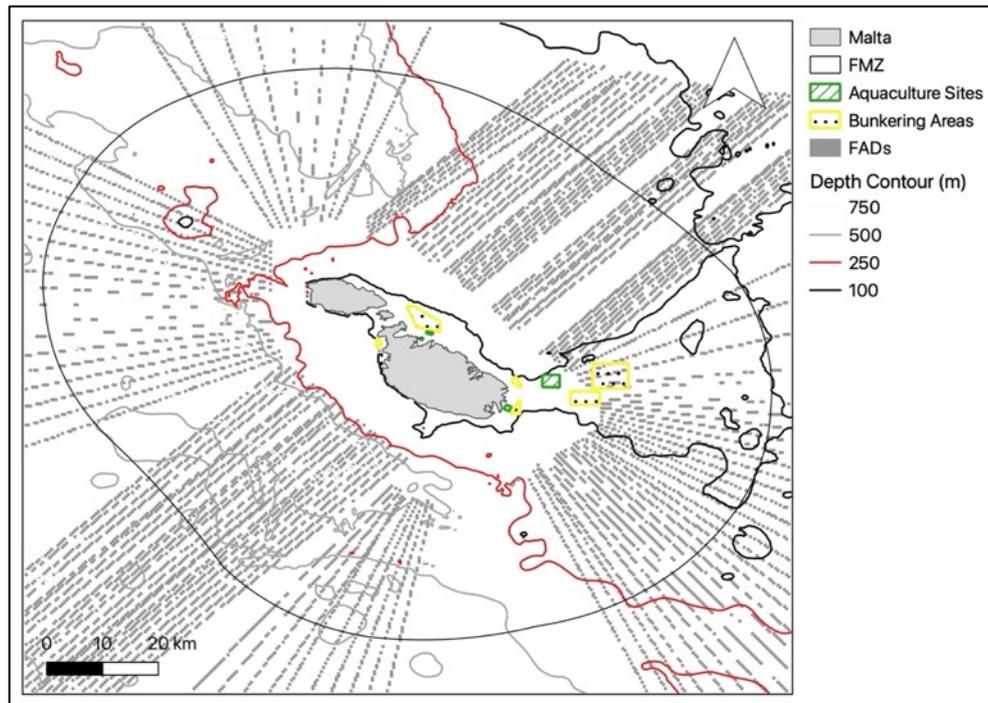


Malta has a fleet of 104 registered vessels actively engaged in artisanal dolphinfish (*Coryphaena hippurus*) fishing (Manfrini et al., 2023), which occurs from mid-August until the end of December. Interesting to note is that each of these vessels deploys a number of FADs, ranging from 30 to 100 FADs per vessel. This adds up to 3,000 to 10,000 possible FAD installations across the region (Manfrini et al., 2023). The extensive deployment of FADs

(Figure 8), when considered alongside the possibility of unreported cetacean entanglements in these devices, raises concerns about the real and potentially underestimated risk posed to local cetacean populations, notably common and bottlenose dolphins (Manfrini et al., 2023; Sechi et al., 2023).

Figure 8

Location of FADs within the FMZ in Malta



Note: The trajectories of FADs were retrieved from the Malta Spatial Data Infrastructure portal (<https://msdi.data.gov.mt/index.html>).

Fish farming, or aquaculture, also offers a potential foraging opportunity for cetaceans, particularly in oligotrophic waters like the Mediterranean Sea. The establishment of aquaculture facilities enhances the productivity of the surrounding areas, subsequently attracting marine mammals, in particular bottlenose dolphins, and leading to an increased presence of these animals in the vicinity of the farms (Díaz López, 2012; Piroddi et al., 2011a). The higher fish density around certain areas reduce the energy expenditure required for foraging in bottlenose dolphins, known for their opportunistic behaviour. Moreover, the availability of discarded or escaping fish during harvesting operations serves as an additional food source, influencing the occurrence and distribution of dolphins in the surrounding regions (Díaz López, 2017; Díaz López et al., 2005).

Aquaculture is associated with several potential consequences for cetaceans, although it is important to note that there have been relatively few documented cases of these interactions (Bath et al., 2023). Nevertheless, certain risks stand out as primary concerns for cetaceans when it comes to aquaculture facilities and operations. According to Bath et al. (2023), these include:

- **Increased Risk of Collision:** Aquaculture often involves the use of boats and vessels for various tasks related to fish farming. This increased maritime activity can increase the risk of collisions between these boats and cetaceans, which may lead to injuries or fatalities.

- Behavioral Changes: The presence of aquaculture facilities can offer cetaceans easier access to food sources. This, in turn, might alter their natural behaviors, as they may be attracted to the readily available fish near the farms. Changes in foraging patterns and increased proximity to human activity are some of the potential consequences.
- Entanglement in Nets: Aquaculture often employs large underwater cages or net systems to contain the farmed fish. Cetaceans, in their movements, could become accidentally entangled in these nets, leading to entrapment and potential harm.

2.5. The Need for a Spatial Analysis in Determining the Impact of Environmental Variables and Anthropogenic Stressors

Species distribution modelling is generally used to describe the relationships between species occurrences and environmental factors. These models can be used to make predictions about the potential distribution of habitats or species in different scenarios, including under future environmental changes (Azzellino et al., 2012; Cañadas et al., 2005). Such modelling exercise is particularly useful for assessing the influence of environmental and anthropogenic stressors on species distributions and their habitats (Fortuna, 2006).

Maximum entropy (MaxEnt) models are widely employed for species distribution modelling based on presence-only records (Elith et al., 2011; Pace et al., 2019). These models enable the prediction of species occurrence in relation to the environmental attributes of the sighting locations. A significant advantage of MaxEnt over other regression-based models, such as generalised linear or additive models (GLMs or GAMs), lies in its ability to achieve high predictive accuracy even with limited sample sizes and opportunistic data (Fernandez et al., 2018). This characteristic makes MaxEnt a valuable tool for ecological research, particularly in situations where data collection may be challenging or when only presence data is available for the species of interest (La Manna et al., 2016). However, it is crucial to consider potential biases, such as sample selection bias, when working with presence-only data in MaxEnt models, as non-random observations could lead to overestimations of species habitat suitability in easily accessible or intensively surveyed areas (Elith et al., 2011).

In MaxEnt models, various environmental variables are frequently employed to assess habitat suitability, encompassing both oceanographic and physiographic features. Significant examples of these variables include sea surface temperature (SST), sea surface salinity (SSS), sea surface chlorophyll-a concentration, depth, bathymetry, and slope. These factors have been investigated as predictors of cetacean presence (La Manna et al., 2016; Pace et al., 2018) and are considered proxies for prey availability, as they influence habitat selection by marine mammals (La Manna et al., 2020). Their inclusion in the models is critical for understanding the ecological requirements and preferences of cetaceans, as they significantly contribute to shaping the distribution patterns of the species across their habitat.

2.6. Current Knowledge on Bottlenose Dolphins and Conservation Efforts in Maltese Waters

The Maltese Islands benefit from a unique combination of geographical, oceanographic, and ecological factors that create a suitable environment for diverse cetacean populations. Located in the passage connecting the western and eastern basins, the surrounding waters experience significant dynamism. Consequently, all eight cetacean species commonly found in the Mediterranean have been reported in the waters surrounding Malta (Notarbartolo di Sciara, 2002). However, the bottlenose dolphin, the common dolphin and the striped dolphin are found

to be the most frequently encountered and the most abundant species in the waters surrounding the Maltese archipelago (Patti et al., 2022; Vella et al., 2023).

The significance of Malta as a Cetacean Critical Habitat (CCH) cannot be overstated. The common dolphin, which is categorised as Endangered in the Red List of the International Union for Conservation of Nature (IUCN), finds crucial habitats within Malta's waters. This acknowledgment and designation as a CCH were officially granted during the ACCOBAMS Meeting of Parties in 2010 (ACCOBAMS, 2010), underscoring Malta's dedication to the conservation of cetaceans. Moreover, Malta has also been considered for inclusion in the proposed Mediterranean Science Commission (CIESM) Pelagian Sea Marine Peace Park, highlighting its role in preserving marine biodiversity and fostering scientific research (Vella et al., 2010). In addition, Malta has been recognised as a Candidate Important Marine Mammal Area (cIMMA) by the Marine Mammal Protected Areas Task Force of the IUCN (<https://www.marinemammalhabitat.org/imma-eatlas/>).

In Malta, the protection of cetaceans is ensured through a combination of regional and international laws and agreements, with a significant responsibility assigned to national legislation. Specifically, the conservation of these species is guaranteed by means of Subsidiary Legislation S.L.549.44, known as the Flora, Fauna and Natural Habitats Protection Regulations, which incorporates the provisions of the Habitats Directive 92/43/EEC into the national legal framework. Notably, Malta is home to three designated Special Areas of Conservation (SACs) (MT0000113, MT0000115, and MT0000116), established with the primary aim of conserving the common bottlenose dolphin and the loggerhead turtle (*Caretta caretta*). This designation was a result of the Project LIFE+ MIGRATE (LIFE11NAT/MT/1070), implemented in 2013 (LIFE+ MIGRATE, 2013).

However, while bottlenose dolphins are commonly found in Maltese waters, as demonstrated in recent assessments conducted to meet the requirements of the MSFD (ERA, 2020), information regarding their abundance is inconsistent, and information on their distribution remains limited.

An earlier estimate conducted by Vella (1998, as cited in UNEP, 2017) suggested the presence of approximately 800 individuals based on aerial surveys. In contrast, more recent research carried out during the LIFE11 NAT/MT/1070 project reported an estimated and corrected abundance of 112 individuals for the year 2014, based on photo-identification data (LIFE+ MIGRATE, 2013). The ambiguity in terms of abundance numbers poses a challenging issue, and it can be attributed to a variety of factors. It may stem from differences in the methodologies used to estimate abundance or from an actual decline in the population. In any case, the exact cause of this discrepancy would require further investigation and a thorough review of the methods used in previous assessments to pinpoint whether the variations are primarily due to methodological differences or a true population decline.

Based on the outcomes of the LIFE11 NAT/MT/1070, the distribution of cetaceans was documented in the After-LIFE Conservation Plan (LIFE+ MIGRATE, 2016b). A kernel density map was generated using an encounter rate calculated for all observed species collectively. The analysis reveals a larger area with a higher likelihood of cetacean presence, located in the deepest regions of the western/north-western survey area. While the map highlights areas where cetaceans were most frequently encountered, it does not provide specific hotspots for bottlenose dolphins alone.

The assessment of bottlenose dolphin distribution in Maltese waters, carried out under the LIFE11 NAT/MT/1070 project, has revealed a random distribution pattern, making it impractical to provide a specific distribution map for this species (LIFE+ MIGRATE, 2016a). Nonetheless, this study did find a consistent preference among bottlenose dolphins for areas with a depth range between 200 meters and 600 meters (LIFE+ MIGRATE, 2016b). In general, the report indicates that the waters surrounding the Maltese Islands do not seem to hold

substantial importance for this specific dolphin species. However, it is worth noting that this conclusion, which differs from prior and subsequent research conducted in Maltese waters (ERA, 2021; Vella, 2004 as cited in UNEP, 2017), may be attributed to the distinct criteria set forth by the HD and the relatively limited scope of the survey. In light of these findings, the three protected areas were established primarily for the loggerhead turtle, for which important habitats were identified; but, because cetaceans can also be found in the same areas, the SACs should nevertheless provide enough protection to the bottlenose dolphin in accordance with the HD (LIFE+ MIGRATE, 2016a).

More details about the bottlenose dolphin's distribution in Malta are provided by Vella (2004, as cited in UNEP) and Patti & Mifsud (2019). Vella's work highlights a clear preference for specific habitats, indicating a tendency for bottlenose dolphins to favour deep, offshore waters that are between 400 and 600 metres deep, but with a notable shift toward coastal areas during the summer and autumn.

On the other hand, Patti & Mifsud's research highlights a year-round concentration of dolphin sightings near the south-eastern aquaculture sites, suggesting a consistent utilization of the southern region by these marine mammals. Conversely, in the absence of fish farms in the north-west, dolphins are observed further offshore.

Despite these insights, both studies lack specificity concerning the environmental variables influencing the dolphins' habitat preferences. Key factors such as water temperature, primary productivity, prey availability, and oceanographic conditions as well as the use of habitat remain unexplored in these works.

The LIFE11 NAT/MT/1070 project identified the threats faced by the targeted species of relevance to the SACs. These threats encompassed macro- and micro-pollution originating from residential, recreational, and industrial activities, including tourism, sports, and leisure. Additionally, it acknowledged the depletion of prey resulting from fishing and the risk of by-catch (LIFE+ MIGRATE, 2013). Moreover, the project mentioned the issue of disturbance caused by shipping and ferry lanes, which could adversely affect the well-being of the protected species. However, it is essential to note that despite recognising these potential threats, the project did not investigate their specific impact on bottlenose dolphins, nor did it assess the spatial exposure of these species to these identified threats. To date, no quantitative nor qualitative analysis of the negative impacts of human activities has been conducted for cetaceans in Maltese waters.

Nature Trust Malta (2015) also reported a list of threats that could affect cetaceans in Maltese waters, including underwater noise, bycatch, entanglement and ingestion of fishing gear, vessel strikes, pollution, and harassment by leisure boats.

However, as of the current literature review, there is a noticeable gap in research concerning the spatial exposure of bottlenose dolphins to risks associated with human activities. No studies have been identified on this subject to date.

In conclusion, the data on bottlenose dolphins available to date appear to be incomplete, making it difficult to determine their distribution accurately and therefore to address specific threats affecting this species. Despite the implementation of protective measures and regulations aimed at conserving these species in SACs, uncertainties persist regarding their habitat preferences and distribution, and the various threats they encounter.

The absence of a clear understanding of bottlenose dolphin distribution in Maltese waters has been explicitly recognized in the Malta's Programme of Measures for the Marine Strategy Framework Directive (ERA, 2023). According to this report, there is acknowledgment of a widespread distribution of bottlenose dolphins in the region. However, the report cites the inability to identify specific areas due to low abundance values as a significant limitation. Furthermore, the report emphasises the importance of conducting dedicated studies to address

both the distribution patterns of bottlenose dolphins and the potential impact of threats on the species.

As demonstrated by the varying estimates of their abundance over the years, there is a need for systematic, long-term monitoring to gather more reliable and detailed information (Mannocci et al., 2018). The possible reasons why this has not occurred yet may be due a lack of funds and resources for carrying out monitoring of highly mobile species living in the marine environment, which is susceptible to significant unpredictability.

Nevertheless, due to the absence of systematic monitoring, the utilization of Species Distribution Models (SDM) tools, such as MaxEnt, has proven to be effective in extracting crucial insights into the species' distribution. This approach optimizes the available data, as discussed in the preceding section (see section 2.6), providing valuable information that can be instrumental in evaluating the impact of various stressors.

3. Methods

3.1 The Study Area

The Maltese archipelago, hereafter referred to as Malta, is a group of islands situated between the eastern and western basins of the Mediterranean Sea (Cassar et al., 2008). Located about 96 km south of Sicily and 290 km north of Libya's coast, it covers a total land area of around 332 km² and includes three main inhabited islands: Malta (246.5 km²), Gozo (65.8 km²), and Comino (2.9 km²), as well as a few small uninhabited islets (Cassar et al., 2008). Malta presents unique biogeographic characteristics, such as an unusually long coastline, higher-than-average rates of endemic species, and a significant genetic distinctiveness among its plants and animals due to its geographical isolation (Deidun, 2010).

Malta's climatic profile is distinguished by hot, arid summers and temperate, moist winters. The annual precipitation is notably modest, accompanied by considerable exposure to sunlight (Galdies, 2022). In recent decades, clear alterations in key climatic variables, including sunshine duration, air temperature, rainfall, wind speed, relative humidity, and SST, have been observed. These changes are linked to the phenomenon of global warming, resulting in warmer ambient temperature and a reduction in regional humidity levels compared to pre-1990 conditions (Galdies, 2022).

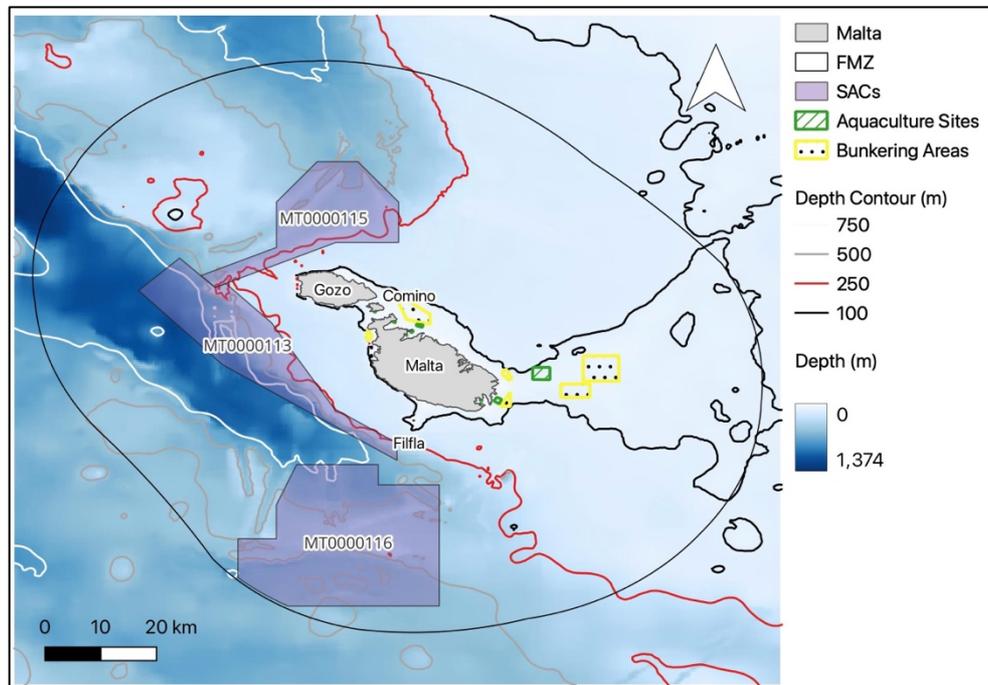
From a geological perspective, Malta is situated on the Pelagian Platform (Pedley et al., 1978), which defines a relatively shallow continental shelf between the southern Sicilian region and north-western Libya, demarcating the Ionian Basin from the Western Mediterranean. The north-eastern sector of this platform, known as the Malta Plateau, features a predominantly shallow and flat seafloor topography, characterised by depths typically within the range of 100 to 150 metres (Micallef et al., 2016). In contrast, the western part of the platform encompasses the Malta Graben, an elongated depression with significantly greater bathymetric depths (Civile et al., 2021). Additionally, the platform acts as a primary corridor for Atlantic waters that enter via the Gibraltar Strait and move eastward, known as Modified Atlantic Water (MAW; Millot & Taupier-Letage, 2005).

The study area includes Malta's maritime boundary, extending to 25 nautical miles from the baseline. This boundary coincides with the Fisheries Management Zone (FMZ) designated by Malta's authorities for managing and regulating fishing activities within its waters. The total area of the study region is approximately 11,980 km², surrounding the archipelago.

Malta has designated 4,138 km² of marine waters for conserving significant marine habitats and species, complying with the Habitats Directive and Birds Directive. This area represents over 35% of Malta's coastal and marine waters within the 25-nautical-mile FMZ boundary. Among the Marine Protected Areas that have been established under the Flora, Fauna, and Natural Habitats Protection Regulations (S.L. 549.44), three offshore areas (MT0000113, MT0000115, and MT0000116) represent the SACs designated for the protection of the bottlenose dolphin and the loggerhead turtle, forming part of the European Natura 2000 Network (**Figure 9**).

Figure 9

Study Area Located within Malta's Fisheries Management Zone (FMZ) and Marine Protected Areas Designated as Natura 2000 Special Areas of Conservation (SACs) for the Bottlenose Dolphin and the Loggerhead Turtle in Maltese Waters



3.2 Data Sources for Bottlenose Dolphin Sightings

Data on the occurrence of bottlenose dolphins in the study area were retrieved from the available datasets owned by the ERA and BirdLife Malta. Such datasets result from separate dedicated surveys carried out within the FMZ, covering coastal and offshore areas around the Maltese archipelago, over a nine-year period (2012 – 2021). Specifically, for the purpose of this study, the following data sources were used:

- 1) EU LIFE+ Malta Seabird Project (LIFE10 NAT/MT/000090). Between 2012 and 2013, BirdLife Malta' collected opportunistic data on cetaceans during vessel-based surveys aimed at identifying marine important bird areas within Malta's FMZ. The significant effort allowed for the collection of substantial data on cetaceans, for a total of 196 sightings ($n = 196$), of which 65 are bottlenose dolphins ($n = 65$).
- 2) LIFE+ MIGRATE (LIFE11 NAT/MT/1070). The project used visual and acoustic vessel-based surveys on cetaceans, carried out in 2013 and 2014. Fifty ($n = 50$) sightings of cetaceans were reported, of which 38 were bottlenose dolphins ($n = 38$).
- 3) LIFE BaĦAR for N2K (LIFE 12/NAT/MT/000845). During offshore surveys performed in the summers of 2015 and 2016, cetaceans were recorded through occasional sightings. Thirty-eight sightings ($n = 38$) were documented, of which 15 were bottlenose dolphins ($n = 15$).
- 4) EMFF 8.3.1 Marine Environmental Monitoring (GF/Admin/40/2020). Vessel-based surveys were carried out in the summer 2021 in two offshore Natura 2000 sites, MT0000115 and MT0000116. A total of 21 sightings ($n = 21$) of cetaceans were recorded, including six sightings of bottlenose dolphins ($n = 6$). One aerial survey was also

conducted to monitor the presence of cetaceans across the FMZ, which resulted in the detection of five groups of cetaceans ($n = 5$), including one ($n = 1$) group of bottlenose dolphins. The project contributed seven sightings ($n = 7$) to the dataset.

One hundred and twenty-five ($n = 125$) geolocated sightings obtained from the different initiatives (**Table 2**) were initially converted into Comma-Separated Values (CSV) for the analysis. Subsequently, a data quality check was executed to remove duplicates. The sightings were therefore reprojected using the software QGIS 3.28.9 “Firenze” (QGIS, 2023) in the World Geodetic System 1984 (WGS84) coordinate reference system (**Figure 10**).

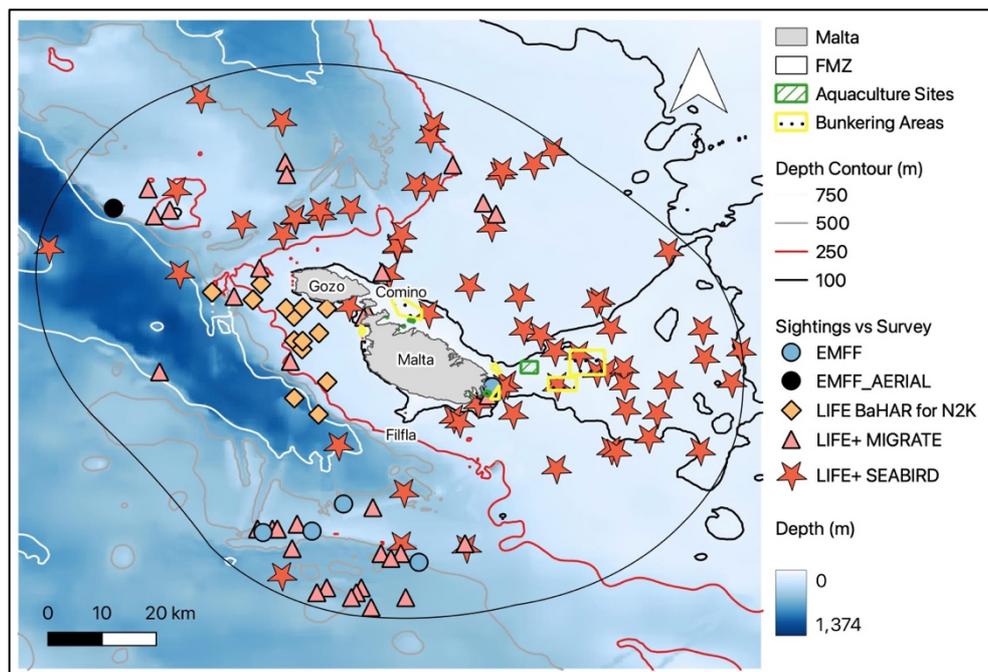
Table 2

Description of the Datasets Used in the Analysis

Initiative	Method	Period	# Records
LIFE+ MIGRATE	Systematic vessel-based line transects	2013-2014	38
EU LIFE+ Malta Seabird Project	Systematic vessel-based line transects	2012-2013	65
LIFE BaHAR for N2K	Non-systematic vessel-based survey	2015-2016	15
EMFF 8.3.1 Marine Environmental Monitoring	Systematic vessel-based line transects in MT0000115 and MT0000116	2021	6
	Aerial line transects	2021	1

Figure 10

Distribution of Bottlenose Dolphin’s Sightings Recorded between 2012 and 2021 within The Fisheries Management Zone (FMZ) during All Survey Initiatives Considered in the Study



The diverse datasets included in this study represent the most extensive and substantive repositories of cetacean sighting data available for the study area, encompassing various projects conducted over multiple years and employing different survey methods. Nonetheless, temporal gaps within the data and a potential sampling bias are acknowledged and will be addressed in the analysis, thus ensuring the rigor and reliability of the findings.

Finally, although the majority of sightings were observed during the spring and summer months, all recorded sightings were included in the analysis due to their occurrence throughout all seasons.

3.3 Spatial Analysis of Model Predictors and Anthropogenic Activities Using QGIS

3.3.1 Environmental Predictors

The software QGIS was used for SDM generation (see Chapter 3.4). Selected variables, which include bathymetry, slope, aspect, SST, sea surface salinity SSS, chlorophyll-a, and dissolved oxygen, were intentionally chosen due to their documented influence on bottlenose dolphin habitat preferences and occurrences, as highlighted in prior research (Giralt Paradell et al., 2019; La Manna et al., 2016, 2020; Pace et al., 2019).

To be incorporated into the SDM, both static variables (depth, slope, aspect) and dynamic variables (mean SST, mean SSS, chlorophyll-a, dissolved oxygen) were converted into raster files. To facilitate this process, a grid comprising 360 columns and 317 rows was employed, with the extent slightly exceeding the boundaries of the actual study area. This adjustment was made to meet the shape requirements according to the input format specifications of the SDM. All the raster files were reprojected to align with the WGS84 coordinate reference system.

The depth was retrieved from the General Bathymetric Chart of the Oceans (GEBCO, 2023), which provides elevation data in meters for ocean and land. The bathymetry data were downloaded in form of a GeoTIFF file, from the atlas available online for user-defined areas (<https://download.gebco.net>), on a 15 arc-second (about 450 meters) resolution.

The bathymetry raster file was used for the computation of seafloor slope, defined as the percentage rate of alteration between a specific point and its neighbouring surroundings (referred to as slope hereafter) and expressed in degrees. The same raster file was used for the determination of “seafloor” aspect, representing the compass direction that a slope is oriented towards (referred to as “aspect” hereafter). Both elements were calculated using raster analysis tools in QGIS.

Raster files of dynamic variables (SST, SSS, chlorophyll-a, dissolved oxygen) were generated using the E.U. Copernicus Marine Service Information (<https://marine.copernicus.eu>), which represents the marine part of the Earth observation component of the European Union’s Space program. The information services provide the state-of-the-art ocean information by combining satellite and in-situ observations.

Sea Surface Temperature data were obtained using the High Resolution L4 Sea Surface Temperature Reprocessed product, based on observations from multiple satellite sensors. The SST data were extracted from the CMEMS Reprocessed (REP) Mediterranean (MED) dataset, featuring a spatial resolution of $0.05^\circ \times 0.05^\circ$ (CMEMS, 2023a). The data were finally converted from Kelvin to Celsius using the Raster Calculator in QGIS.

Chlorophyll-a and dissolved molecular oxygen data were retrieved from the Mediterranean Sea Biogeochemical Reanalysis product with a resolution of $0.042^\circ \times 0.042^\circ$ (ca. 4 km), extracted at -1 m elevation (CMEMS, 2023b), where chlorophyll-a is expressed as mass concentration in sea water (mg/m^3) and dissolved molecular oxygen is given in mole concentration in sea water (mmol/m^3). The product is obtained by means of the MedBFM

model, which produces forecasts and reanalysis assimilating satellite data of surface chlorophyll and in-situ profiles of chlorophyll and nitrates.

Salinity was retrieved from the Mediterranean Sea Physics Reanalysis product, generated by a hydrodynamic model from the Nucleous for European Modelling of the Ocean (NEMO) and the OceanVAR variational data assimilation scheme, featuring a resolution of $0.042^\circ \times 0.042^\circ$ (ca. 4 km), extracted at -1 m elevation (CMEMS, 2023c).

Daily and, when accessible, multi-year data for each dynamic variable were collected within the time span of January 1, 2012, to December 31, 2021. The average for each dynamic variable across the whole period was obtained using Climate Data Operators (CDO), a collection of command-line tools that are used to manipulate and aggregate NetCDF climate data (<https://code.mpimet.mpg.de/projects/cdo>), and imported into GIS as raster layers.

All raster files containing static and dynamic data were downsampled to the same resolution of the GEBCO bathymetry raster (450 m) using the raster “r.resample” tool found in GRASS GIS. No-data values were filled using the “Fill nodata” tool, which uses inverse distance weighting to obtain values in the no-data regions from the surrounding pixel values. This was necessary in order to fill the spatial gaps along the coastline and ensure a correct functioning of the SDM. Furthermore, the areas within the borders of the Maltese islands were masked out.

Finally, the “Point Sampling Tool” was used to extract numerical information from all the environmental variables to create a correlation matrix. The collinearity between predictors was therefore examined using the Pearson coefficient r . In case of $|r| > 0.7$, indicating a strong correlation and potentially introducing severe bias into model estimation and predictions (Dormann et al., 2013), only one relevant predictor was retained.

3.3.2 Anthropogenic Predictors

Marine traffic density data were obtained from the European Marine Observation and Data Network (EMODnet)’s Human Activities Data Portal (www.emodnet-humanactivities.eu). EMODnet generates marine traffic maps by utilizing Automatic Identification System (AIS) data acquired from Collecte Localisation Satellites (CLS) and ORBCOMM. These maps include recreated ship track lines and encompass various ship types, such as (1) fishing, (2) service, (3) dredging or underwater operations, (4) sailing, pleasure craft, (5) high-speed craft, tug and towing, (6) passenger, (7) cargo, tanker, (8) military and law enforcement, as well as (9) “unknown” and (10) “other” categories. These data are stored in GeoTIFF format and represent vessel density, measured in hours per square kilometre per year, with a spatial resolution of $1 \times 1 \text{ km}^2$.

The density data are available for the years 2017 to 2022, and annual raster data were downloaded for the period from 2017 to 2021. As noted by Saliba et al. (2021), traffic patterns in the Malta Channel remained stable from 2012 to 2020, even during the COVID-19 pandemic. Consequently, this timeframe serves as a reasonable reference for characterizing the previous years to cover the same period as the sightings.

To align with the environmental predictors, yearly averages for the combined data of all ship types were pooled into a single raster file for the period 2017-2021. This computation was performed using the Raster calculator in QGIS. Subsequently, the vessel density raster data underwent the same processing as the environmental predictors, which included downscaling, no-data filling, masking and their integration into a grid of 360 columns and 317 rows, with each cell spanning 450 meters.

Finally, Raster files for each vessel category were averaged between 2017 and 2021, downsampled to match the resolution and extent of the environmental predictors, filled, and masked. While the raster resulting from all vessels combined was used for a successive overlap

analysis, the raster files created for single category were utilised to visually analyse which vessel type has the highest traffic density.

3.3.3 Other Anthropogenic Activities

The spatial distribution of anthropogenic activities, specifically FADs and aquaculture sites, was sourced in the form of a Web Map Service (WMS) from the Malta Spatial Data Infrastructure portal (<https://msdi.data.gov.mt/index.html>).

Regarding FADs, their positions are represented as predefined trajectories, outlining their potential areas of deployment. In other words, the lines displayed in the WMS do not indicate the actual locations of FADs but rather delineate the paths along which they may be placed. To translate this representation into data, a raster file was generated by exporting the WMS layer in QGIS. In this raster, transect lines were assigned a value of 1, while all other areas were given a value of 0. The same grid and resolution as the environmental and anthropogenic predictors were maintained.

To identify aquaculture locations, data from the WMS layer were similarly exported. Within this export, areas designated as aquaculture sites were given a value of 1, while all other areas retained a value of 0. This data export adhered to the identical grid and resolution parameters as the previously acquired raster datasets.

Finally, it is important to clarify that the trajectories of FADs and the locations of aquaculture sites were solely utilized for the purpose of illustrating potential overlap with the distribution of the bottlenose dolphin. These specific data sets were not integrated into the model itself but were instrumental in assessing the spatial relationships between dolphin presence and these anthropogenic features.

3.4 Modelling Bottlenose Dolphins' Potential Distribution within the Study Area

3.4.1 Selection of MaxEnt for Species Distribution Modelling

In order to predict the potential distribution of the bottlenose dolphin within the study area, the software MaxEnt version 3.4.4 (available at <http://www.cs.princeton.edu/~schapire/maxent/>) was used.

MaxEnt is a machine learning method based on the maximum entropy principle, extensively used in habitat suitability and species distribution modelling (S. J. Phillips et al., 2006). This SDM proves particularly advantageous when there are limited survey data and small sample size (Wisiz et al., 2008) and is known to provide highly accurate predictions in terms of habitat suitability (Merow et al., 2013; Phillips et al., 2006).

Dolphins, as highly mobile species, exhibit behaviours that often involve extended periods spent underwater (Shane, 1990). This presents a significant challenge when it comes to their detection. Due to the underwater nature of their activities, it can be difficult to determine whether the absence of dolphin sightings in a specific area reflects their absence or is simply a result of their temporary unobservable state (Elith & Leathwick, 2009). In essence, this ambiguity arises because their underwater activities remain largely masked, making it challenging to definitively categorize an absence as true or false in the absence data.

Consequently, the model chosen for this study is well-suited to this context since it adopts an approach where the non-observation of a species is considered as an aspect of the background rather than an absence, in alignment with the findings of Fernandez et al. (2022). In fact, the model relies exclusively on the recorded locations where dolphin sightings have been confirmed, usually referred to as presence-only data. Given the difficulty in establishing true

absence data for this species (Lobo et al., 2010), utilizing presence-only data provides a practical approach for predicting their potential distribution. This approach capitalizes on the information available from known sightings and leverages environmental data to model the species' potential distribution within the study area, acknowledging the complexities associated with detecting these highly mobile and frequently submerged animals (Fernandez et al., 2022).

3.4.2 MaxEnt's Operational Framework

The MaxEnt process first utilises a dataset containing the confirmed presence-only records of the species object of the study (Merow et al., 2013). Concurrently, it incorporates a set of environmental predictors distributed across a predefined landscape, corresponding to the study area and divided into grid cells. Within this landscape, MaxEnt systematically selects background locations, serving as a basis for comparison with the known presence locations. Importantly, at these background sites, the species' presence status remains unknown, creating a contrast between observed presences and potential absences. Subsequently, MaxEnt compares the environmental conditions observed at presence locations with those identified at the chosen background locations.

Building upon this contrast analysis, MaxEnt proceeds to estimate the likelihood of species occurrence throughout the study area, resulting in a Relative Occurrence Rate (ROR; Merow et al., 2013). Consequently, it generates a continuous predictive map, revealing the probability of species presence across various locations within the landscape. The resultant probability distribution serves as an indicator of habitat suitability for the species under study (Merckx et al., 2011). This predictive map ranges from 0 (low habitat suitability) to 1 (high habitat suitability), identifying the probability score of occurrences for each location on the map based on how suitable it is for the species in study. Such presence-background modelling is particularly useful because it helps address the challenges associated with integrating data collected using diverse methodologies over an extended time span (Breen et al., 2016; Pace et al., 2019).

Furthermore, as elucidated by Phillips et al. (2006), ensuring the performance of the predictive model is of utmost importance. To achieve this, a two-step process is followed. The initial step involves model calibration, where the algorithm refines its parameters and establishes predictive relationships. This is done using a dedicated portion of the available data, referred to as the training dataset. Subsequently, the model undergoes validation using an independent set of data, separate from the training data, ensuring that it is evaluated on its ability to provide reliable predictions.

To evaluate the prediction, a common approach is to consider the receiver operating characteristic (ROC) curve, which plots the number of correct predictions of species presences (Sensitivity) against the number of correct predictions of species absences (Specificity). The value used to measure the ROC is the Area Under the Curve (AUC) that defines that the prediction is not better than random if the value is equal to 0.5 (S. J. Phillips & Dudík, 2008).

Nonetheless, the applicability of the AUC for model evaluation is not without its reservations. Lobo et al. (2008) raised questions about its limitations, and it has been demonstrated that AUC can potentially overestimate model quality when both test and training data are influenced by similar sampling biases (Veloz, 2009). In addition, it is important to acknowledge that AUC values often appear higher for species with limited habitat ranges relative to the study area described by the environmental data, as explained by Phillips (2005).

Warren et al., (2014) have demonstrated that using the Akaike Information Criterion corrected for small sample sizes (AICc) provided an effective method to evaluate different models and select the one that is most likely to represent the underlying processes that generated the data.

Furthermore, this method allowed to fine-tune the model parameters to reduce model complexity while considering sampling bias (Warren & Seifert, 2011).

3.4.3 The MaxEnt Modelling Process: Parameter Selection, Variable Importance and Evaluation

The software MaxEnt is equipped with a predefined set of default parameters, encompassing output specifications, the selection of feature classes, regularization parameters, and the number of replicates (Phillips, 2005). However, it's important to note that default parameters may not consistently produce the most optimal model output (Morales et al., 2017) and numerous studies demonstrated improvements with species-specific tuning (Elith et al., 2011; Merow et al., 2013; Warren & Seifert, 2011). Therefore, customization and careful consideration of parameter choices were applied to the present study, facilitated by the use of the RStudio package “ENMeval” (Muscarella et al., 2014).

The package “ENMeval” version 2.0.4 was used to choose the most suitable model configurations to run the MaxEnt model. The package, as described in Kass et al. (2023), conducts ecological modelling across a range of user-defined settings, covering various combinations. It subsequently carries out cross-validation to assess the performance of these models and provides data tables to assist in the selection of the configuration parameters to ensure balance between goodness-of-fit and model complexity.

In the context of this study, the package’s input data included the non-correlated predictor raster files, described in the previous section, and generated using QGIS, as well as the bottlenose dolphins’ occurrence file. ENMeval computes a range of evaluation metrics and presents them in the form of a table. One of these metrics is the AICc, which accounts for both model goodness-of-fit and complexity. The model exhibiting the smallest $\Delta AICc$ value, typically $\Delta AICc = 0$, is considered the most favourable choice among the existing set of models. (Warren & Seifert, 2011). In correspondence of this value, an indication of which feature classes and regularization parameter should be used is provided. In addition to the use of the AICc method, the model was evaluated using the AUC and the omission rate.

As a result of the ENMeval computation, hinge, linear, and quadratic feature classes were chosen to run the model in Maxent, along with a regularization parameter set at 1. These features are used to build response curves that show how the estimated species ROR changes with different predictor values and are essential for assessing how well the model aligns with biological expectations (Merow et al., 2013).

A k -folds cross-validation approach was employed to ensure reliable predictive performance. This method divides the total dataset into a predefined number of subsets, in this case, set at 10. The model utilizes $k-1$ of these subsets as training data, with the remaining one reserved for testing. This procedure is iterated k times, guaranteeing that each subset serves as the testing data exactly once (Merow et al., 2013).

The complementary log-log transform (cloglog) was chosen as the preferred output because it is recognized as the most suitable method for representing the habitat suitability for the species (S. J. Phillips et al., 2017).

Given that MaxEnt models are trained based on the available data, the potential for these models to inherit biases arises when the data is influenced by uneven or selective sampling. As a result, the model’s predictions may reflect where intensive sampling occurred rather than the true preferences of the species, as discussed by Phillips et al. (2009). When sampling bias is not properly addressed, MaxEnt models can lead to misleading inferences about species distributions (Merow et al., 2013).

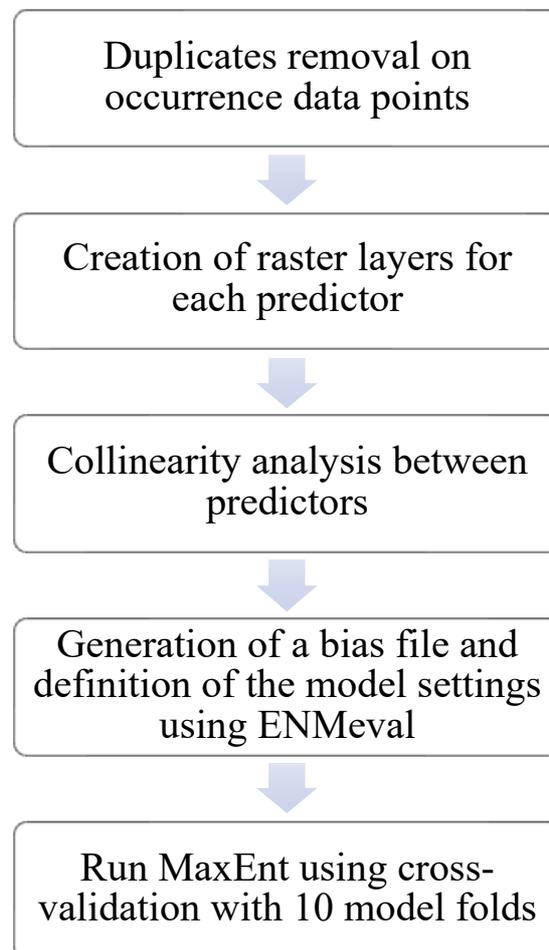
To address this issue, particularly in light of the integration of distinct datasets in this study, it is assumed that some regions of the study area may have been sampled more frequently than

others. To address potential sampling bias, given the integration of diverse datasets in this study, a file was created in RStudio and incorporated into the model using the software's dedicated feature. This bias file was created by performing a kernel density estimation (KDE), which estimates the spatial density of bottlenose dolphin presences based on their occurrences (Warren et al., 2014). This method allows the file to serve as a template for extracting background points within effort areas, mitigating the impact of uneven or selective sampling (Pace et al., 2018).

Ultimately, the model was executed using the file containing the sightings' locations and the raster files containing uncorrelated environmental and anthropogenic predictors. The methodology used to perform the MaxEnt model used in this study is summarised in the flow chart represented in **Figure 11**.

Figure 11

MaxEnt Modelling Flow Chart



A jackknife analysis was performed to evaluate the contribution of individual environmental variables to the model and to explain the importance of each variable in determining species occurrences. This analysis method assesses how well the model performs when each predictor is omitted one at a time, allowing for the measurement of variable importance, through a systematic approach involving three distinct phases (Phillips et al., 2005):

- **Exclusion of Variables:** the variables are individually excluded, allowing for an examination of the model's performance when a particular variable is omitted, highlighting the impact of each variable in isolation.
- **Single Variable Assessment:** the model is evaluated while considering only one variable at a time, providing insights into the influence and predictive power of each variable when it is the sole focus of the analysis.
- **Integration of All Variables:** all variables are considered together, demonstrating how their interactions and contributions as a group influence the overall model performance.

By running the model with each predictor removed, the models' performance was therefore compared to understand the influence of specific variables on the model's accuracy.

The modelling process began with all initially selected uncorrelated environmental variables included. Subsequently, variables exhibiting a negative contribution to the model, as indicated by a negative test gain on the jackknife analysis, were identified. In response, the model was re-executed, this time excluding these variables (Breen et al., 2016). A negative test gain serves as an indicator that a particular variable may have limited importance for the model, and its exclusion offers an opportunity to simplify the model's complexity without substantial loss in accuracy (Phillips, 2005).

In addition, the jackknife test percent contribution was used as an additional metric to assess the importance of each variable in predicting the species' distribution. In particular, those with a higher test percent contribution were considered to have the most substantial impact on the model's performance (Pace et al., 2018).

Finally, response curves were generated to illustrate how the estimated ROR changes in response to variations in a specific environmental predictor variable (Elith et al., 2011; Merow et al., 2013; Phillips, 2005). These curves are graphical representations of how the probability of species presence is influenced by individual environmental factors.

3.4.4 Generation of a Habitat Suitability Map for Bottlenose Dolphins

A habitat suitability map was created by importing the ASCII file derived from MaxEnt's cloglog output into QGIS and converting it into a raster file, using the WGS84 coordinate reference system. The map presents a range of values spanning from 0 (indicating a low habitat suitability) to 1 (signifying a high habitat suitability) across the study area and serves as a suitable basis for the subsequent overlap analysis, as discussed in Chapter 3.5.

To enhance map visualization, the "reclassify by table" raster analysis tool was used to represent the presence probability in four classes of equal size (0 – 0.25 = Very Low, 0.25 -0.5 = Low, 0.5 – 0.75 = Moderate and 0.75 – 1 = High). This approach simplified the representation and improved map clarity by highlighting areas with a higher likelihood of occurrence.

3.5 Calculating the Exposure of Bottlenose Dolphins to Anthropogenic Stressors

To explore the relationship between the bottlenose dolphin habitat suitability and human activities, including vessel traffic and FADs, an overlap analysis was conducted using QGIS's "Raster Calculator".

Given the skewed distribution of the vessel density data, a logarithmic transformation was initially applied to all density raster files for each category and for all vessels combined. While each category was used to visualise the distribution of the traffic density, only the raster file obtained from all vessels combined was used for the overlap analysis.

The data belonging to all vessels combined raster file were subsequently normalized to a range between 0 and 1 using the following formula computed in the “Raster Calculator” (Awbery et al., 2022):

$$N_i = \frac{V_i - \min(V)}{\max(V) - \min(V)}$$

In this equation, N_i represents the normalized value for each individual cell within the vessel density raster, and V_i indicates the value of each specific cell in the original vessel density raster.

FADs distribution raster did not require normalization, as their features were already given a value of 1 during the generation of the layer.

Subsequently, an exposure index was obtained to measure the overlap between the potential distribution of bottlenose dolphins and two distinct factors: vessel traffic density and the presence of FADs. Importantly, these factors were considered separately in the calculation.

The exposure index (Exp_i) was calculated for each cell as the product of the anthropogenic stressor considered (P_i) and the bottlenose dolphins’ potential distribution (O_i), as indicated in the formula:

$$Exp_i = P_i * O_i$$

This index provides an assessment of the exposure of bottlenose dolphins to anthropogenic stressors (Awbery et al., 2022) within each cell and was calculated for both vessel traffic density and the spatial distribution of FADs. The resultant maps of relative exposure risk represent regions ranging from low risk (0) to high risk (1) for potential interactions between dolphins and anthropogenic stressors within the study’s geographical area.

The map representing the risk exposure to vessel traffic was finally reclassified using the raster analysis tool “reclassify by table” to highlight the areas of higher exposure, based on three equal intervals identifying areas of low ($Exp_i < 0.33$), moderate ($0.33 < Exp_i < 0.66$) and high exposure ($Exp_i \geq 0.66$).

The raster file containing the index calculated along the FAD trajectories, as a result of the overlap analysis, was converted into a shapefile to simplify the representation of the risk exposure. The shapefile was employed to identify segments of the trajectories with a high index ($Exp_i \geq 0.66$), accentuating areas where the likelihood of overlap between dolphin presence and FAD presence is more pronounced.

In conclusion, it is important to acknowledge two significant aspects. Since the study does not account for seasonal variation, this approach allows for a broad evaluation of the potential impact of these factors on the potential distribution of bottlenose dolphins within the study area. Lastly, the presence of additional human activities was taken into account in the spatial analysis, including aquaculture sites and bunkering areas, as supplementary factors to draw comprehensive conclusions.

4. Results

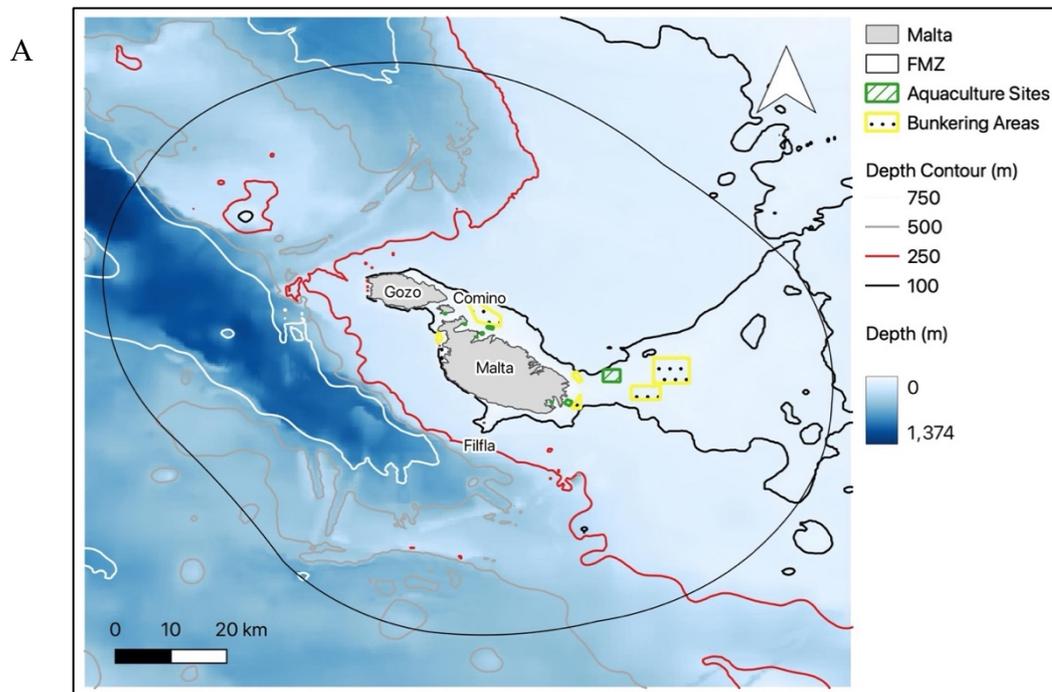
4.1 Description of Environmental and Anthropogenic Predictors

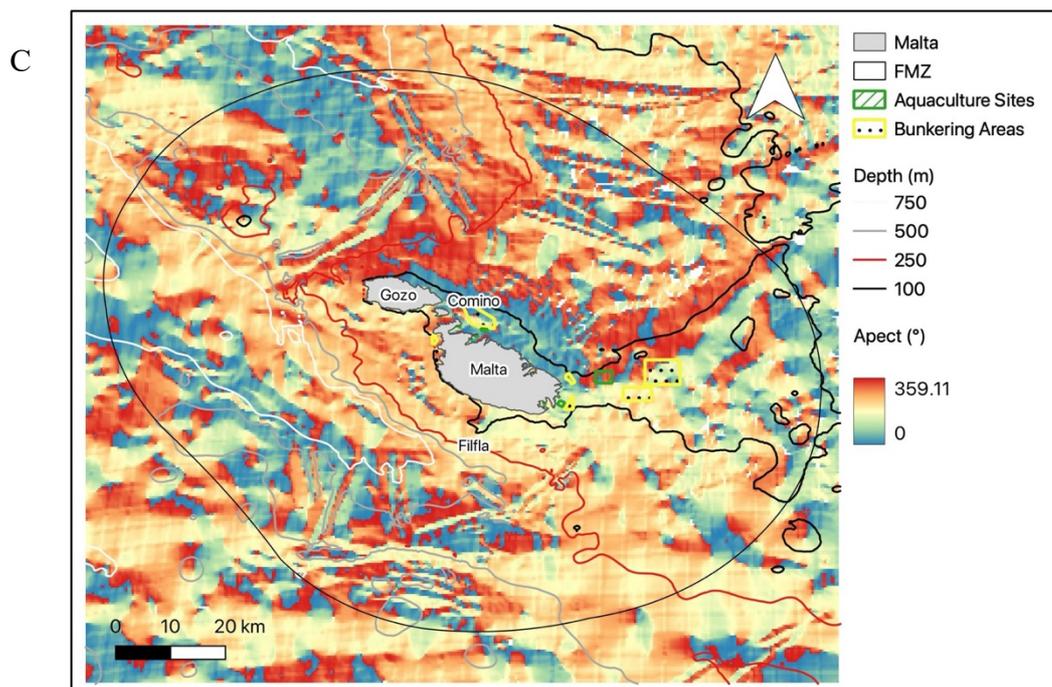
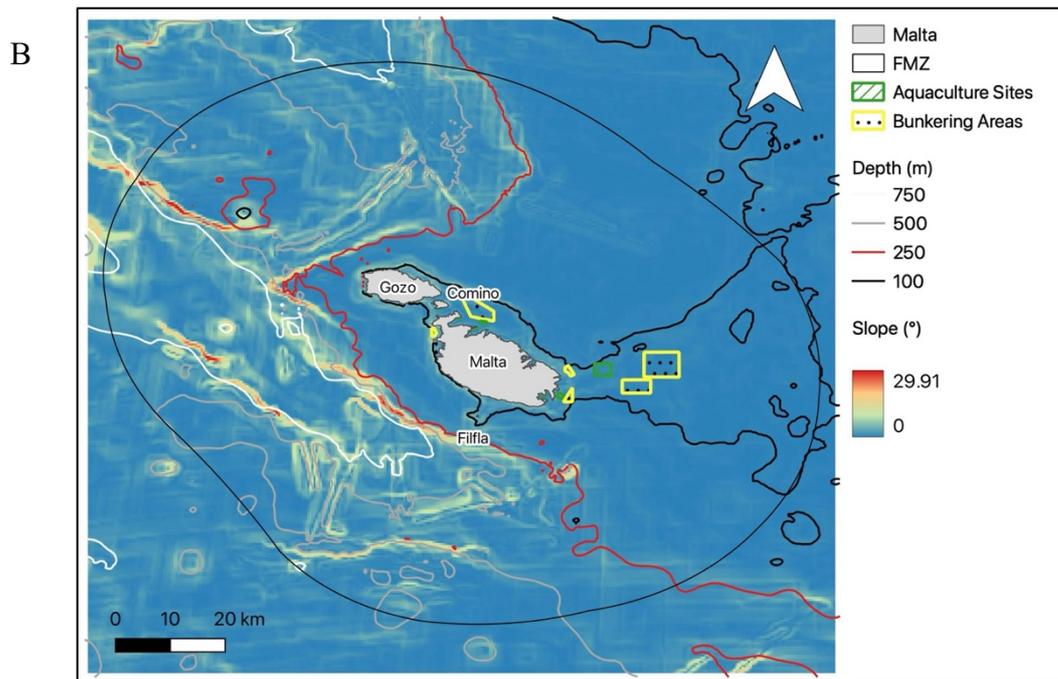
4.1.1 Depth, Slope, and Aspect

The seafloor around the Maltese archipelago is distinguished by an uneven continental shelf (Mueller et al., 2020; **Figure 12**). Moving eastward, the shelf extends significantly offshore. In the northern half of the archipelago, a steep escarpment marks the edge of the shelf. On the western side, the shelf takes on a narrower profile, with its edge situated very close to the coastline. Further west, beyond the Maltese Islands, the Malta graben trends from north-west to south-east, revealing depths of up to 1300 metres within the study area.

Figure 12

Seafloor Topography Around the Maltese Archipelago: (A) Depth, (B) Slope, (C) Aspect





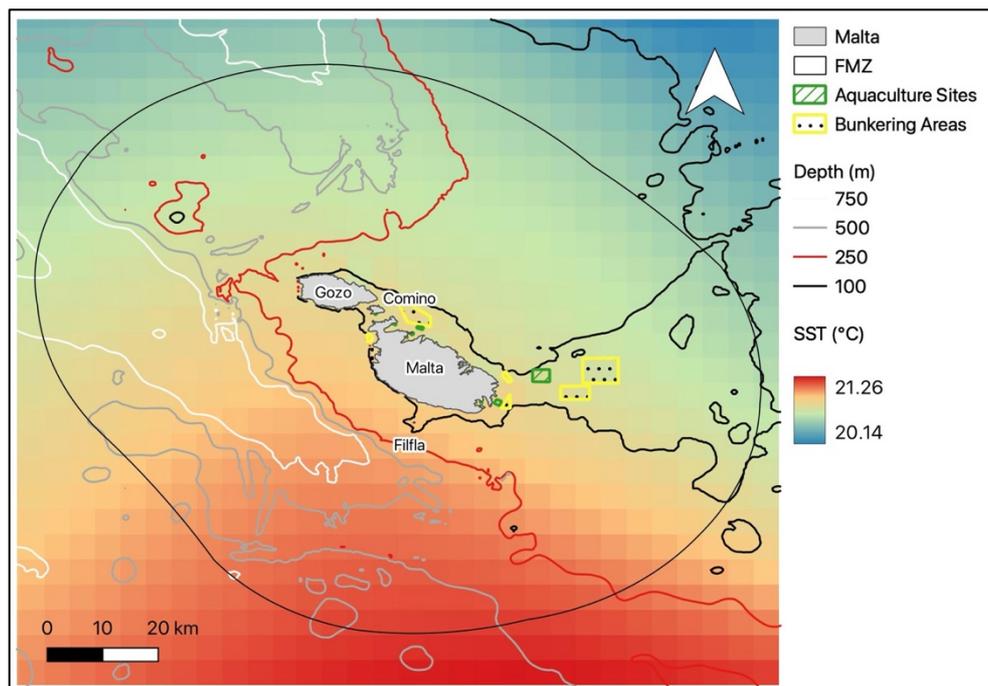
Note: The bathymetric data were retrieved from the GEBCO Atlas (<https://download.gebco.net>). Slope and aspect were obtained using the software QGIS.

4.1.2 Temperature, Chlorophyll-a, Dissolved Oxygen and Salinity

The map of SST, averaged between 2012 and 2021, illustrates a distinct pattern of warmer waters in the southern sector of the study area, extending towards the southwestern regions and exhibiting moderate warmth up to Filfla Island (**Figure 13**). The temperatures gradually shift to colder values in coastal areas on the eastern side of the archipelago and in the offshore waters across the remaining area of the study region.

Figure 13

Spatial Distribution of SST Averaged between 2012 and 2021 (°C)

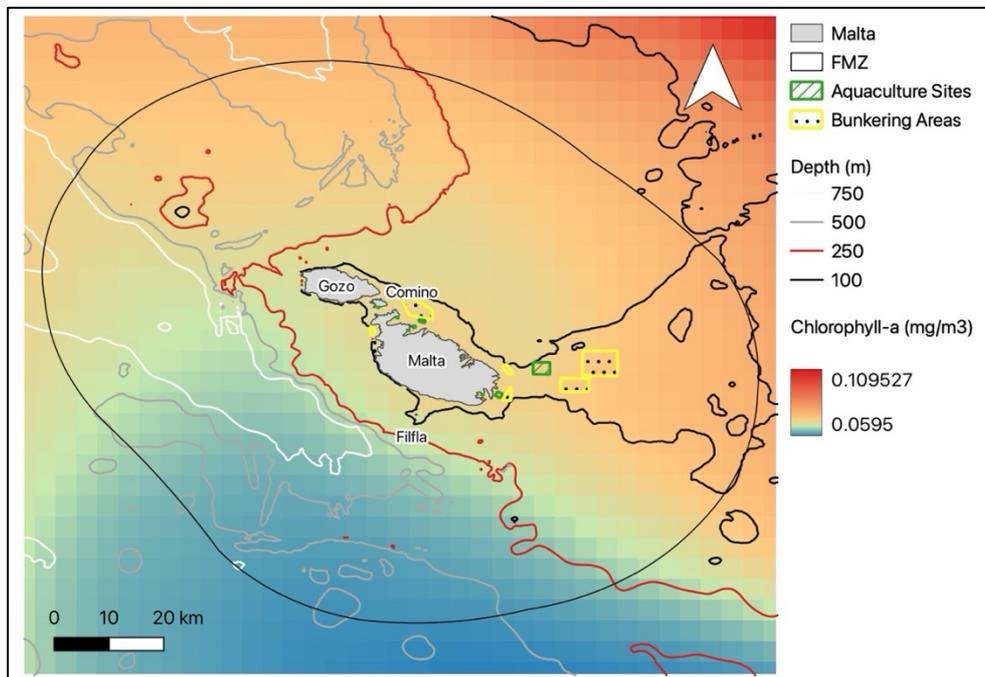


Note: Retrieved from the E.U. Copernicus Marine Service Information (<https://marine.copernicus.eu>). Red indicates high temperatures; blue indicates low temperatures.

The spatial distribution of chlorophyll-a concentrations, averaged over the period 2012-2021 and illustrated in **Figure 14**, reveals a distinct gradient in the waters to the west and south of the archipelago. Intermediate concentrations are observed within the range of the 100 m and 250 m isobaths, while higher concentrations are notable on the continental shelf, with a progressive increase observed in the waters farther east and offshore.

Figure 14

Spatial Distribution of Chlorophyll-a Concentrations Averaged between 2012 and 2021 (mg/m³)

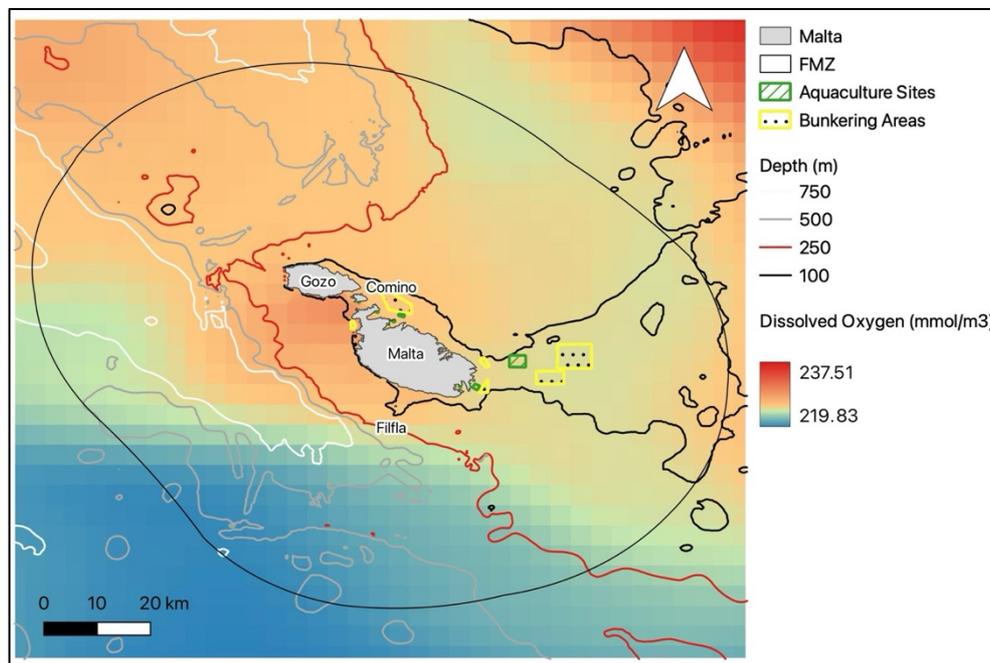


Note: Retrieved from the E.U. Copernicus Marine Service Information (<https://marine.copernicus.eu>). Red indicates high concentrations; blue indicates low concentrations.

Dissolved oxygen levels observed between 2012 and 2021 exhibit a moderate distribution in coastal areas, reaching peak concentrations in the western waters off Comino Island (**Figure 15**). Conversely, notably low values are observed in the southern region beyond the 250-meter isobath. A discernible gradient exists from the northwest to the southeast, although low dissolved oxygen values are also present on the continental shelf extending from the southeast of Malta.

Figure 15

Spatial Distribution of Dissolved Oxygen Averaged between 2012 and 2021 (mmol/m³)

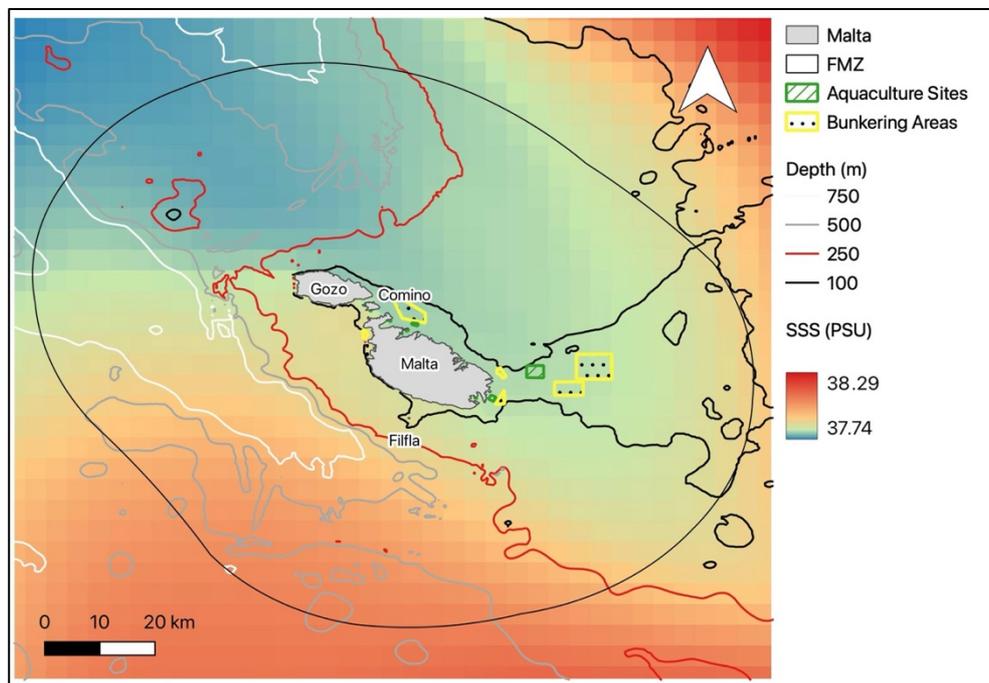


Note: Retrieved from the E.U. Copernicus Marine Service Information (<https://marine.copernicus.eu>). Red indicates high concentrations; blue indicates low concentrations.

Figure 16 illustrates the spatial distribution of SSS for the period 2012–2021. The map distinctly displays a demarcated offshore region characterised by higher values in the southwestern portion of the study area. Furthermore, some regions close to the archipelago’s western coast — specifically, the western side of the channel that separates Malta and Gozo — show moderate to high SSS values. On the other hand, the northwest region exhibits lower SSS values, whereas intermediate values are predominant throughout the continental shelf.

Figure 16

Spatial Distribution of SSS Averaged between 2012 and 2021 (PSU)



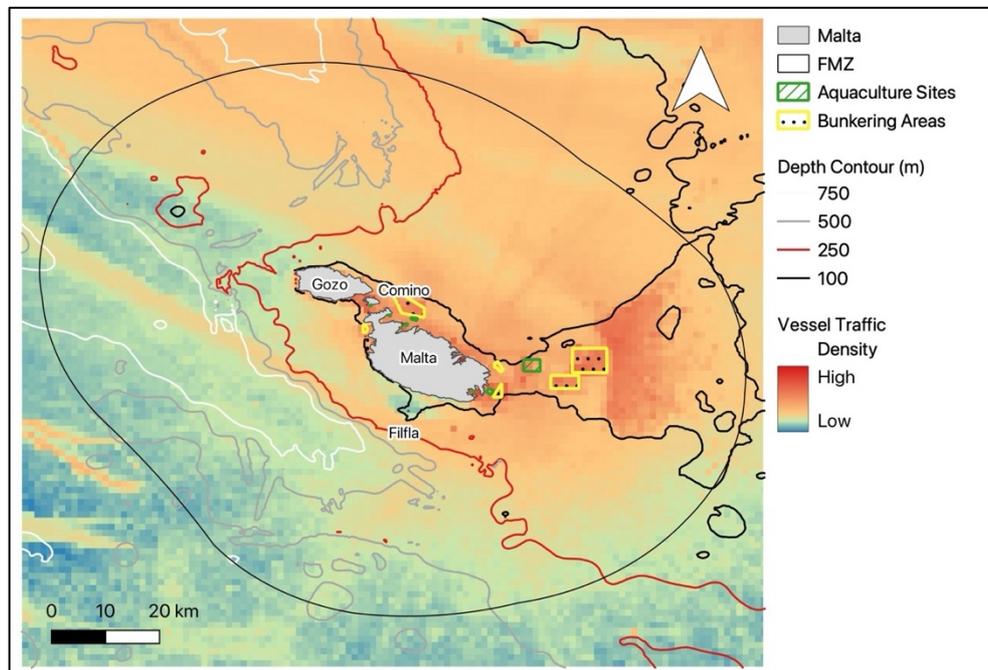
Note: Retrieved from the E.U. Copernicus Marine Service Information (<https://marine.copernicus.eu>). Red indicates high salinity; blue indicates low salinity.

4.1.3 Vessel Traffic Density

The vessel density data, obtained from the EMODnet's Human Activities Data Portal and subjected to logarithmic transformation (**Figure 17**), shows a widespread distribution of marine traffic across the entire survey area. Remarkably, there is a distinct concentration of vessel presence on the eastern side, coinciding with the principal shipping lane situated in the channel between Malta and Sicily. Of particular significance are the regions displaying the highest vessel traffic density, including the eastern coastline of the island of Malta, the waters surrounding Comino in the channel between Malta and Gozo, and the bunkering areas located in the south-eastern waters off Malta.

Figure 17

Vessel Density within the Study Area Averaged between 2017 and 2021 and Log-Transformed (hrs/km²)



Note: Marine vessel traffic information was retrieved from the EMODnet’s Human Activities Data Portal (www.emodnethumanactivities.eu) and include all types of vessels. Red indicates high vessel traffic density; blue indicates low vessel traffic density.

4.2 Collinearity Among Predictors

To investigate collinearity among predictors, a preliminary correlation matrix was produced (**Table 4.1**). It found strong relationships between four variables: dissolved oxygen, chlorophyll-a, SSS, and SST, with SST being negatively correlated to chlorophyll-a and dissolved oxygen, SSS being negatively correlated to dissolved oxygen, and chlorophyll-a being positively correlated to dissolved oxygen. To avoid introducing redundant information that could compromise the model’s predictive accuracy, only the variable chlorophyll-a was included in the analysis, while dissolved oxygen, SSS and SST were excluded. This decision was made because incorporating chlorophyll-a into the model would account for the effects of dissolved oxygen, SSS and SST (Dormann et al., 2013). Furthermore, chlorophyll-a has been employed as a key indicator of dolphin occurrence in the Mediterranean Sea, particularly in relation to periods of high primary productivity (La Manna et al., 2016).

Table 3

Correlation Matrix Showing the Pearson's Coefficient "r" between Environmental Predictors

	All Vessels	Depth	Apect	SST	Slope	SSS	Dissolved Oxygen	Chlorophyll a
All Vessels	1							
Depth	0,19303	1						
Apect	-0,032618	0,040505	1					
SST	-0,063775	-0,26015	-0,049726	1				
Slope	-0,064896	-0,26449	-0,099391	0,10436	1			
SSS	-0,13942	-0,18601	-0,075622	0,69088	0,02041	1		
Dissolved Oxygen	0,07124	0,28989	0,085364	-0,81979	-0,047946	-0,78145	1	
Chlorophyll a	0,099108	0,44805	0,043179	-0,93563	-0,18194	-0,5688	0,80518	1

Note: Variables showing a strong linear correlation, where $|r| > 0.7$ (Dormann et al., 2013), are highlighted in bold.

4.2 Impact of Environmental Variables and Human Activities on the Distribution of Bottlenose Dolphins

To determine the potential distribution of dolphins using MaxEnt, the number of sightings included in the study was reduced to 123 ($n = 123$) after removing duplicate records.

The model was initially executed using 10-fold cross-validation and a regularization parameter set to 1, incorporating all non-correlated variables as predictors and selecting only hinge features, as indicated by the ENMeval analysis. The results of the jackknife analysis of test gain in this first run were negative for aspect and slope. These outcomes indicated that the model's performance worsened when attempting to predict species distribution using these variables individually, leading to their exclusion.

Consequently, a second run of the model was performed. This time, linear, hinge, and quadratic features were considered, based on the ENMeval analysis, focusing exclusively on positive predictors. These predictors included vessel density (all vessels), chlorophyll-a, and depth.

The estimates of relative contributions of the environmental and anthropogenic predictors to the Maxent models are shown in **Table 4.2**, averaged over the 10 replicate runs. It is evident from the table that depth emerges as the most influential variable in terms of predictive power, followed by vessel density and chlorophyll-a.

Table 4

Estimates of Permutation Importance and Variable Contribution of Environmental and Anthropogenic Predictors.

Variable	Percent contribution (%)	Permutation importance
Depth	56	66
All Vessels	37.8	10.2
Chlorophyll-a	6.2	23.8

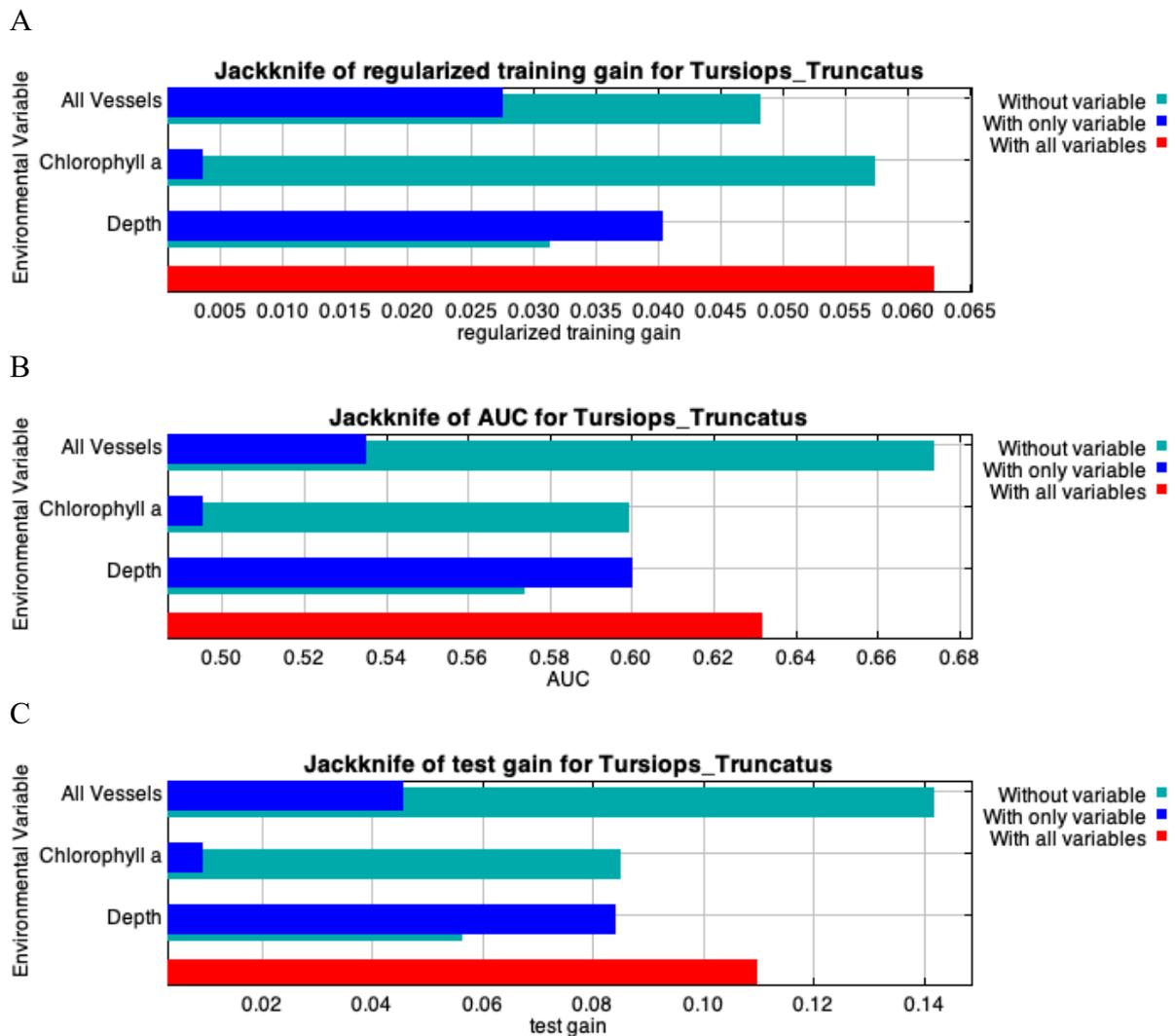
In the following bar charts produced by MaxEnt (**Figure 18 A**), the jackknife analysis emphasizes that when used in isolation, the variable "depth" exhibits the highest training gain, signifying its substantial standalone importance as a predictor (Phillips, 2005). In addition, the most significant decrease in the model performance, training gain and test gain occurs when the variable "depth" is excluded (**Figure 18 A, B, C**), indicating that it contains the most

information that are not present in the other variables (Phillips, 2005). The model performance decreases also when omitting “chlorophyll-a”, meaning that this variable is providing important information, and when it is removed from the model, the model’s ability to predict or explain the target variable (e.g., species distribution) is reduced.

Importantly, it should be noted that when the variable “vessel density” is excluded from the model, the resulting model exhibits higher AUC and test gain compared to the complete model (Phillips, 2005). This observation underscores that vessel density contributes to a reduction in model performance and can be considered as the weakest predictor (**Figure 18 B, C**).

Figure 18

Jackknife Analysis of Predictors Importance of Training Gain (A), AUC (B) and Test Gain (C)



Note: The analysis illustrates the importance of individual variables through a three-step process: first, by excluding each variable (light blue), second, by considering only one variable at a time (shown in blue), and finally, by examining the combined impact of all variables (represented in red).

In summary, the results of the modelling exercise underscore the significance of seafloor topography as a key factor influencing the distribution of bottlenose dolphins. The topography

of the seafloor plays an essential role in defining the preferred habitats and movement patterns of the dolphins, offering insights into their habitat preferences and the areas where they are more likely to be encountered.

Furthermore, the model suggests that chlorophyll-a concentration may also be a contributing factor to the presence of dolphins in specific regions. Chlorophyll-a, as an indicator of primary productivity and the availability of prey species, can influence the distribution of bottlenose dolphins by shaping the distribution of their food sources.

Conversely, the influence of vessel density on the presence of dolphins is less pronounced. Vessel density is a weaker predictor, meaning that the presence of boats and ships in an area has a relatively minor impact on the distribution of bottlenose dolphins. While vessel activity can potentially affect dolphin behaviours and stress levels, it is not as prominent a factor as seafloor topography and chlorophyll-a concentration in shaping their distribution patterns.

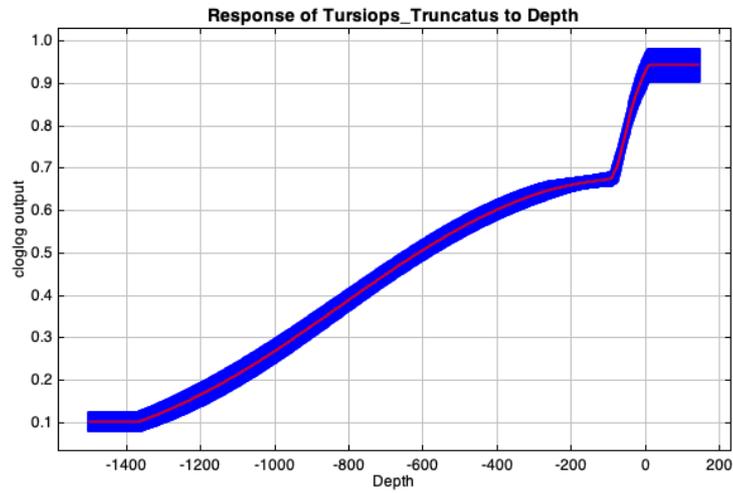
An indication on how the predictors influence the predicted probability of bottlenose dolphins presence is given by the results of the response curves (**Figure 19**) generated by the model. In particular, the results can be explained as follows:

- Depth: the probability of species presence in regions is higher in water depths between 0 and 100 meters (**Figure 19 A**). This implies that the species predominantly inhabits a relatively shallow depth range within the study area, though there is a moderate probability observed up to a depth of 600 meters.
- Chlorophyll-a: concentration levels show an inverse relationship with the likelihood of species presence. As chlorophyll-a levels increase, the likelihood of species presence decreases. However, a higher probability of species presence is evident within the range of 0.06 to 0.07 mg/m³ (**Figure 19 B**). This suggests that the species exhibits a preference for regions characterized by moderate to high chlorophyll-a concentrations.
- Vessel Density: the probability of species presence decreases as vessel traffic increases (**Figure 19 C**). This implies that the presence of high vessel traffic may have a negative impact on the species or deter it from occupying areas with heavy maritime activity.

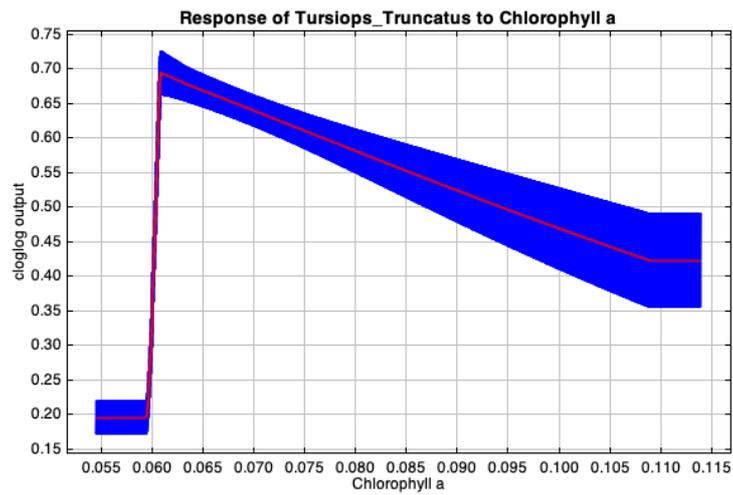
Figure 19

Response Curves Indicating the Influence of Depth (A), Chlorophyll-a (B) and Vessel Density (C) on the Presence of Bottlenose Dolphins

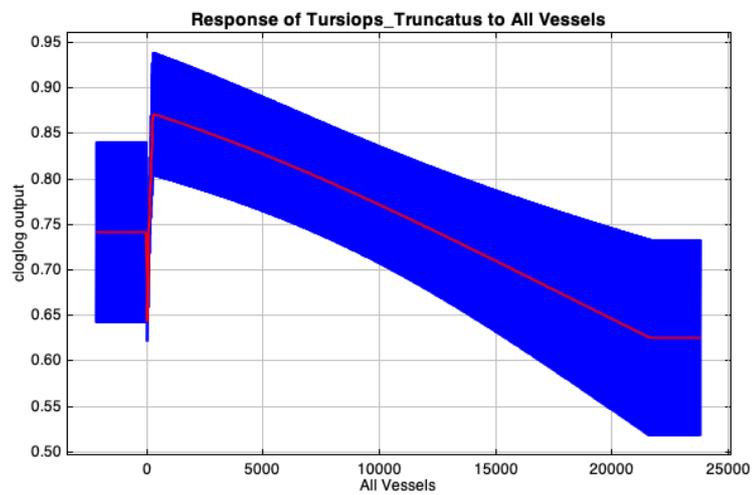
A



B



C

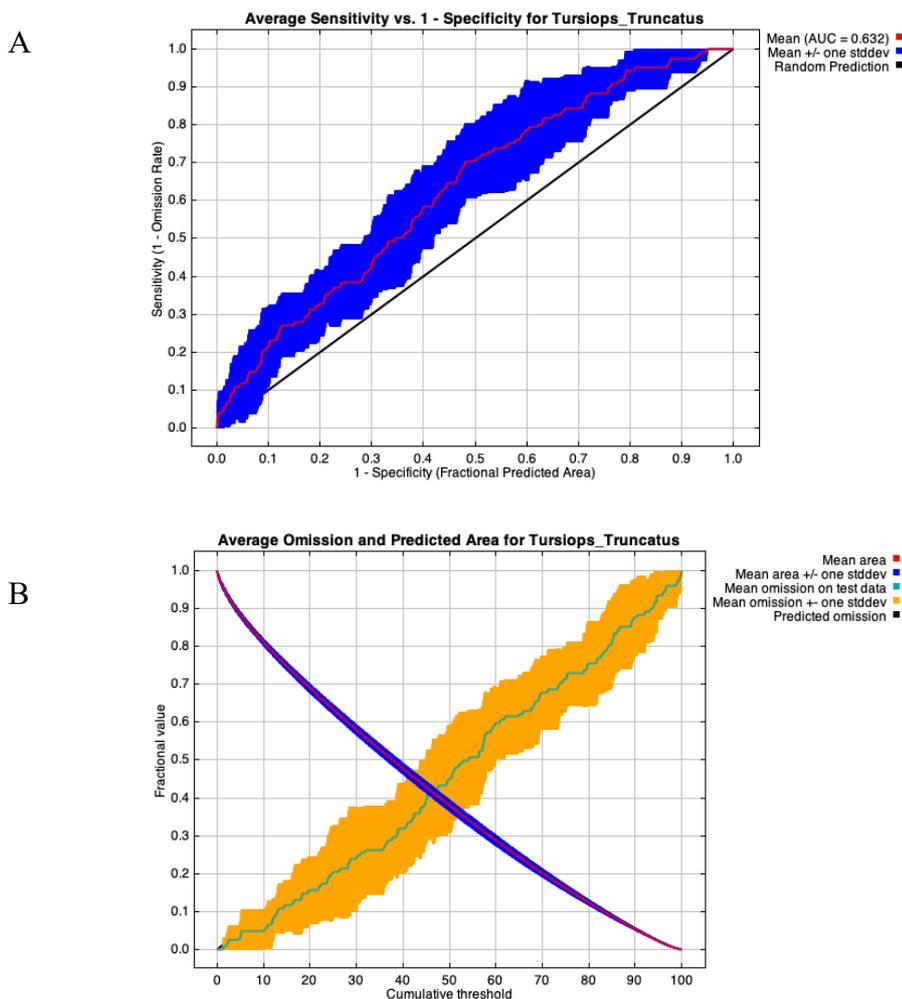


The results of the ENMeval analysis, which led to the selection of the parameters used to run the model in terms of regularization and feature class types, and the bias file are reported in Appendix I. Specifically, the parameters corresponding to a $\Delta AICc$ of 0 were the ones chosen for the model's execution.

The 10 replicate runs of the MaxEnt final model produced an average AUC of 0.632 on test data, with a standard deviation of 0.056, indicating that the model performs better than a random model would (Merow et al., 2013; Phillips & Dudík, 2008), and that the model's performance is consistent across different subsets of the data (**Figure 20 A**). In addition, the test omission closely matches the predicted omission (**Figure 20 B**), supporting the reliability of the model's results (Phillips & Dudík, 2008). Finally, following La Manna et al. (2023), the difference between the train-AUC and the test-AUC was also considered relevant in defining the robustness of the model. Notably, the observed value, as low as 0.038, aligns with findings by La Manna et al. (2023a), falling within the range of 0.005 to 0.102.

Figure 20

ROC curve (A) and Omission Rate vs Predicted Area (B) for Bottlenose Dolphins



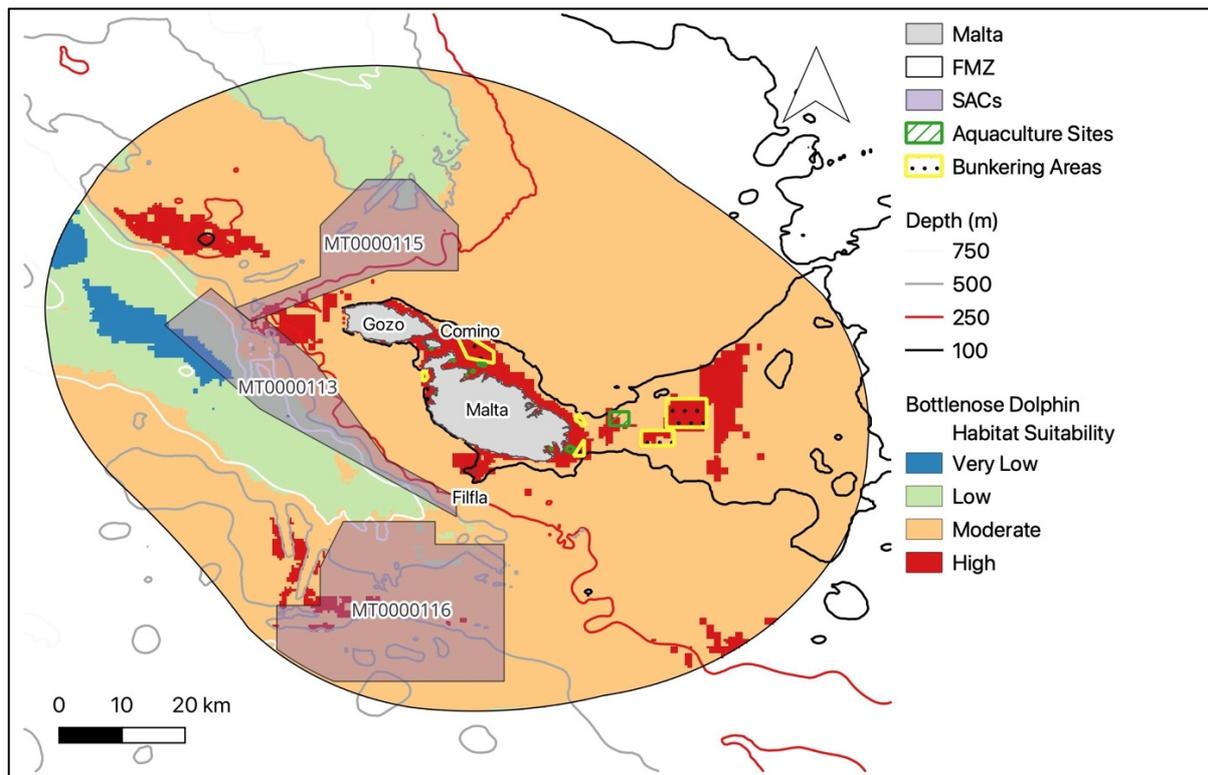
4.3 Predicted Distribution of Bottlenose Dolphins

The predictive map of bottlenose dolphin potential distribution, obtained through the MaxEnt modelling exercise, reveals significant variations across the study area, with a widespread moderate habitat suitability across the study area, and regions of high habitat suitability. Particularly, high habitat suitability scores are observed in distinct geographic areas within the FMZ (Figure 21), which include:

- The area along the eastern coast of both Malta and Gozo, including the Comino channel, shows an elevated probability of the presence of dolphins. Additionally, this region extends offshore to south-east, within the 100 m bathymetric line.
- Heading to the southwestern section of Malta island, including the vicinity of Filfla island, another area emerges as a favourable habitat for bottlenose dolphins.
- Moving towards the north-western coast of Malta island and the western side of the Comino channel, another region proves a higher likelihood of dolphin presence.
- Furthermore, the model predicts that bottlenose dolphins may inhabit deeper waters to the northwest of Gozo, as well as deeper offshore waters to the southwest of Malta, which are both marked by an increased likelihood of dolphin presence.

Figure 21

Potential Distribution Map for Bottlenose Dolphins within the FMZ based on the output of the MaxEnt Predictive Model



Note: The colour scale represents bottlenose dolphin habitat suitability, with red areas indicating highly suitable areas.

The map provides a comprehensive representation of bottlenose dolphin habitat suitability, clearly delineating specific regions with a pronounced probability of dolphin presence, while

also revealing a broader distribution pattern closely associated with seafloor depth. Notably, bottlenose dolphins demonstrate a distinct preference for specific depth ranges within their habitat. However, although the map illustrates that bottlenose dolphins are highly likely to inhabit shallow waters, particularly those with depths around 100 meters, it is essential to acknowledge that their distribution is not limited to these shallower areas. The predictive modelling exercise indicates that these dolphins can also be encountered in deeper waters, reaching depths of up to 600 meters. This may suggest their adaptability to a range of seafloor depths and their capacity to inhabit a diverse range of marine habitats within the study area.

4.4 Exposure of Bottlenose Dolphins to Anthropogenic Stressors

4.4.1 Spatial Distribution and Impact Assessment of Vessel Traffic Exposure

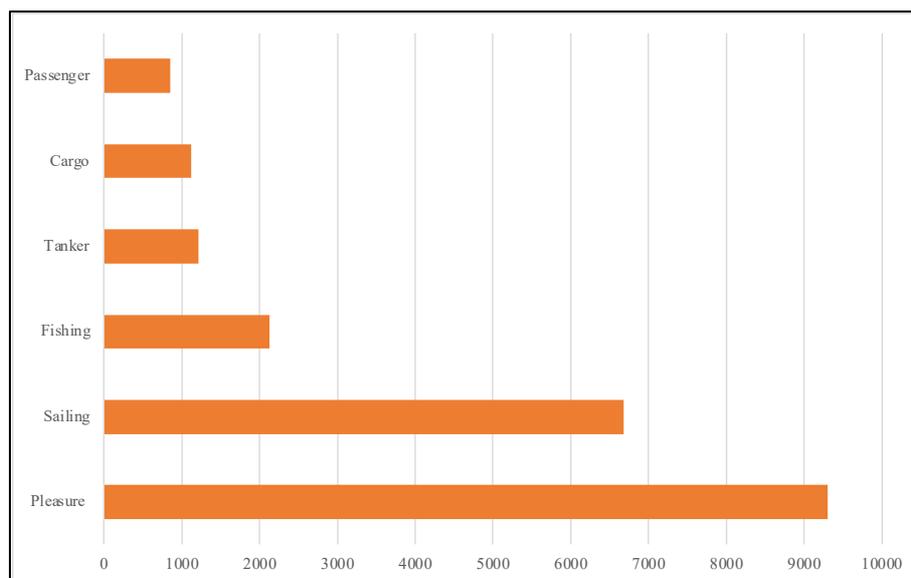
4.4.1.1 Analysis of Vessel Traffic Patterns and Densities

The analysis entailed the examination of areas where a convergence is observed between two significant factors: the distribution of the bottlenose dolphin and the density of vessel traffic. In other words, it identified regions where these two aspects intersect.

Out of the 13 vessel categories included in the analysis, those having the highest maximum density values recorded within the study area are reported in **Figure 22**. As indicated in the graph, pleasure crafts and sailing vessels show the highest vessel traffic density peak. Although this does not necessarily imply that they are the most prevalent traffic category, it does imply that these groups engage in particularly intense vessel activity at specific areas or times, typically during the summer months when demand for maritime tourism is stronger (National Statistics Office, 2023).

Figure 22

Maximum Density for Single Vessel Categories Observed between 2017 and 2021 (hrs/km²)



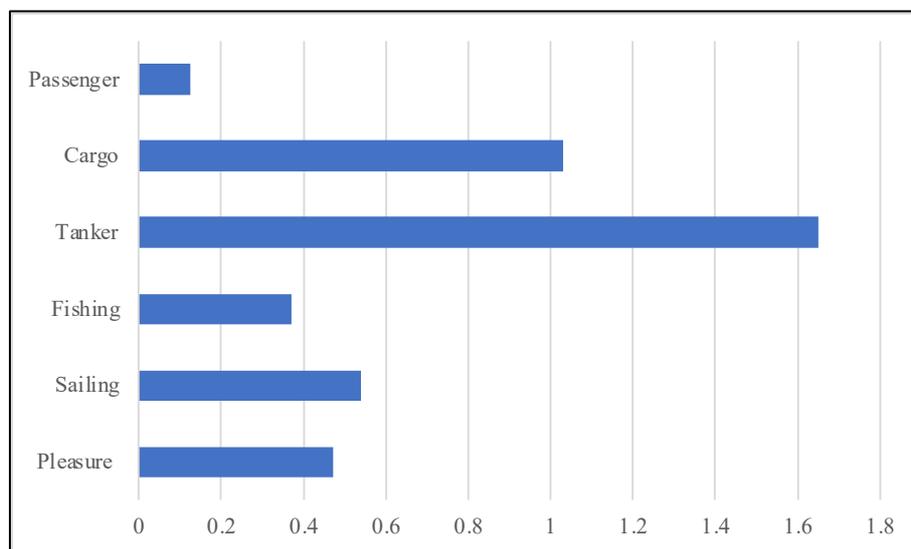
Note: Vessel traffic information for each type of vessel was retrieved from the EMODnet's Human Activities Data Portal (www.emodnethumanactivities.eu).

However, when the maximum density values are compared to the mean density values (**Figure 23**), it is clear that the maximum values are significantly higher than the mean values for the majority of categories. While there are locations with very high vessel activity (as indicated by the maximum values), the mean values are lower, indicating that these high-density regions are not representative of the overall study area.

Tanker and cargo vessels, in particular, have significantly higher mean densities when compared to the other categories. This suggests that their traffic activity is distributed more evenly across the study area, with fewer extreme peaks in traffic density. Pleasure crafts and sailing vessels, on the other hand, have the highest maximum densities and moderate mean densities. This indicates that while there are certain areas where these vessels are highly active, their overall activity is variable in space and time.

Figure 23

Mean Density for Single Vessel Categories Observed between 2017 and 2021 (hrs/km²)



Note: Vessel traffic information for each type of vessel was retrieved from the EMODnet's Human Activities Data Portal (www.emodnethumanactivities.eu).

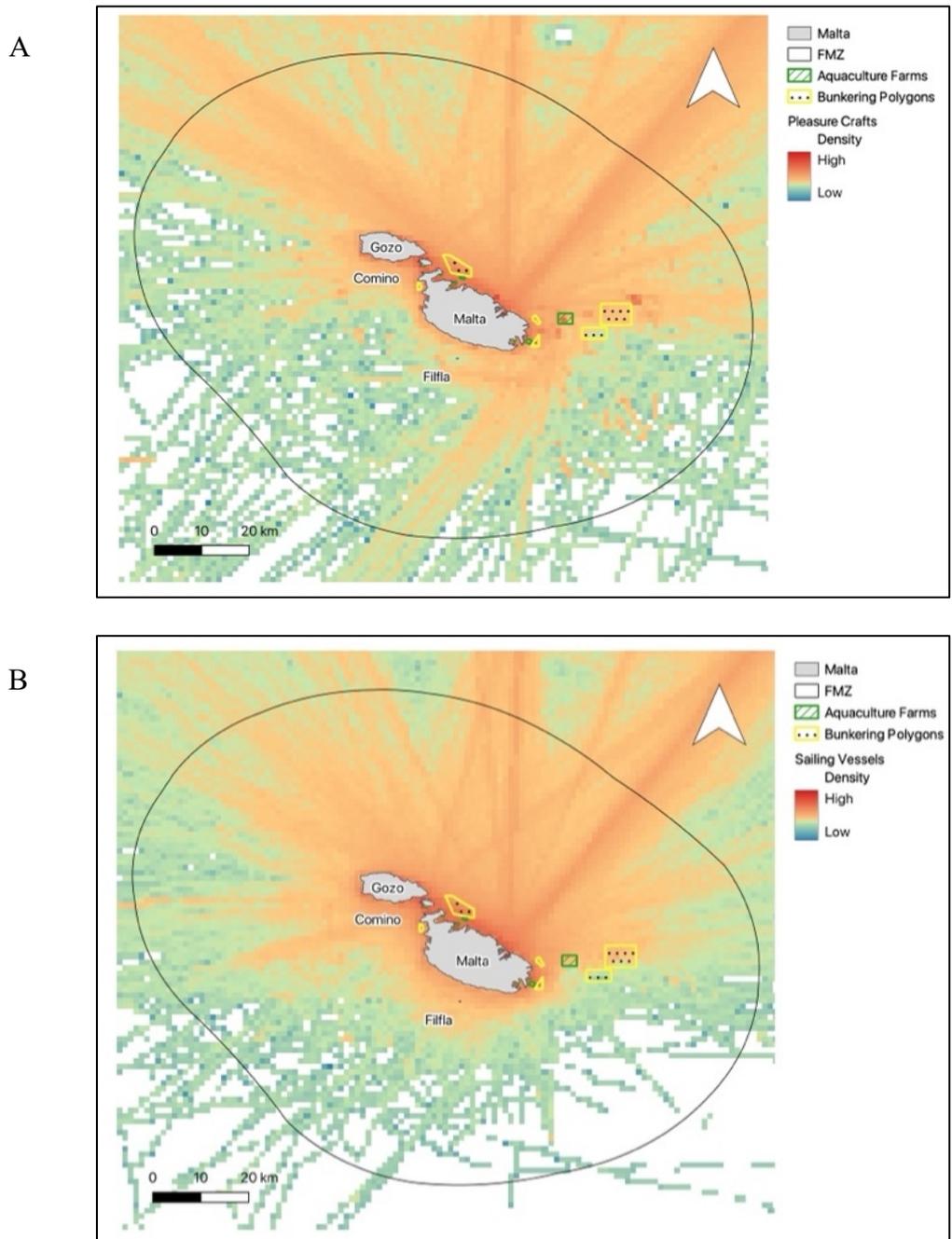
Finally, the distribution of vessel density reveals distinct patterns for each category in specific areas within the study region for the observation period, as shown in **Figure 24** and described below:

- The relative density of pleasure crafts and sailing vessels is notably higher near the coastlines and between Malta and Sicily. Interestingly, these two categories exhibit very similar distribution patterns, indicating that they tend to frequent the same or similar areas.
- Fishing Vessels exhibit a scattered distribution with areas of high density, especially observed near aquaculture sites, which confirms a strong association between fishing activities and aquaculture locations.
- Cargo and Tanker vessels demonstrate a similar distribution of density, characterized by high-density regions found in close proximity to bunkering areas, reflecting the importance of these locations in cargo and tanker operations.

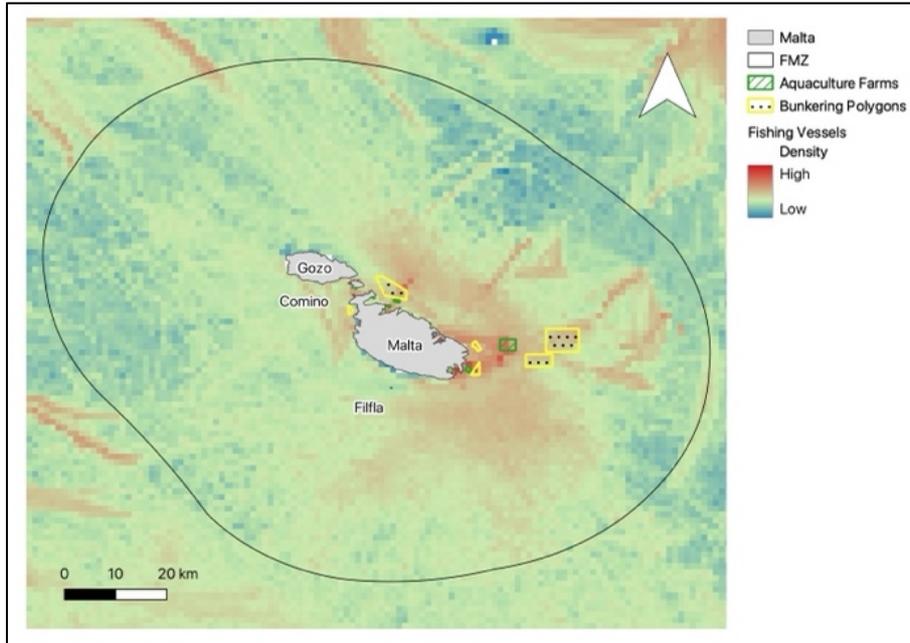
- Passenger Boats exhibit the highest relative density between Malta and Sicily and between Malta and Gozo, due to the transportation demand between the islands.

Figure 24

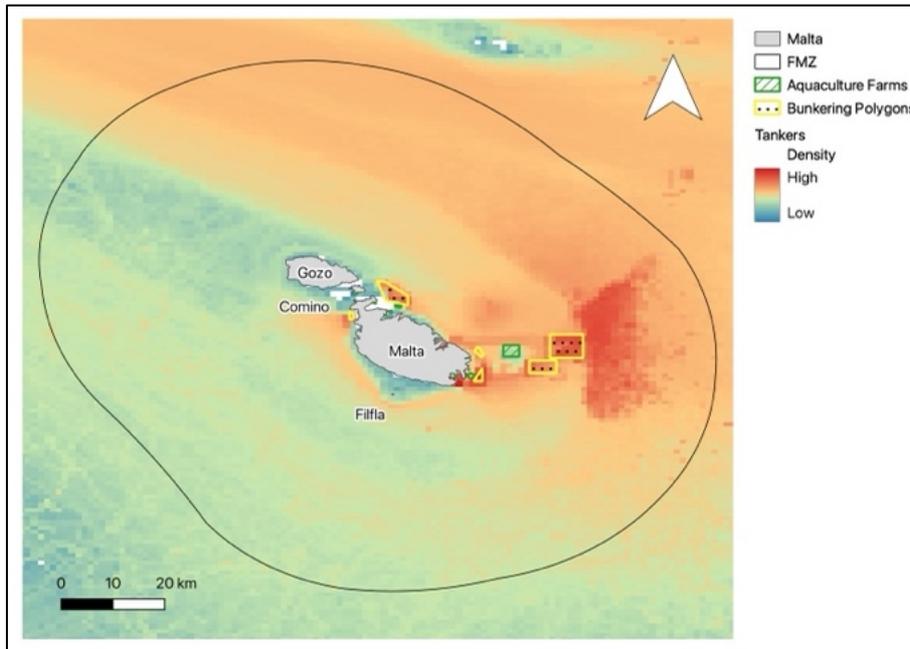
Vessel Density Distribution by Category within the Study Area, Averaged between 2017 and 2021 and Log-Transformed (Hours per Square Kilometre per Year), for (A) Pleasure Crafts, (B), Sailing Vessels, (C) Fishing Vessels, (D) Tankers, (E) Cargo Vessels, (F) Passenger Vessels



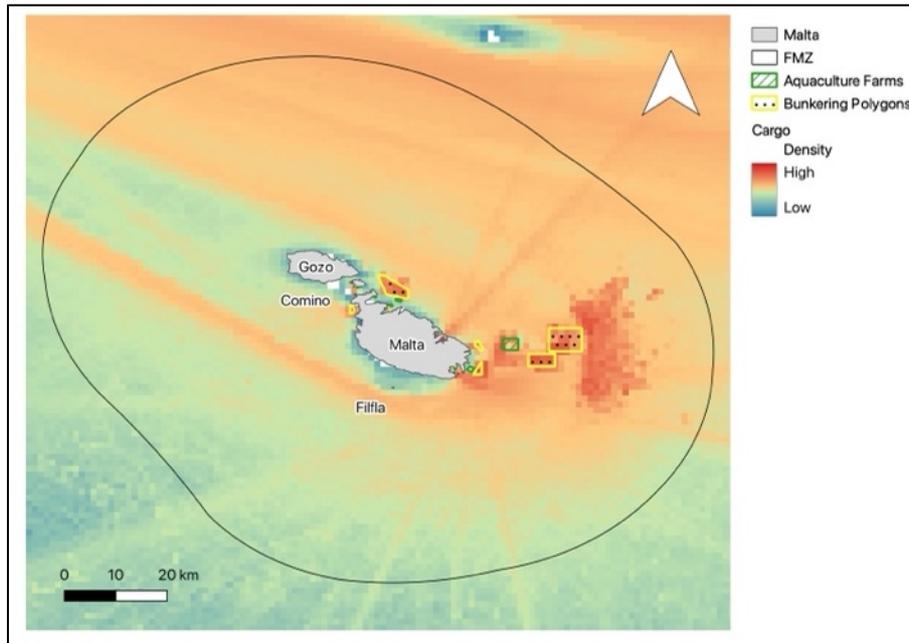
C



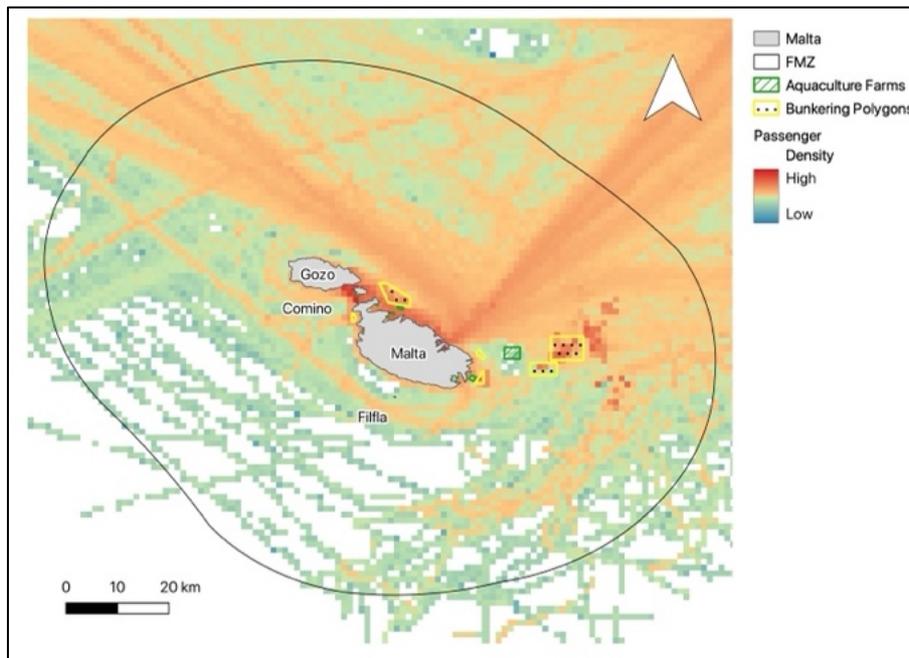
D



E



F

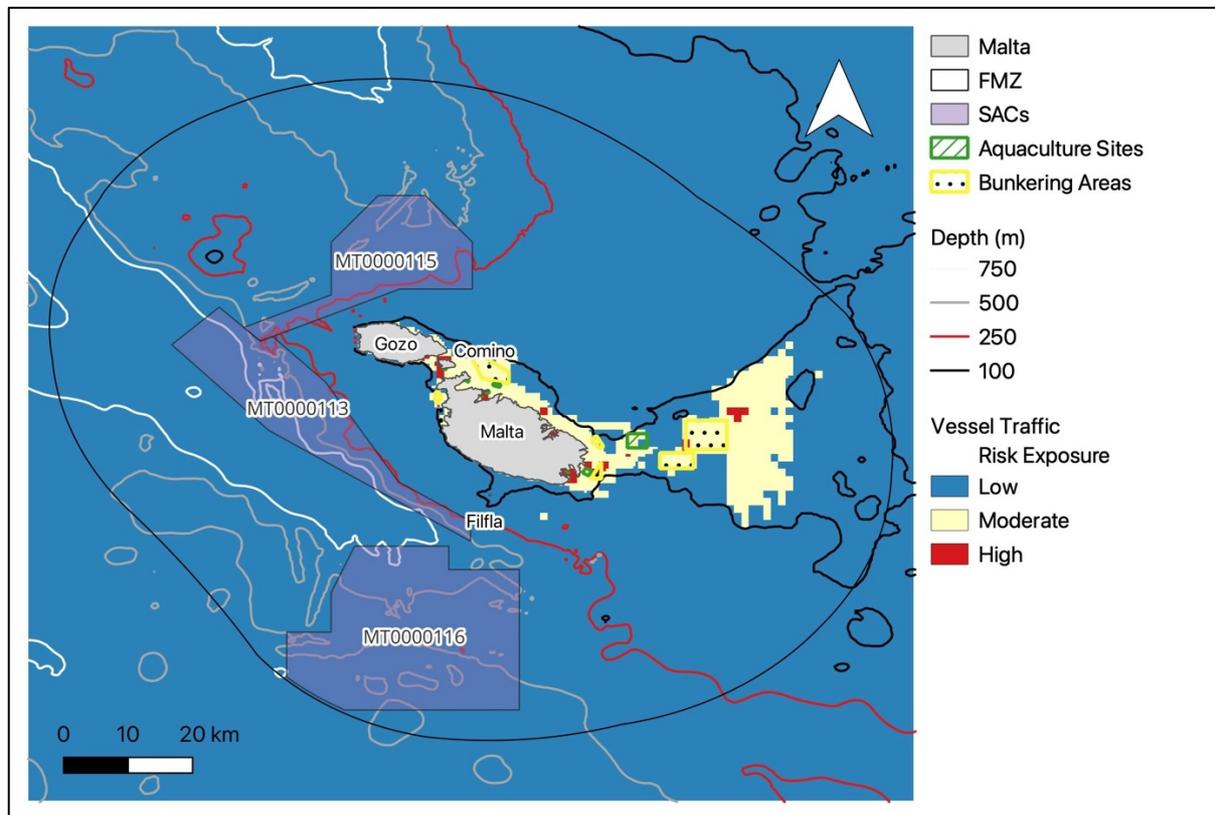


4.4.1.2 Assessing Vessel Traffic Exposure and Impact Zones on Bottlenose Dolphins

The overlap analysis (**Figure 25**) revealed a large area of moderate traffic exposure to bottlenose dolphins, primarily concentrated in the eastern portion of the study area, where maritime traffic is densely clustered, especially in proximity to the coastline and around bunkering sites.

Figure 25

Spatial Representation of the Total Traffic Exposure for Bottlenose Dolphins within the Study Area based on the Risk Exposure Index Obtained from the Overlap Analysis



Note: Red areas indicate high exposure of bottlenose dolphins to vessel traffic, while yellow areas represent moderate exposure.

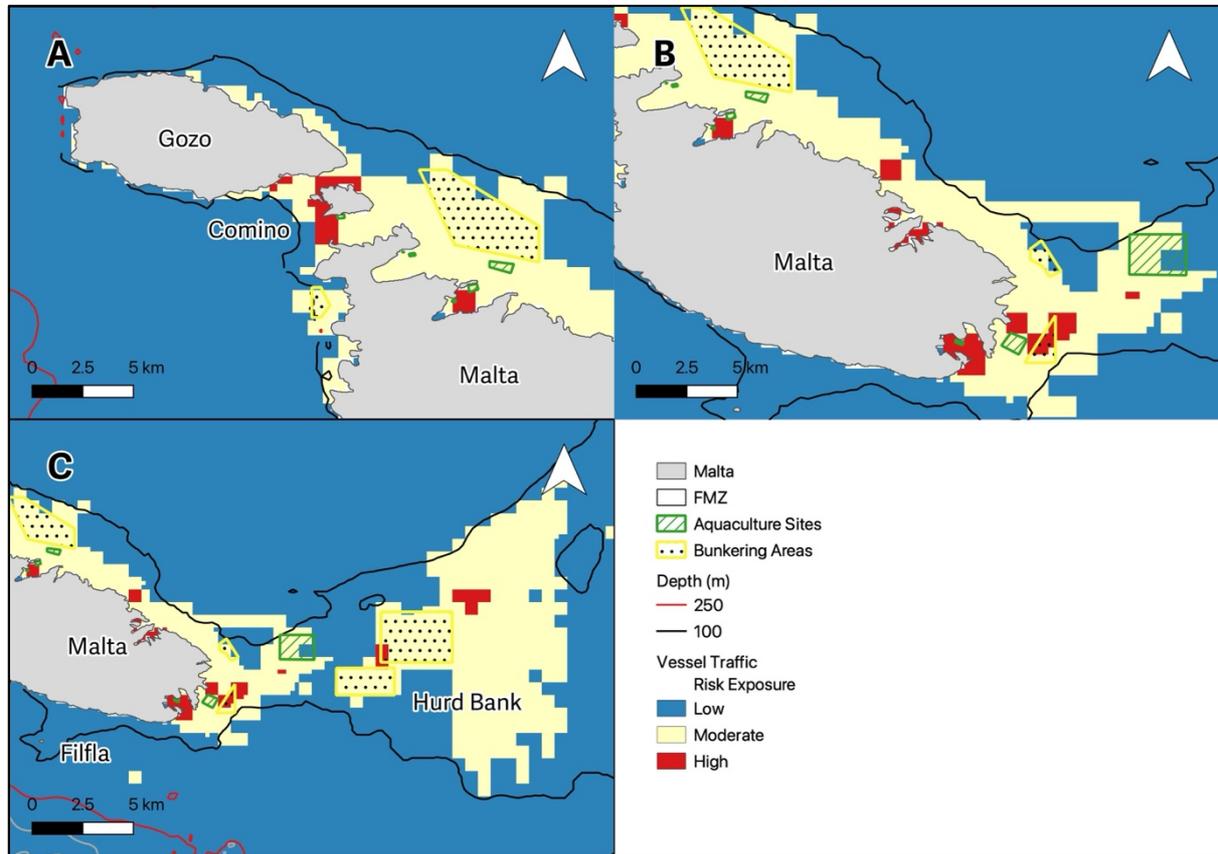
Furthermore, significant traffic exposure and therefore increased risk for the bottlenose dolphin population is concentrated in specific areas. These include four main areas:

- The Comino channel, which is a vital maritime corridor, also exhibits high traffic exposure, due to passage of passenger boats that connect Malta and Gozo and a substantial activity from pleasure crafts and sailing vessels (**Figure 26 A**). Their presence may be most likely particularly pronounced during the summer months, when the touristic activities increase (National Statistics Office, 2023).
- The area between the aquaculture site and the bunkering area along Malta's south-eastern coast (**Figure 26 B**). In this location, fishing vessels display a higher density surrounding the fish farms near the shore, as do tankers and cargo vessels moving between the southernmost bunkering area and the Marsaxlokk Harbour.
- The area in proximity of the south-eastern offshore bunkering area (Hurd Bank, **Figure 26 C**). In this area the high concentration of vessels is due to bunkering activities for cargo vessels and tankers.
- The ports of Valletta and Marsaxlokk, being key transport hubs, experience high levels of maritime traffic due to tankers and cargo vessels and overlap with suitable areas for bottlenose dolphins (**Figure 26 C**).

Regions characterized by high traffic exposure, where a significant likelihood of interactions between dolphins and vessels is evident, are of particular concern due to the potential increased impact of maritime activities on marine life.

Figure 26

Spatial Representation of the Areas of High Risk Exposure to Vessel Traffic



Note: Red areas indicate high exposure of bottlenose dolphins to vessel traffic, while yellow areas represent moderate exposure.

However, attention should also be directed toward areas of moderate exposure. While they may not exhibit the same intensified probability of interactions between dolphins and vessels as high exposure regions, these areas are not to be overlooked. Four main areas of moderate exposure can be identified on the map:

- The region extending from the high-exposure zone in the Comino channel to the port of Valletta along the eastern coast of Malta, where passenger vessels, pleasure crafts, and sailing vessels contribute to higher traffic density.
- The north-western coast of Malta, characterized by the presence of tankers in the bunkering area and pleasure crafts due to the concentration of tourist activities, particularly around popular beaches.
- The north-eastern bunkering area and aquaculture sites, where a variety of vessel types are found, indicating exposure from different maritime activities.
- A larger area in the vicinity of the furthest bunkering areas off the southeast coast of Malta, where tankers, passenger, cargo, and fishing vessels are intensely present.

The presence of bottlenose dolphins in areas of moderate exposure still signifies a level of vulnerability, worsened by the geographical extent of the impact and the potential cumulative impact by different maritime activities.

4.4.2 Spatial Distribution and Assessment of FADs Exposure

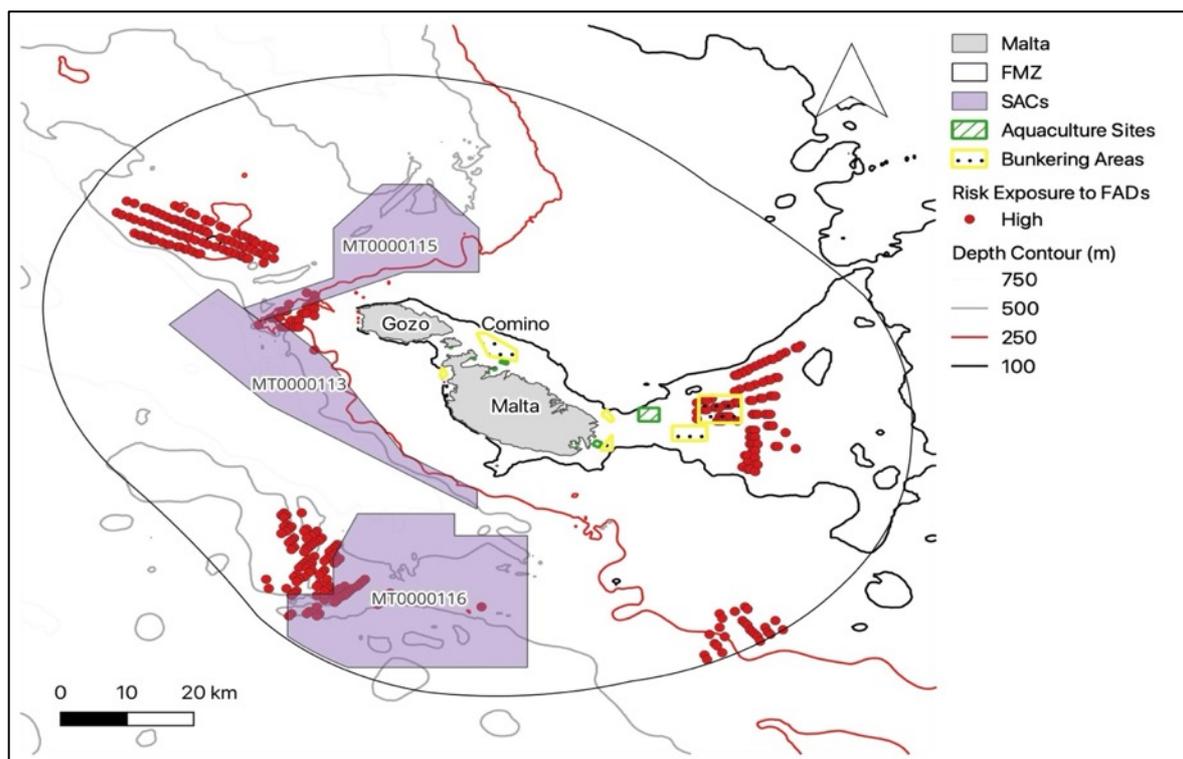
The trajectories of FADs are mapped across the entire study area, describing a widespread potential presence. However, it is crucial to underline that the presence of these mapped trajectories does not guarantee the continuous presence of FADs in those specific locations. FADs are deployed strategically and are not permanently anchored in every marked trajectory.

Furthermore, the deployment of FADs is a seasonal practice, predominantly occurring from August to December. During this period, fishing activities intensify, leading to a higher likelihood of overlap between FADs and dolphins' presence.

Despite the seasonal and intermittent nature of FAD deployment, three main areas within the study region present a higher risk exposure. In particular, as highlighted in **Figure 27**, these areas are situated off the northern coast of Gozo, off the south-eastern coast of Malta and off the western coast of Filfla. These locations are points of concern due to their elevated potential for interactions between bottlenose dolphins and FAD-related fishing activities.

Figure 27

Distribution of High-Risk Areas for Interactions between Bottlenose Dolphins and Potential Deployment of FADs



Note: FAD trajectories were retrieved from the Malta Spatial Data Infrastructure portal (<https://msdi.data.gov.mt/index.html>). The map shows in red the locations where the interactions are more likely to occur.

5. Discussion

5.1 MaxEnt Model Evaluation

The modelling exercise used in this study proved particularly useful to provide the first analysis of the distribution of the bottlenose dolphin in Maltese waters by maximising the use of the available information.

Although the use of AUC to determine the accuracy of the model has been questioned by several authors, this metric is still commonly used to describe the predictive power of the modelling exercise (La Manna et al., 2016, 2020, 2023a; Pace et al., 2018, 2019; Ranù et al., 2022). In SDM, a good model is usually defined as one that obtains AUC values > 0.7 (Swets, 1988). However, alternative and supplementary methodologies have been suggested for assessing model performance in MaxEnt (La Manna et al., 2023). This is because the AUC cannot be deemed a flawless measure of accuracy in presence-only models, given the fact that the MaxEnt uses presence data and contrasts it with randomly selected background points instead of considering true absences (Lobo, Jiménez-Valverde & Real, 2008).

Hence, for the present study, the model evaluation adhered to a methodology introduced by La Manna et al. (2023a). While an AUC value of 0.632 might suggest moderate discrimination capability and predictive accuracy (Swets, 1988), the model's robustness was proved by considering additional metrics beyond the AUC alone. The assessment incorporated factors such as the standard deviation of average AUC, the difference between train-AUC and test-AUC values, and the alignment between test omission and predicted omission (La Manna et al., 2023a; Merow et al., 2013; Phillips & Dudík, 2008).

The resulting moderate values of AUC may be due to the introduction of the bias file, possibly affecting the model quality (Veloz, 2009), and to the spread distribution of sightings over a large area, a factor known to reduce AUC values (Phillips, 2005). Nevertheless, this outcome reflects the opportunistic nature of the bottlenose dolphin itself, where the species' presence is widely dependent on the availability of prey, as further detailed in the subsequent sections.

Finally, the decision to incorporate linear, quadratic, and hinge features in the model served to streamline its complexity, ensuring that it did not exhibit signs of overfitting. The inclusion of these features allowed for a balanced and well-fitted model that appropriately captured the principal patterns without being overly influenced by noise or irrelevant details. This thoughtful selection contributed to the model's effectiveness in generalising to new, unseen data, reinforcing its robustness and reliability in addressing the study's objectives.

5.2 Bottlenose Dolphin Modelled Distribution and Drivers of Habitat Suitability

The study highlights a significant preference among bottlenose dolphins for shallow waters, particularly over the continental shelf, within a depth range of up to 100 meters. Their distribution spans the entire coastal areas of the archipelago, characterised by shallow waters and gentle slopes, excluding deeper and steeper areas beneath the cliffs on the western side of Malta and on the north and western sides of Gozo. Additionally, another area characterised by high habitat suitability extends to the shallow south-eastern waters on the continental shelf, in the proximity of the Hurd Bank. This observation aligns with previous research carried out in different regions of the Mediterranean Sea, emphasising the prevalence of bottlenose dolphin sightings on the continental shelf (Gnone et al., 2011, 2022; La Manna et al., 2016; Pace et al., 2021). However, the study reveals an additional suitable area in offshore waters, where depth reaches 600 meters. Moreover, two areas north-west of Gozo exhibit a similar preference, with depths reaching 250 metres.

The highly suitable areas identified in shallow waters include the aquaculture facilities situated along Malta's eastern coast, as well as on the shelf area that extends to the Hurd Bank. The abundance of wild fish around aquaculture sites, particularly pelagic zooplanktivorous fish species, and the possibility of feeding on uneaten fish feed and discarded farmed fish make them appealing to this species. This represents an opportunity for dolphins to increase the quantity and quality of their food while decreasing the amount of time and energy they spend foraging, matching with their well-known behavioural plasticity (Reynolds et al., 2013). Furthermore, it represents a consistent source of food for dolphins all year, compensating for the lack of fish prey due to their change in distribution in response to seasonal changes in SST and primary productivity (Díaz López, 2012; Díaz López et al., 2005; López, 2006; Piroddi et al., 2011). The presence of dolphins in these areas is confirmed by fishermen's accounts, indicating a substantial perceived increase around the fish farms in Malta since 2017, as documented in the study conducted by Terribile and Laspina in 2022

These findings deviate, in part, from prior research in the region. While studies conducted by Vella (2004, as cited in UNEP, 2017) and during the LIFE+ MIGRATE Project (LIFE+ MIGRATE, 2016b) have indicated a preference for deep offshore waters with depths ranging from 400 to 600 metres, the present research underscores a clear inclination towards the shallow waters on the continental shelf. Vella (2004, as cited in UNEP, 2017) proposed that dolphins might approach the shore more closely in summer and autumn, while the results of the LIFE+ MIGRATE Project reported the presence of bottlenose dolphins exclusively in coastal waters adjacent to fish farms (LIFE+ MIGRATE, 2016b). It is important to note that neither study explicitly designated coastal and shallow areas as a preferred habitat.

The presence of bottlenose dolphins in a few deep offshore regions may imply two hypotheses: dolphins may move between shallow and deep regions depending on the most favourable environmental conditions and presence of prey, or this could indicate the existence of a distinct offshore population, as suggested by Patti et al, 2022. Indeed, these two theories could potentially provide explanations for why the distribution of bottlenose dolphins appeared scattered in the results of the LIFE+ MIGRATE Project's study. Further exploration and analysis, incorporating additional factors such as seasonality, group size, and composition, could help validate or refine these hypotheses.

5.2.1. Depth

The significance of depth as the primary driver of distribution becomes evident through its high scores as an explanatory variable in the MaxEnt modelling exercise, aligning with existing literature where depth is consistently identified among the most important predictors (Breen et al., 2016; La Manna et al., 2016, 2020; Pace et al., 2019). This can be attributed to the influence of depth on the availability and distribution of prey species, which consequently affects the distribution of bottlenose dolphins (Pace et al., 2019). Bottlenose dolphins are observed to feed on species residing at various levels of the water column, encompassing benthic, demersal and pelagic species, typically found in shallow waters up to 200 metres (Blanco et al., 2001; Neri et al., 2023).

Studies conducted in various regions of the Mediterranean Sea revealed a varied diet, which reflects the species' ability to exploit different food resources (Bearzi et al., 2009; Blanco et al., 2001; Milani et al., 2018). Notably, the bottlenose dolphin is known to exhibit behavioural plasticity that allows it to adapt its feeding strategies and capitalise on human activities, particularly fishing operations (Reynolds et al., 2013).

Overall, demersal species emerge as a predominant component in the western Mediterranean Sea, where European hake (*Merluccius merluccius*) is the most commonly found in bottlenose dolphins' stomach content analyses (Blanco et al., 2001; Neri et al., 2023). Conversely, in the

eastern Mediterranean, the bottlenose dolphin feeds mainly on benthic species, such as snake blenny (*Ophidion barbatum*), and demersal species, such as bogue (*Boops boops*), while epipelagic species such as round sardinella (*Sardinella aurita*) and European pilchard (*Sardina pilchardus*) also part of their diet (Bearzi et al., 2009; Milani et al., 2018). Other species commonly considered of great importance for the bottlenose dolphin include octopus (*Octopus vulgaris*), and mackerels (*Trachurus sp.*).

Specific information on the diet of the bottlenose dolphin in Maltese waters is currently lacking. Nevertheless, insights into depth preferences in relation to prey species can be gleaned. A study conducted by Terribile & Laspina (2022) revealed a substantial interaction with artisanal fishery practices, indicating cuttlefish (*Sepia officinalis*) and saddled seabream (*Oblada melanura*) as the primary species susceptible to depredation in Malta. Notably, these fish species inhabit shallow waters on the continental shelf.

The suitability of the Maltese shelf for bottlenose dolphins can be further attributable to its role as the primary spawning area for a substantial portion of its demersal resources (DFA, as cited in Dimech et al., 2005), including the European hake mainly found on the continental shelf between depths of 100 and 200 metres (Borg et al., 2023; Fiorentino et al., 2003).

These patterns provide further evidence that habitat suitability is significantly associated with depth and is higher in shallow and coastal waters. However, the pelagic character of some of the fish species found in Malta, such as mackerels, may be the driver of bottlenose dolphins' distribution in offshore areas (Bonanno et al., 2015).

5.2.2. Chlorophyll-a

Chlorophyll-a emerges as the second most influential explanatory variable of dolphins' distribution, due to the high level of permutation importance resulting from the jackknife analysis. Given the distribution of chlorophyll-a and considering that the highest habitat suitability is associated with moderate to high concentrations, the hypothesis that bottlenose dolphins are more likely to be found in shallow and coastal regions in Malta is reinforced. The study indeed revealed a strong tendency to avoid areas with low concentrations of chlorophyll-a, primarily located in deep offshore waters in the south-western region.

Nevertheless, this study shows that habitat suitability declines as chlorophyll-a concentrations increase. Although the results cover a similar range of chlorophyll-a concentration values found in research carried out in Lampedusa by La Manna et al. (2016), a partial divergence can be observed. In La Manna et al.'s study, the predicted presence of bottlenose dolphins in Lampedusa initially declined until chlorophyll-a reached intermediate values, but the results showed an increased predicted presence with increasing chlorophyll-a concentrations.

The decrease in bottlenose dolphin habitat suitability, evident in the response curve of the current study as chlorophyll-a concentrations increase, can be attributed to the nutrient input from intense the human activities occurring around the Maltese Islands, particularly marine traffic (Farrugia et al., 2016; Fossi & Lauriano, 2008). This input enhances the abundance of phytoplankton biomass, potentially rendering those areas less suitable for dolphins.

Chlorophyll-a's ecological importance as a predictor is made clear by its role as a key indicator of phytoplankton productivity, which determined its application in this study as a proxy for prey availability. Given that phytoplankton forms the foundation of the marine food web, its abundance is fundamental to support the entire marine ecosystem, while, at the opposite end of the food chain, bottlenose dolphins exist as apex predators. The co-occurrence of chlorophyll-a and bottlenose dolphins finds explanation in the relationship between abundance of prey species that occupy the intermediate levels of the food web and the spatial distribution of primary productivity (Smith et al., 1986).

The low minimum and maximum average concentrations of chlorophyll-a found over the course of the period under observation emphasise the oligotrophic nature of Malta's waters (Farrugia et al., 2016). However, a spatial difference between coastal and offshore waters is evident and consistent with previous studies describing coastal waters as more productive than offshore (Colella et al., 2016). Given the high energetic demands of bottlenose dolphins as top predators, coastal productive waters represent a preferred habitat that can fulfil their energy requirements, particularly in the oligotrophic context of Maltese waters (Mannocci et al., 2018).

Additionally, it is known that chlorophyll-a values exhibit significant seasonal variation (Gauci et al., 2021), due to the impact of climatic variables such as wind speed and temperature, while the interannual variation is negligible (Colella et al., 2016). Given the absence of a specific focus on seasonality in this study, it is important to clarify that the inferred habitat suitability primarily stems from geographical factors rather than the influence of seasonal variations, thus reinforcing the preference of bottlenose dolphins for shallow and coastal areas characterised by moderate-to-high average chlorophyll-a levels rather than deep offshore waters.

5.2.3 Correlated Environmental Variables

The analysis revealed a strong inverse correlation between SST and chlorophyll-a, indicating that areas with lower chlorophyll-a, notably the deeper regions in the south-west portion, coincide with warmer average temperatures. These findings align with established research by Behrenfeld et al. (2006), which found warm surface waters and strong water column stratification are associated with lower levels of chlorophyll-a. Consequently, the analysis of the distribution of chlorophyll-a, given its high spatial correlation with SST, logically leads to the conclusion that bottlenose dolphins exhibit a preference for shallower areas with moderate-to-low temperatures and avoid those characterised by warmer SSTs.

Another important finding of the study is the positive correlation between dissolved oxygen and chlorophyll-a, and the inverse correlation between dissolved oxygen and SST, which are consistent with the findings of Saliba (2017) in Maltese waters. This suggests a preference for colder, productive, and well-oxygenated shallow waters, which also represent the conditions most favourable for prey aggregation (Methion et al., 2023).

5.2.4 Vessel Traffic

The inclusion of vessel traffic as a predictor in the model was aimed at understanding the influence of the variation of this variable on the habitat suitability of bottlenose dolphins around the Maltese archipelago, knowing that this region is characterised by a high density of maritime activities (Galdies & Refalo, 2015). Although this predictor significantly contributed to the model's predictive power, it reveals a smaller impact on habitat suitability compared to depth and chlorophyll-a, making it the third variable of importance in shaping the modelled distribution of the species. This implies that bottlenose dolphins tend to inhabit areas in close proximity to human activities, but while the influence of vessel traffic on the distribution of dolphins appears to be relatively modest, the predicted habitat suitability diminishes as the level of traffic intensifies. This suggests that this variable still exerts an impact on their habitat use and tends to be progressively less tolerated.

This duality in the findings suggests that dolphins are resilient to boat traffic until it reaches a threshold that becomes intolerable, indicating that dolphins coexist with human activities but tend to avoid areas where the disturbance is too high (La Manna et al., 2013). In particular, this

resilience can be explained by the behavioural plasticity and the compromise that bottlenose dolphins accept when the benefits of food availability are higher than the costs of being exposed to the risks caused by the presence of humans (Reynolds et al., 2013).

Responsive avoidance behaviour has been documented in relation to various factors associated with vessel type and behaviour, predictability, magnitude, frequency, timing, and location (La Manna et al., 2013; Papale, Azzolin, & Giacoma, 2011; Pirota et al., 2015). Specifically, dolphins exhibit adverse reactions to motorised vessels characterised by erratic and unpredictable behaviour, especially when such occurrences are frequent and concentrated in both space and time. Conversely, when in the vicinity of fishing boats, characterised by consistent navigation speed and direction, dolphins tend to modify their acoustic behaviour to maintain feeding while remaining within the area (La Manna et al., 2013).

The tolerance that determines the proximity of high habitat suitability to human activities can be attributed to different factors. For example, fishing areas not only provide convenient locations for dolphins to forage, aligning with productive habitats that support a rich marine ecosystem, but dolphins also capitalise on fishing operations through depredation, obtaining easily accessible food in the process (Bonizzoni et al., 2022). Furthermore, the consistent navigation speeds and linear routes characteristic of fishing vessels enable dolphins to maintain their foraging activities by employing adaptive strategies, including acoustic adaptation, as described above.

Similarly, in regions crossed by ferry boats, such as the channel between Malta and Gozo where this type of disturbance represents a regular and predictable variable, dolphins may adjust their behaviour in the presence of these vessels (Luís et al., 2014). Moreover, in the proximity of bunkering areas, prevalent vessel types, such as cargo vessels and tankers, exhibit fixed-route behaviour, with a large majority remaining stationary, resulting in minimised physical disturbance (Pirota et al., 2015). Additionally, the presence of anchored boats offers a potential foraging opportunity, aided by the shadow effect and the concentration of organic matter, fostering prey aggregation (Gooding & Magnuson, 1967).

Considering that pleasure crafts exhibit the highest density peaks and the most significant variability in both space and time, particularly concentrated around the coast, this type of marine traffic appears to be less tolerated and to affect the distribution of dolphins, causing displacement from the most suitable areas (Rako et al., 2013). However, a more detailed investigation of the influence of different vessel types on a shorter temporal scale is needed, considering the seasonality of some activities, particularly those related to maritime tourism, and the seasonal distribution of the dolphin population.

These results confirm that dolphins are indeed present on the continental shelf and are closely associated with vessel traffic, emphasising their behavioural plasticity and ability to take advantage of human activities to a certain extent of tolerance.

5.3 Risk Exposure to Anthropogenic and Environmental Stressors

5.3.1 Risk Exposure to Vessel Traffic

The study shows that bottlenose dolphin habitat preferences and maritime traffic coexist, with a notable overlap that is primarily concentrated along the archipelago's eastern coastline. This pattern underlines the substantial exposure of dolphins to maritime traffic pertaining to different activities and across diverse regions.

Negative reactions to vessel disturbance have been consistently documented, specifically when vessels approach within a proximity of 200 metres to dolphins, irrespective of the type of activity (Papale, Azzolin, & Giacoma, 2011; Pirota et al., 2015; Piwetz, 2019). These

adverse reactions manifest in the disruption of various essential activities, including feeding, social interactions, and resting. Additionally, dolphins exhibit avoidance behaviours in response to the perceived disturbance caused by the close proximity of vessels (Papale, Azzolin, & Giacoma, 2011).

5.3.1.1 Leisure Boats

Leisure boating, referring to privately owned or touristic pleasure crafts and sailing vessels, emerges as the major cause for concern due to its significant overlap with the habitat suitability of bottlenose dolphins. This concern arises from the fact that leisure boats share significant spatial proximity with the natural distribution of dolphins, creating a scenario where their activities intersect with critical marine environments. The issue is worsened by the fact that leisure boats exhibit extremely high-density values, especially in specific areas, with the waters surrounding Comino being particularly problematic.

The majority of the evidence suggests that these activities make bottlenose dolphins more vulnerable and degrade their preferred habitat, which can result in either short-term relocation within the impacted area or longer-term exclusion from their natural habitats. (Bejder et al., 2006; Fortuna, 2006)

In areas characterized by high tourism-driven leisure yachting, leisure boating emerges as the primary contributor to anthropogenic disturbance (Rako et al., 2013). The combination of loud, low-frequency noise and erratic behaviour amplifies the disruptive impact of pleasure boats on the marine environment. These combined factors contribute to habitat degradation, leading to specific instances where the abundance of dolphins has been reduced, and their distribution has been altered (Rako et al., 2012, 2013). These disturbances are recognised as enduring influences that impact the long-term habitat use patterns of bottlenose dolphins (Fortuna, 2006). Additionally, the short-term disruptions caused by leisure boating and non-targeted touristic activities, especially if repeated, carry implications for long-term impacts on crucial aspects such as survival and reproduction (Clarkson et al., 2020).

This is particularly pertinent in highly competitive nautical tourism locations like the Maltese archipelago, where intense leisure boating occurs, especially during the summer (Gauci Carlton, 2018). A notable 15% increase in Malta's pleasure craft licences granted in 2021, fuelled by the country's thriving tourism industry (Business Today, 2023), raises concerns, especially if no measures are implemented to limit interactions between leisure boaters and dolphins and to prevent harassment incidents. Malta's allure as a tourist destination and its exponential growth in tourism over the years (Deloitte, 2022), with leisure remaining the main purpose of visit for the vast majority of the arrivals (Attard, 2019). However, this comes at an environmental cost. In the case of dolphins, this is evident in pleasure boaters neglecting measures to approach dolphins responsibly, leading to instances of harassment (Lovinmalta, 2023).

While sailing vessels do not appear to elicit negative reactions from dolphins when under sail (Papale, Azzolin, & Giacoma, 2011), they do become a source of underwater low-frequency noise when they switch their mode of propulsion to engines. An important recent study carried out in Malta by Filletti et al. (2023), has identified sailing vessels as contributing to the highest Sound Pressure Levels (SPL) levels detected underwater, together with passenger and cargo vessels. This noise emission is characterised by low-ranging frequencies and is particularly intense in locations like the Grand Harbour. Notably, the study found that the emission of low-frequency noise from sailing vessels is considerably higher on weekends, possibly indicating increased maritime activity during that time due to touristic activities. Finally, the results of the present study show a significant overlap between sailing vessels coastal routes and areas frequented by pleasure crafts. This implies that sailing vessels, specifically those primarily

intended for tourism and leisure, may demonstrate behaviours similar to those typically associated with power-driven pleasure crafts and expose dolphins to the same risks.

Despite the study underscores the significant exposure of bottlenose dolphins to the stress exerted by leisure boating, this exposure is likely underestimated. The reason for this underestimation is attributed to the fact that smaller pleasure boats and jet skis, which are coastal, fast, and known for erratic behaviour, are not equipped with Automatic Identification System (AIS). AIS is mandated only for vessels exceeding 300 Gross Tons (GT) according to the International Maritime Organization regulations in 2023 (IMO, 2023).

According to Wells et al. (2008), areas with intensified traffic from small boats and jet skis amplify the risk of collisions, posing a heightened threat to the well-being of coastal bottlenose dolphins. The erratic nature of these vessels, coupled with their tendency to approach animals closely and travel at significant speeds, contributes to the elevated risk. Injuries resulting from vessel strikes, while frequently survivable, pose the greatest risk to coastal bottlenose dolphins, with small boats and jet skis identified as the primary culprits (Dwyer et al., 2014; Wells et al., 2008). These incidents, often caused by unpredictable behaviour and high-speed navigation, can have severe consequences, ranging from potential fatality to disruptions in reproductive processes. Solitary bottlenose dolphins that seek interactions with humans, face a higher risk of fatal collisions, as exemplified by a tragic incident in the Netherlands. In this case, a highly sociable solitary dolphin washed ashore dead, displaying clear signs of a propeller collision (IJsseldijk et al., 2020).

The surge in commercial marine mammal watching activities, commonly referred to as “whale watching,” has emerged as a growing concern. Despite being initially perceived as benign and sustainable, this practice can lead to habitat alterations and disturbances, especially when a good code of conduct for approaching the animals is not adopted (Bejder et al., 2022). In Malta, only one company holds the required permit to conduct whale-watching activities, adhering to the ACCOBAMS guidelines for responsible whale watching (ACCOBAMS, 2022). However, some tour operations in Malta are advertising dolphin viewing without the required regular permit (F. Soster, personal observation). This is particularly problematic because these operators fail to adhere to the recommended code of conduct for cetacean viewing, adopting behaviours that are detrimental and dangerous for the animals (ACCOBAMS, 2010).

In conclusion, the impacts described above, particularly the disturbances caused by loud, low-frequency noise and erratic behaviour from leisure boating, have evident consequences for dolphins. One significant effect is the potential displacement of dolphins from their usual coastal habitats to areas farther from the coast, which may be less suitable. This pattern of displacement has been described in previous studies conducted in the Mediterranean (Gonzalvo et al., 2008, 2014; La Manna et al., 2023a; Papale, Azzolin, & Giacoma, 2011; Rako et al., 2013).

5.3.1.2 Fishing Vessels

Fishing vessels’ distribution overlaps significantly with the distribution of bottlenose dolphins, especially in the south-eastern coastal and offshore waters in proximity of the aquaculture sites. These areas are often characterised by intense vessel activities involved in the fish farming operations, such as maintenance, feeding and harvesting.

Dolphins demonstrate remarkable adaptability in the presence of boats associated with aquaculture operations, allowing them to take advantage of foraging opportunities, particularly during harvesting operations (Díaz López, 2012). The benefits of accessing food near fish farm activities appear to outweigh the risks, fostering a coexistence in which dolphins adjust their behaviour to meet their needs.

However, it is critical to recognise that threats to dolphins continue to exist in this context. Fish farm workers intentionally feeding discarded fish (F. Soster, personal observation) pose a significant risk to the population. Such food provisioning practises can disrupt dolphins' natural behaviour and lead to habituation, impairing dolphin calves' ability to learn essential feeding behaviours if adults obtain food directly from humans (Mann & Sergeant, 2003). Furthermore, this behaviour could have a negative impact on fish farm operations, potentially causing disruptions if dolphins encounter resistance while attempting to obtain food from fish farm workers (Díaz López, 2017).

The well-documented interactions between dolphins and fishing activities are widely known, and this phenomenon has been the focus of many studies (Bonizzoni et al., 2022). Bonizzoni et al. (2021) have given detailed insights into these interactions. In particular, observations show that dolphins prey on trawlers in a depredatory manner. Since these fishing operations provide dolphins with alternative sources of food, it has been discovered that the close relationship between dolphin behaviour and active trawlers has a significant impact on both the distribution and behaviour of dolphins. In Malta, interactions are particularly problematic for artisanal fisheries rather than trawling, as highlighted by Laspina, Terribile & Said (2021).

In the current study, the overlap between dolphin habitat suitability and non-aquaculture-related fishing activities is moderate in coastal areas, while offshore, it is confined to the continental shelf off the southeast coast of Malta. This suggests a seemingly limited impact of fisheries on dolphin distribution due to the moderate overlap with fishing activities.

A potential explanation for this limited overlap could be attributed to the fact that the dataset used for this study only includes tracks from vessels equipped with AIS. In Malta, a significant 98% of the fishing fleet is constituted by small-scale vessels engaged in artisanal fisheries that are typically smaller than 12 metres (Fisheries Control Directorate, n.d).

Given that AIS-equipped vessels might not fully represent the extensive small-scale fishing activities, there is a possibility that the impact of these smaller vessels on the distribution of bottlenose dolphins, is underestimated. For a more comprehensive understanding, the study should have considered boats equipped with Vessel Monitoring Systems (VMS), which has become mandatory for every fishing vessel in Malta only recently, as per legislative amendments (S.L.425.07, amended by L.N. 191 of 2023).

However, it is essential to acknowledge that most interactions between bottlenose dolphins and artisanal fisheries primarily occur in the areas surrounding fish farms, as emphasized by Terribile and Laspina (2022). This underscores that the majority of these interactions take place in coastal regions, suggesting that the coastal impact of small-scale fishing activities is substantial. The increasing frequency of these interactions has prompted the testing of acoustic deterrent devices (ADD) to dissuade dolphins from depredate small-scale fisheries, yielding promising results in terms of reduced depredation incidents (Terribile & Laspina, 2022). Nevertheless, the potential impact of ADD on dolphins, particularly in terms of their food intake and distribution, remains largely unexplored.

Adding to the complexity of this subject, fishing gear itself poses inherent risks, potentially causing injuries through entanglement or ingestion. Instances of entanglement in lines or nets can lead to severe consequences, including the loss of appendages or disruptions to essential behaviours like swimming and feeding (Wells et al., 2008).

5.3.1.2 Cargo Vessels and Tankers

Tankers and cargo ships demonstrate a distribution pattern that is predominantly offshore, deviating from coastal areas. The most concentrated zones for these vessels are identified in bunkering areas, which are necessary for their refuelling operations. This offshore concentration is a reflection of the logistical and operational necessities inherent to these large

maritime vessels. Additionally, a noteworthy density of tankers and cargo vessels is observed in close proximity to harbours, particularly at the Grand Harbour and Marsaxlokk. This intensified presence near harbours signifies a strong association with port activities, trade, and logistical operations, which are crucial for the economy of the Maltese Islands (Times of Malta, 2023).

In terms of their interaction with dolphins' suitable areas, the overlap is concentrated around the two harbours and offshore in the vicinity of the south-eastern bunkering sites. Interestingly, this overlap is more pronounced with tankers than cargo vessels, given the higher mean density of tankers and their peak concentrations in these regions.

In proximity to harbours, the excessive underwater SPL and the persistent low-frequency characteristics of the surroundings (Filletti et al., 2023) may induce altered acoustic behaviours and communication patterns in bottlenose dolphins. Studies indicate that, in response to similar conditions, dolphins tend to reduce the frequency of their calls and adjust the acoustic frequency range. This adaptive strategy is aimed at mitigating the impact of masking caused by the low-frequency sounds emitted by engines in the area. Notably, the consequences of these adjustments are particularly serious for social interactions, especially in mother and calf pairs (Bas et al., 2017; Luís et al., 2014).

In addition, the presence of large cargo vessels and tankers in inshore waters creates a constraint on the surface-level lateral movement opportunities for dolphins. Observations indicate that dolphins in these areas alter their usual movement patterns by increasing their frequency of diving to avoid collisions. This alteration is particularly notable in mother and calf pairs, as calves have limited diving abilities (Piwetz et al., 2019).

Conversely, in bunkering areas, the risk of potential collisions with dolphins can be considered low due to the typically slow speed or stationary behaviour of vessels in these areas that do not seem to have an impact on the distribution of the animals. Furthermore, the availability of open space without physical constraints allows dolphins the freedom to move without encountering significant obstacles or hazards.

Despite the lower risk of collisions, bunkering areas contribute significantly to habitat degradation, primarily due to pollution. Although bunkering is a routine operation, the process involves the transfer of fuels and other substances between vessels, involving a risk of oil spills and posing a threat to the overall health and integrity of the habitat (Kamal & Kutay, 2021). While the risk of collisions may be minimised in bunkering areas, the ecological impact of potential oil spills remains a significant concern.

The waters surrounding Malta present elevated risks of oil spills and discharges (Galdies, 2008). While individual incidents may be perceived as insignificant, the cumulative impact arising from repeated small events poses a substantial threat to the marine environment (Galdies, 2008), directly affecting bottlenose dolphins. Research has revealed that, even in the absence of oil spills in a given year, bottlenose dolphins exhibit elevated levels of polycyclic aromatic hydrocarbons (PAHs), petroleum-derived substances, in their tissues due to the transit of oil tankers (García-Álvarez et al., 2014). Although the impacts of PAHs on cetaceans have not been thoroughly explored, the effects of these compounds are known to be carcinogenic for humans and animals (López-Berenguer et al., 2023).

Notably, the south-eastern bunkering areas, which are heavily utilised by cargo vessels and tankers due to their strategic location providing shelter from the prevailing north-westerly wind, present a particularly high risk due to the overlap with suitable habitat for dolphins.

Regrettably, the current lack of data hinders the ability to assess the impacts of this environmental stressor on ecosystems and species. As of 2019, the Environment and Resources Authority (ERA, 2019) notes the unavailability of comprehensive information, emphasising the need for enhanced data collection and monitoring efforts to better understand and address

the potential consequences of maritime activities on the marine environment and on bottlenose dolphins in this region.

5.3.1.3 Passenger Vessels

Vessels dedicated to passenger transportation, including ferries, fast ferries, and cruise ships, exhibit significant overlap with the suitable habitats of bottlenose dolphins. This overlap is notably concentrated in coastal areas, with locations such as the channel between Malta and Gozo and the Grand Harbour experiencing high densities of both maritime activities and dolphin presence.

However, given the predictable nature of their schedule, their impact on bottlenose dolphins is more closely associated with loud and low-frequency and habitat degradation, than abrupt behavioural disruptions and redistribution (Arcangeli et al., 2013; Luís et al., 2014).

Notably, these passenger vessel activities intensify during the summer months, corresponding to increased inbound and domestic tourism, as indicated by the National Statistics Office (NSO, 2023). The heightened maritime traffic during the summer season underscores the importance of understanding and managing the potential impacts on bottlenose dolphins, particularly in these coastal areas where tourism-related activities and marine mammal habitats intersect, as expressed in previous chapters.

5.3.2 Risk Exposure to FADs

Fish Aggregating Devices (FADs) do not significantly overlap with coastal regions but pose a risk in offshore areas chosen by bottlenose dolphins as their preferred habitat. Notably, a clear association is observed in regions off Gozo and the south-west of Malta, indicating potential threats to dolphins in these offshore habitats.

Even though the exposure to marine traffic was not detected in these areas, the exposure to FADs emphasizes that dolphins may face risks from fisheries engaged in the common dolphinfish catch. However, quantifying the actual exposure to this type of risk remains challenging, as these areas merely represent a potential overlap with FAD deployment trajectories and not with actual gears. However, the findings offer crucial insights into the interaction between the distribution of bottlenose dolphins and artisanal fisheries. Since the practice is seasonal, assessing the effective overlap of this activity with the presence of dolphins should consider seasonal changes in distribution and the actual locations of FADs.

A significant overlap with FADs trajectories is also visible in areas where bunkering activities occur, exposing dolphins to multifaceted challenges and impacts. While FADs offer an alternative foraging opportunity, they concurrently pose a risk of entanglement (Manfrini et al., 2023). As discussed earlier, the benefits derived from the shadow effect of FADs, aiding in finding food, outweigh the associated risk of entanglement.

In 2019, Malta implemented a series of management measures to regulate the utilisation of Fish Aggregating Devices (FADs) in accordance with the guidelines outlined in Recommendation GFCM/43/2019/1 by the General Fisheries Commission for the Mediterranean (GFCM, 2019). These measures include important regulations such as allowing only authorised vessels that have been notified to the GFCM to deploy FADs. Additionally, to mitigate the risk of entanglement, the use of biodegradable materials in the construction of FADs is recommended and the importance of maintaining and promptly removing FADs when not in active use is stressed. These measures collectively aim to promote sustainable and responsible practices in the deployment and management of FADs, aligning with international recommendations for the conservation of marine ecosystems. Despite the implementation of

these regulations, incidents of entanglement persist in Malta and abroad (Manfrini et al., 2023; Sechi et al., 2023; F. Soster, personal observation), indicating an ongoing issue, whose extent remains uncertain and requires a more in-depth investigation.

5.3.3 Risk Exposure to Environmental Stressors

The present study did not explicitly identify the spatial overlap of environmental stressors with the distribution of bottlenose dolphins, nor did it examine specific climate change scenarios. However, the observed preference for a particular range of chlorophyll-a concentrations suggests that alterations in environmental parameters could pose significant risks to the dolphins.

The rise in sea surface temperatures (SST) due to climate change is linked to shifts in chlorophyll-a distribution, affecting the presence of phytoplankton in coastal areas, especially in nearshore waters sensitive to variations in nutrient input, often in the form of sediments. This sensitivity may lead to undesirable effects such as eutrophication, negatively impacting the health of coastal sea areas and contributing to habitat degradation (Gauci et al., 2021).

In general, ocean warming holds the potential to modify phytoplankton blooms and overall productivity by impacting mixed-layer shoaling (Fiedler, 2018). Specifically, marine heatwaves can disrupt chlorophyll-a levels, affecting the entire marine food web and directly influencing fish populations. The effects vary with latitude due to diverse limiting environmental factors, such as nitrate concentrations. In particular, marine heatwaves tend to decrease chlorophyll concentrations in the tropics and mid-latitudes, while high latitudes experience increases (Noh et al., 2022).

The repercussions of ocean warming extend to fish stocks, influencing productivity and the overall structure of ecosystems. Changes in primary production cascade to secondary production, affecting the transfer of energy to higher trophic levels, ultimately impacting the distribution of both predators, like bottlenose dolphins, and fishing activities (La Manna et al., 2023b).

The findings of the current study reveal a substantial aversion of bottlenose dolphins to regions characterised by low chlorophyll-a concentrations, raising concerns about potential risks associated with extreme events caused by climate change to the well-being and distribution of these dolphins. In particular, the frequency of marine heatwaves has doubled over the last two decades, causing mass mortality events of marine organisms across the Mediterranean Sea (Garrabou et al., 2022). In addition, the latest Ocean State Report, carried out by Copernicus Marine Service, has documented record-breaking marine heatwaves observed in the summer of 2022, surpassing previous occurrences in terms of intensity, duration, and overall surface impact (Copernicus, 2022). The escalating frequency and severity of these extreme events is particularly worrisome, especially for coastal benthic and demersal fish species (Garrabou et al., 2022). Consequently, the repercussions of these events can have a significant impact on dolphins' distribution if their prey are affected.

To gain a more thorough understanding of this aspect, it is necessary to conduct a comprehensive analysis that takes into account detailed records of marine heatwaves in Malta and considers seasonal variations in chlorophyll-a and dolphins' distribution. Nevertheless, the current research holds the potential to establish a foundational understanding of the potential changes associated with the interactions between marine heatwaves, chlorophyll-a concentrations, and bottlenose dolphin's habitat preferences.

6. Conclusion

6.1 Key Findings

The exploration of bottlenose dolphin habitat preferences and the assessment of human activities' impact are receiving increased attention across the Mediterranean Sea (Awbery et al., 2022; Genov, 2022; La Manna et al., 2023a; Pace et al., 2021). Despite this increased regional focus, the same level of attention does not seem to extend to Maltese research institutions and government bodies, where the situation appears to be relatively underexplored and underrepresented in the existing body of research, also explaining the lack of conservation measures in place for this species.

Acquiring the necessary information for the conservation of protected cetacean species becomes difficult in the absence of long-term studies and comprehensive systemic surveys. Nonetheless, by maximising the information at hand, well-informed choices can be made, and practical plans can be put into place for the conservation of cetaceans.

This study represents the first effort to offer a thorough depiction of bottlenose dolphin habitat use in Malta and to provide insights into any evidence of the impacts of human activities, such as maritime traffic and fishing operations, while assessing the species' exposure to such activities. In contrast to earlier research, this study went above and beyond by providing a detailed map outlining the specific areas where bottlenose dolphins are more likely to be found and the specific preferences for certain habitats. Additionally, what sets it apart is the emphasis on mapping the distribution in relation to the oceanographic context and generating a quantitative and spatial assessment of the risk exposure to various human-induced threats. Rather than relying solely on qualitative observations, this study employed rigorous analyses to determine the extent to which these threats influence the dolphins' habitat.

Given the fragmented data available on the occurrence of the bottlenose dolphin in Maltese waters, all resources published between 2012 and 2021 were used to run a SDM. The MaxEnt approach emerged as a particularly effective tool for understanding the contribution of oceanographic features and human presence to the habitat preferences of this species in Malta. Additionally, incorporating anthropogenic activities into the model proved to be effective and crucial in highlighting a certain degree of intolerance for boat disturbance. This inclusion is particularly relevant as human activities, especially vessel traffic, have become integral components of the dolphins' environment.

Notably, the findings revealed that bottlenose dolphins are primarily linked to shallow and coastal regions due to the significant influence of seafloor topography and chlorophyll-a concentration, indicating a close relationship between the dolphins and the surrounding ecological parameters. Because human activities are concentrated in shallower and coastal waters, the study found a significant overlap between the suitable habitat for the species and vessel traffic, mainly related to tourism and leisure boating. However, a strong interaction with artisanal and professional fishing activities was also observed in offshore areas.

The study reveals that all suitable areas for bottlenose dolphins are impacted by either vessel traffic or fishing, with a moderate level of influence observed across most regions and some areas experiencing higher degrees of risk exposure. Furthermore, the analysis of maritime traffic patterns in the study indicates a consistent and significant disturbance in coastal and shallow regions, suggesting that areas suitable for bottlenose dolphins are subject to an influence that is not sporadic but constant.

Although the impact of climate change could not be understood from this study, the strong impact of environmental variables on dolphins' distribution suggests a potential vulnerability to extreme events, such as marine heatwaves, that might affect the availability of food.

6.2 Limitations of the Study

The modelling exercise conducted in this study was subject to various limitations that warrant consideration in the interpretation of results.

First of all, the fragmented nature of the data collected over an extended timeframe, with a significant gap between the last survey and the previous one, posed a challenge to the comprehensive understanding of bottlenose dolphin distribution. Additionally, the non-uniform distribution of sightings dispersed throughout the wide geographic scope of the study area may have introduced biases into the model, affecting the accuracy of predictions (Phillips, 2005). The creation of a bias file was therefore necessary and proved effective to mitigate the potential bias arising from the non-homogeneous sampling effort (Phillips et al., 2009). This facilitated the reduction of spatial autocorrelation, typically linked to clustered sightings, and corrected for seasonal bias resulting from a more concentrated effort during spring and summer.

In terms of environmental conditions, the creation of predictor layers involved an averaging and interpolation process, potentially influencing the representation of actual spatial and temporal variations in these conditions. The limited set of predictors chosen for the study, although common in this type of analysis, may not encompass all factors influencing dolphin distribution. Notably, variables such as prey abundance, distribution, and categorical factors like fish farms were not included, limiting the interpretability of the model (La Manna et al., 2023a). The strong association of bottlenose dolphins with human activities further complicates prediction, necessitating the consideration of additional biological factors. Therefore, considering more variables, such as categorical variables, including the locations of the fish farms, and more detailed information on the distribution of prey, would have enhanced the accuracy of the model. However, these kinds of variables are often difficult to represent and quantify (La Manna et al., 2023a).

The static nature of the model, devoid of considerations for seasonality and social factors like group size and composition, represents a further limitation. Seasonal variations in hydrographic and biological variables are critical, and understanding their influence is essential for a thorough investigation (Methion et al., 2023). The absence of these considerations in the current study hampers the ability to draw robust conclusions about potential changes in bottlenose dolphin habitat preferences in response to seasonal fluctuations in anthropogenic activities and environmental conditions.

The overlap analysis, focusing solely on AIS boats and not accounting for vessels equipped with Vessel Monitoring Systems (VMS), represents another limitation. This choice has led to an underestimation of the impact, particularly regarding small-scale fisheries. Additionally, the exclusion of small leisure boats, which lack satellite tracking systems, further diminishes the comprehensiveness of the impact assessment.

Concerning Fish Aggregating Devices (FADs), the use of trajectories instead of actual locations limits the understanding of their impact. Furthermore, since FADs are seasonal, an analysis that considers the seasonal distribution of dolphins is imperative for a more accurate assessment.

6.3 Recommendations

6.3.1. Prospects for Future Research

The study showed how information gathered from different resources and using a modelling exercise can support scientific research to produce robust baseline data on the bottlenose

dolphin in Malta. However, although the current research addresses the existing gap in knowledge regarding the distribution of bottlenose dolphins and identifies specific areas of overlap between the species and human activities, it is acknowledged that further efforts are required to explore various aspects, including temporal variability and social dynamics, as elaborated in the following paragraphs.

The study has considered year-round bottlenose dolphin occurrence data and made use of information gathered over an extended period to offer a baseline assessment of the suitable habitat. Nonetheless, it is imperative to emphasise the necessity for more detailed research that delves into seasonal variations, concerning both environmental conditions and anthropogenic disturbances. Comprehending the differences between the summer and winter months, when, for example, nautical activities tend to decrease due to the reduced impact of tourism, and tracking the changes in fisheries distribution can contribute to a more comprehensive understanding of ecosystem dynamics. Moreover, considering the bottlenose dolphin's ecological plasticity, incorporating prey distribution into the analysis could be crucial to enhancing the accuracy of the distribution model and to providing deeper insights into the dynamics of how both human activities and dolphin distribution change over seasons as well as the interdependence between the two.

An additional research priority should involve the examination of social aggregation. In particular, including factors such as group size and composition in the analysis would result in a more thorough comprehension of how various suitable regions are used. Furthermore, an exploration of group dynamics in correlation with oceanographic variations would enhance our insight into the distribution patterns of the species. This investigation could also unveil the social dynamics that play a role in shaping their habitat preferences.

Prioritising and carrying out more extensive and systematic efforts are imperative given the results obtained from the present study. Specifically, expanding the data collection to include data on those small boats that are not equipped with AIS is crucial for a more comprehensive investigation into the ecological impacts of the two primary pressures identified in this study. Moreover, exploring potential behavioural changes over time may be essential to understanding whether these pressures induce bottlenose dolphins to redistribute over time.

A suggestion for further studies with regards to interactions with fisheries is to increase the effort in assessing the impact of specific threats associated with FADs, taking into account the actual FAD locations, tracking the abandoned gear, and reporting entanglement events as bycatch.

Finally, modelling the distribution of bottlenose dolphins under various climate change scenarios is advised to investigate the possible effects of climate change on their habitat preferences and spatial patterns. Through the examination of multiple climate change scenarios, possible changes in the dolphins' range could be predicted, thereby enhancing the knowledge base for conservation and management strategies.

6.3.2 Implications for Conservation

The findings of the study not only reveal critical insights into the distribution of bottlenose dolphins in Malta but also carry significant implications for the conservation of this species in the region. One of the key observations is the lack of specific measures in place to safeguard bottlenose dolphins in areas identified as suitable habitats.

Addressing gaps in previous research, this study is aimed at helping identify and understand important habitats for bottlenose dolphins. Despite Malta's existing Programme of Measures for the MSFD (ERA, 2023), the absence of identified hotspots limits the effectiveness of current conservation efforts. The insights obtained from this research, in turn, can guide management practices aimed at mitigating potential threats to the species.

One noteworthy finding is that the SACs previously established for the conservation of bottlenose dolphins are not aligned with the areas that have been determined to be suitable for the species. This misalignment emphasises the need to re-evaluate and expand these conservation sites based on the study's findings.

Furthermore, the research underscores the impact of vessel traffic, particularly from tourism and leisure boating activities, on the distribution of dolphins in coastal areas. The inadequacy of current measures is especially evident in two areas: the Comino Channel, where high vessel traffic resulting in noise and pollution is negatively impacting bottlenose dolphin habitats; and the areas near coastal fish farms in the southeast of Malta, where dolphins are increasingly interacting with fisheries and recreational boats.

While the development of a code of conduct for boaters and the implementation of an awareness campaign are positive steps, the study recommends further and more stringent measures, stressing the importance of developing and adopting a more solid strategy for the protection of the bottlenose dolphin in Maltese waters, not only limited to the SACs.

Following Bejder et al. (2022), recommendations include reduced speed limits, heightened public awareness, and stricter regulation of tourism and traffic around the critical areas identified. First and foremost, lowering speed limits is a critical first step. However, optimal solutions would include not only limited access to the specified regions but also the establishment of designated boat traffic routes.

In the context of interactions with fisheries, effective management approaches would include spatial and temporal restrictions on fishing activities in areas identified as suitable habitat for bottlenose dolphins. For example, adjusting the trajectories in which FADs can be deployed and limiting fishing practices outside important habitats for the species would be a proactive measure to minimize the potential impacts of fishing activity on bottlenose dolphins. However, implementing these approaches is likely to face challenges, especially in regions like Malta where the fishing industry, in general, holds significant power. Therefore, it is important that fishing practices strictly adhere to the regulations set forth by the GFCM to ensure sustainability. The GFCM has already proposed mitigation measures to diminish the impact of FADs, including the use of gear designed to reduce the likelihood of entanglement when a cetacean comes into contact with it and the prompt recovery of the gear after use to prevent abandonment and mitigate potential risks.

Finally, in order to direct conservation efforts with a strategic and knowledgeable approach to the protection of this species, a Conservation Management Plan (CMP) for the bottlenose dolphin would be essential in the first place. By establishing specific conservation objectives and implementing targeted management strategies, the plan would support the species' long-term survival.

In conclusion, the study's implications extend beyond the identification of suitable habitats, urging a comprehensive reconsideration of current conservation measures. The study advocates for a more context-specific approach, considering the intricate relationship between bottlenose dolphins and their environment. Implementing these recommendations is crucial for effective conservation, ensuring the sustainable coexistence of bottlenose dolphins and human activities in Maltese waters.

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Appendix I

Figure S1

Results from the ENMeval Modelling Exercise Used to Identify the Feature Types. The Feature Types Selected are those Suggested for $\Delta AICc = 0$

fc	rm	time	arg	auc.train	auc.diff.avg	auc.diff.std	auc.val.avg	auc.val.std	or.10p.avg	or.10p.std	or.mtp.avg	or.mtp.std	AICc	delta.AICc	w.AIC	ncoof	
1	L	1	fc.LQ.m.1	0.576842846	0.056663874	0.045389566	0.588072593	0.067122149	0.090394615	0.090627011	0.098333333	0.098333333	0.026352314	2.7845554407492	5.482313657	0.02940937	3
2	LO	1	fc.LQ.m.1	0.598287066	0.06177162	0.046997744	0.56607995	0.06895372	0.107051282	0.107051282	0.06895372	0.06895372	0.026352314	#####	6.19042738	0.020744418	4
3	H	1	fc.H.m.1	0.63928819	0.067275847	0.059226858	0.589729423	0.068046474	0.091666667	0.107223661	0.016666667	0.016666667	#####	#####	2.945584725	0.105079455	16
4	LOH	1	fc.LOH.m.1	0.634682122	0.06318941	0.061084399	0.59538801	0.070386479	0.107051282	0.103585107	0.033333333	0.033333333	#####	#####	0	0.458284835	14
5	LOHPT	1	fc.LOHPT.m.1	0.640228205	0.055093489	0.062088857	0.598886686	0.06311861	0.08877949	0.085052398	0.025	0.025	#####	#####	8.174183757	0.007893679	19
6	LOHPT	1	fc.LOHPT.m.1	0.652593867	0.06834784	0.071373995	0.582456607	0.068288385	0.124338914	0.088531848	0.033333333	0.033333333	#####	#####	11.96741615	0.001154633	20
7	L	2	fc.L.m.2	0.576701919	0.05617125	0.045842432	0.567865749	0.067039273	0.090394615	0.090627011	0.098333333	0.098333333	#####	#####	7.022598104	0.013883529	3
8	LO	2	fc.LQ.m.2	0.586742747	0.058827521	0.047786364	0.582400594	0.065782144	0.107051282	0.103585107	0.068333333	0.068333333	#####	#####	7.598498482	0.010254782	4
9	H	2	fc.H.m.2	0.606783216	0.063291698	0.062186499	0.575042303	0.073166675	0.088358974	0.086227943	0.016666667	0.016666667	#####	#####	11.88758188	0.001195662	10
10	LOH	2	fc.LOH.m.2	0.616557391	0.070089914	0.05768292	0.587182104	0.079748897	0.107051282	0.095847089	0.033333333	0.033333333	#####	#####	8.130069276	0.007665285	12
11	LOHPT	2	fc.LOHPT.m.2	0.62103946	0.063257607	0.063368824	0.600378917	0.078356382	0.116025641	0.106553697	0.025	0.025	#####	#####	1.195086445	0.252130719	10
12	LOHPT	2	fc.LOHPT.m.2	0.626123946	0.055391758	0.046167453	0.567503007	0.06604619	0.098076623	0.098447392	0.008333333	0.008333333	#####	#####	4.857271723	0.044650033	12
13	L	3	fc.L.m.3	0.576597917	0.055391758	0.046167453	0.567503007	0.06604619	0.098076623	0.098447392	0.008333333	0.008333333	#####	#####	8.596226768	0.008419739	3
14	LO	3	fc.LQ.m.3	0.58535697	0.056775522	0.050793744	0.561556564	0.067164305	0.107051282	0.103585107	0.068333333	0.068333333	#####	#####	12.16177308	0.001037282	5
15	H	3	fc.H.m.3	0.58933574	0.058670345	0.048924876	0.569318504	0.064984386	0.107692308	0.1044957	0.016666667	0.016666667	#####	#####	19.61419457	2.5233661985506E-05	7
16	LOH	3	fc.LOH.m.3	0.600534324	0.063000377	0.054879889	0.576320417	0.073235247	0.115384615	0.111929922	0.033333333	0.033333333	#####	#####	9.434508061	0.004068928	9
17	LOHPT	3	fc.LOHPT.m.3	0.608378661	0.060604843	0.05857109	0.578982001	0.069516897	0.115384615	0.111929922	0.041666667	0.041666667	#####	#####	6.1980529	0.02085145	8
18	LOHPT	3	fc.LOHPT.m.3	0.611957198	0.060604843	0.05857109	0.578982001	0.069516897	0.115384615	0.111929922	0.041666667	0.041666667	#####	#####	7.824198553	0.009164998	9
19	L	4	fc.L.m.4	0.576320854	0.054500688	0.04671256	0.567034332	0.0681101	0.098076623	0.091339586	0.008333333	0.008333333	#####	#####	10.1824253	0.002818707	3
20	LO	4	fc.LQ.m.4	0.576320854	0.054500688	0.04671256	0.567034332	0.0681101	0.098076623	0.091339586	0.008333333	0.008333333	#####	#####	12.23084359	0.001012142	4
21	H	4	fc.H.m.4	0.602016985	0.057837534	0.034501478	0.582838137	0.063281617	0.107692308	0.1044957	0.025	0.025	#####	#####	2.75368013	#####	6
22	LOH	4	fc.LOH.m.4	0.595531799	0.062987248	0.055786878	0.57239111	0.074827483	0.115384615	0.111929922	0.033333333	0.033333333	#####	#####	15.82087164	0.000168142	8
23	LOHPT	4	fc.LOHPT.m.4	0.600877948	0.058581732	0.055492219	0.571009836	0.069165725	0.107051282	0.117542733	0.041666667	0.041666667	#####	#####	20.04058199	2.0388177255044E-05	10
24	LOHPT	4	fc.LOHPT.m.4	0.600877948	0.058581732	0.055492219	0.571009836	0.069165725	0.107051282	0.117542733	0.041666667	0.041666667	#####	#####	20.04058199	2.0388177255044E-05	10
25	LO	5	fc.LQ.m.5	0.57599387	0.053225296	0.047256959	0.566423338	0.065424986	0.105789231	0.10586092	0.008333333	0.008333333	#####	#####	11.88568265	0.001198798	3
26	LO	5	fc.LQ.m.5	0.57599387	0.053225296	0.047256959	0.566423338	0.065424986	0.105789231	0.10586092	0.008333333	0.008333333	#####	#####	11.88568265	0.001198798	3
27	H	5	fc.H.m.5	0.61004765	0.055710031	0.034887093	0.578840403	0.061222812	0.107692308	0.1044957	0.016666667	0.016666667	#####	#####	36.15300975	#####	5
28	LOH	5	fc.LOH.m.5	0.58871917	0.06358473	0.0521218	0.565811934	0.073874803	0.11474359	0.116896161	0.033333333	0.033333333	#####	#####	20.0432827	#####	8
29	LOHPT	5	fc.LOHPT.m.5	0.55098026	0.05723505	0.05676127	0.564634887	0.068222519	0.107051282	0.117542733	0.041666667	0.041666667	#####	#####	23.556659718	#####	9
30	LOHPT	5	fc.LOHPT.m.5	0.55098026	0.05723505	0.05676127	0.564634887	0.068222519	0.107051282	0.117542733	0.041666667	0.041666667	#####	#####	23.556659718	#####	9

Figure S2

Bias File Used in the MaxEnt Modelling Exercise to Improve Predictability and Reduce Sampling Bias

