

Cetacean distribution and habitat modelling in the NE Atlantic Ocean

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Marine Biology Master of Science Thesis | 2023

University of Algarve, Portugal

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The cover photograph is an original (*Delphinus delphis* – short-beaked common dolphin)

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Ana-Maria Purcari

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Ana-Maria Purcari

Abstract

The world's ocean, central to life on our planet, is rapidly deteriorating due to human activities. Cetaceans, many of which hold the position of apex predators, play a pivotal role in upholding the integrity of marine ecosystems, serving as indicators of ecosystem health and productivity. However, the conservation of these species is hindered by the scarcity of available data concerning their occurrence and distribution patterns. Ecological niche models are useful in studying habitat suitability concerning the environmental preferences of the species. Combining data from platforms of opportunity and citizen science can overcome difficulties in collecting marine data. This study aimed to model habitat suitability for the most sighted cetacean species: the short-beaked common dolphin (*Delphinus delphis*), common bottlenose dolphin (*Tursiops truncatus*), fin whale (*Balaenoptera physalus*), and minke whale (*Balaenoptera acutorostrata*) in the Algarve region, South Portugal. Seasonal habitat preference for the target species was investigated using the Maximum Entropy Model for the period 2019-2022. The results show that cetaceans are highly dependent on the coastal habitats of the Algarve, likely due to upwelling events and notable topographic features such as capes, that lead to resource-rich waters. For the short-beaked common dolphin, chlorophyll-a concentration was a key predictor, reflecting prey availability. Models revealed distribution differences between inshore and offshore populations of the common bottlenose dolphin. Fin whales use this area as a migratory corridor, moving between high latitude feeding grounds and low latitude breeding grounds. Minke whales are considered residents in Portuguese waters, present year-round but more reported in spring and summer. Given the great importance of cetaceans for the planet's well-being and the rapid increase in economic activities in the Algarve, these findings should influence future marine protected area plans to preserve the biodiversity and associated cultural and economic benefits.

Keywords: cetaceans, ecological niche modelling, MaxEnt, habitat suitability, Portugal, NE Atlantic.

Resumo em Português

A presença humana estendeu-se a todas as partes dos oceanos da Terra, provocando a rápida deterioração dos ecossistemas marinhos devido às alterações climáticas e às atividades antropogénicas. Esta degradação pode conduzir estes ecossistemas a um ponto de instabilidade, afectando as comunidades naturais e os serviços vitais que prestam à humanidade. Para evitar tais resultados, as estratégias de conservação e gestão devem basear-se nos conhecimentos científicos mais recentes sobre a ecologia das espécies.

Os cetáceos, que englobam as baleias de barbas, e as baleias com dentes, representam o maior grupo de mamíferos marinhos. Muitas destas espécies são predadores de topo, desempenhando um papel crucial na manutenção da integridade dos ecossistemas marinhos, refletindo a sua saúde e produtividade. No domínio marinho, as actividades humanas exercem um impacto mais significativo nos ecossistemas costeiros, sendo os predadores marinhos de topo, como muitas das espécies de cetáceos, particularmente vulneráveis devido às suas características e história de vida. Quando estas espécies se encontram nas regiões costeiras, enfrentam ameaças como a degradação do habitat, as capturas acessórias, a depleção de presas, o turismo e a poluição. Dada a complexidade do ambiente oceânico, a sua compreensão e gestão constituem um desafio. Muitos estudos têm-se concentrado na ecologia e no estado de conservação destes predadores de topo, que podem actuar como espécies emblemáticas, importantes para a decisão de medidas de conservação e indicadores de biodiversidade. As evidências apoiam a ideia de que a protecção destes predadores de topo e dos seus habitats aumenta a biodiversidade e a saúde geral do ecossistema, tornando-os componentes cruciais da gestão marinha e dos esforços de conservação.

A região costeira do Atlântico Ibérico tem águas produtivas com variadas características topográficas que albergam uma vasta gama de espécies de cetáceos. Devido ao aumento

das atividades marítimo-turísticas no Algarve, que impõe pressão sobre o habitat, esta área necessita de estudos de ecologia de cetáceos para possíveis futuras medidas de conservação. Os estudos de distribuição das espécies, nomeadamente, a modelação do nicho ecológico, permitem conhecer os comportamentos ecológicos e os padrões de distribuição geográfica. As embarcações comerciais de observação de cetáceos e as iniciativas de ciência cidadã podem fornecer dados valiosos para apoiar estes estudos, ultrapassando os desafios na recolha de dados. Esses desafios são essencialmente o acesso a embarcações que realizem saídas com elevada frequência semanal. A identificação de habitats adequados com elevada abundância de espécies pode ajudar a inverter o declínio das populações de cetáceos causado pela interferência humana.

O estudo teve como objetivo estabelecer modelos de nicho ecológico para o golfinho-comum-de-bico-curto, o roaz-corvineiro e duas baleias de barbas (baleia-comum e baleia-anã) no Atlântico Norte, focando os seus padrões de distribuição sazonal ao longo das águas costeiras do Sul de Portugal. Esta investigação é particularmente significativa, uma vez que, tanto quanto sabemos, é a primeira a incorporar a modelação de habitat para baleias de barbas nesta região. Esta investigação analisou dados recolhidos ao longo de quatro anos por embarcações comerciais de observação de cetáceos e plataformas de ciência. Foram utilizados modelos de nicho ambiental para identificar os factores que afectam a distribuição dos cetáceos na região, identificando habitats que poderão requerer esforços de gestão e conservação. Espera-se que os resultados contribuam para a identificação de potenciais áreas fundamentais para os cetáceos nas águas costeiras do sul de Portugal continental.

A investigação foi efectuada na região do Algarve uma área que apresenta diferentes profundidades de zonas costeiras, incluindo o Parque Natural da Ria Formosa, e de mar aberto, influenciadas por diferentes sistemas de marés e de correntes oceânicas. Foram recolhidos dados sobre golfinhos-comuns-de-bico-curto (*Delphinus delphis*), roaz-corvineiro (*Tursiops truncatus*), baleias-comuns (*Balaenoptera physalus*) e baleias-anãs (*Balaenoptera acutorostrata*) a partir de embarcações comerciais de observação de cetáceos, plataformas de ciência cidadã e observações a partir de terra, de 2019 a 2022.

Variáveis ecológicas, como latitude, longitude, sazonalidade, batimetria, declive batimétrico, distância à costa, temperatura da superfície do mar e concentração de clorofila-a, foram utilizadas para modelar as preferências sazonais de habitat. A preferência de habitat para as espécies-alvo foi investigada utilizando Modelo de Entropia Máxima. A importância relativa das variáveis ambientais foi avaliada utilizando a importância da permutação, e a exatidão do modelo final foi avaliada utilizando a área sob o parâmetro da curva do receptor-operador.

Foram criados modelos de nicho ambiental para as espécies-alvo com base em dados de 2139 avistamentos de golfinhos-comuns-de-bico-curto, 1087 de roaz-corvineiro e 128 de baleias de barbas (comum e anã). É de realçar que a maioria dos avistamentos ocorreu durante o verão e a primavera. Uma vez que as observações são oportunisticas e se desenrolam com mais intensidade nos meses em que há mais turistas. A análise de colinearidade não indicou correlações fortes entre as variáveis de previsão. Os modelos foram inicialmente executados com todos os cinco fatores de previsão, reduzindo-os gradualmente com base na sua importância relativa. Os modelos demonstraram um excelente desempenho preditivo, com valores médios do parâmetro da curva do receptor-operador superiores a 0,9.

Apesar do excelente desempenho do modelo, foram registadas algumas limitações como sejam o uso de presenças, em vez de presenças-ausências, e os enviesamentos sazonal e geográfico. Os modelos de presença-ausência são mais precisos na estimativa da distribuição real das espécies. No entanto, para espécies altamente móveis e oceânicas, a obtenção de registos de ausência reais constitui um desafio particularmente complicado de ultrapassar. Os conjuntos de dados oportunistas das plataformas de observação estão limitados às zonas costeiras onde operam as empresas de observação de cetáceos. Este enviesamento costeiro pode afetar o desempenho preditivo dos modelos fora da área de estudo e afetar a precisão global do modelo. Os esforços de amostragem do estudo foram influenciados pelos operadores turísticos, com uma maior recolha de dados durante a época de verão. Desafios como a pandemia de COVID-19 também contribuíram para a limitação do número da recolha de dados.

Para o golfinho-comum-de-bico-curto, a concentração de clorofila a foi um preditor-chave da distribuição, refletindo a disponibilidade de presas. O habitat de Sagres mostrou uma adequação distinta, provavelmente devido a fortes eventos de upwelling que influenciam a abundância de presas. A preferência por águas mais quentes no inverno, em torno do Cabo de Santa Maria, também foi destacada. No caso do roaz-corvineiro, foram observadas diferenças de habitat entre as populações costeiras e offshore, com factores como a distância à costa e a batimetria a desempenharem papéis significativos. A população offshore esteve presente durante todo o ano ao longo da isóbata de 200 m. As águas costeiras do Cabo de Santa Maria apresentaram uma elevada aptidão para esta espécie durante todo o ano, o que pode ser devido à elevada biodiversidade e produtividade causada pela Ria Formosa. Os golfinhos roazes são conhecidos por habitarem águas costeiras pouco profundas e entrarem nas lagoas em busca de alimento. No que respeita às baleias de barbas, os modelos realçaram o carácter migratório destas espécies. Os resultados sugerem que as águas algarvias servem de corredor migratório para as baleias-comuns, que se deslocam entre zonas de alimentação a alta latitude e zonas de reprodução a baixa latitude. Ao contrário das baleias-comuns, as baleias-anãs são consideradas residentes nas águas portuguesas. Estiveram presentes durante todo o ano, mas foram mais registadas na primavera e no verão. Tendem a preferir águas mais profundas, no limite da plataforma continental. As áreas altamente adequadas em torno dos cabos de São Vicente e Santa Maria podem ser áreas atrativas para as baleias de barbas devido a eventos de afloramento e disponibilidade de presas.

O estudo realça a forte dependência das espécies de cetáceos dos habitats costeiros da região do Algarve, caracterizados por eventos de upwelling significativos e características topográficas proeminentes que conduzem a águas ricas em recursos biológicos. Apesar das limitações registadas, as plataformas oportunísticas de observação, como os barcos de observação de cetáceos e a ciência cidadã, podem fornecer dados valiosos. Dado o declínio da biodiversidade e da saúde dos ecossistemas, é necessária mais investigação para compreender melhor a relação entre a distribuição geográfica das espécies e os habitats mais adequados para os cetáceos. Tal conhecimento pode ajudar a implementar

medidas de conservação eficazes e a regular melhor as actividades humanas nos 'hotspots' de cetáceos.

Palavras-chave: cetáceos, modelação de nicho ecológico, MaxEnt, adequação do habitat, Portugal, Atlântico Nordeste.

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List of abbreviations

ASW	Atlantic Surface Water Current
AUC	Area Under the Receiver-Operator (ROC) Curve
aut	Autumn
BRT	Boosted Regression Tree Model
chl _a	Chlorophyll-a
CTA	Classification Tree Analysis
dist_shore	Distance to shore
DSM	Density Surface Model
ENFA	Ecological Niche Factor Analysis
ENM	Ecological Niche Modelling
ENMs	Ecological Niche Models
GAM	Generalised Additive Model
GBIF	Global Biodiversity Information Facility
GBM	Generalised Boosted Model
GLM	Generalized Linear Model
GPS	Global Positioning System
K	Kelvin
lat	Latitude
lon	Longitude
m	Meters
MARS	Multivariate Adaptive Splines
MaxEnt	Maximum Entropy Model
mg/m ³	Milligrams per cubic meters
MOW	Mediterranean Outflow Water Current
nm	Nautical Miles
OPO	Observation Platform of Opportunity
PEEZ	Portuguese Economic Exclusive Zone
PI	Permutation Importance Parameter
RF	Random Forest Model

SD	Standard Deviation
spr	Spring
sst	Sea Surface Temperature
sum	Summer
SVM	Support Vector Machines
VIF	Variance Inflation Factor
win	Winter

1 | State of the art

Cetaceans are large, misunderstood creatures of the sea that have always been a part of human history through whaling, culture and fishing stories, economy, education, and tourism (Brito & Sousa, 2011). They are divided into two different infraorders, Mysticeti: the elegant baleen whales and Odontoceti: the hunter-toothed whales (Wursig et al., 2018). Most of them live in this boundless blue environment that is highly understudied and foreign to most people. Thus, their conservation is affected by the limited data on their occurrence and distribution patterns. And in this regard, the species present in the coastal waters of South Portugal are no exception. However, through a niche-based modelling approach, we can provide insight into how cetaceans use their habitat and what factors influence their distribution. Nowadays, more and more attention must be directed towards them as we realise how crucial they are for the planet.

1.1 | Cetacean ecology

1.1.1 | Worldwide distribution

Suborder Cetacea includes two infraorders: Mysticeti (baleen whales) and Odontoceti (toothed whales, dolphins, porpoises), comprising 14 families (International Whaling Commission, 2022). Cetaceans are secondary marine forms that live permanently in aquatic environments. They are found in all oceans and most of the seas of the world, from polar regions (Vacquié-Garcia et al., 2017) to temperate (Goetz et al., 2015) and tropical waters (Forcada, 2018; Díaz-Torres et al., 2022), as well as in riverine habitats (Das et al., 2022). Many are migratory species that alternate seasonally between habitats, from neritic to abyssal feeding grounds and from coastal to offshore migratory routes and breeding grounds (Forcada, 2018; Delarue et al., 2022; Herr et al., 2022).

1.1.2 | Habitat

Cetaceans are associated with a variety of oceanic features. Some species associate

with ice edges (Vacquié-Garcia et al., 2017), with the continental shelf or its edges (Kiszka et al., 2007), with seamounts (Dede et al., 2022), and some with shorelines (Ingram & Rogan, 2002; Ballance, 2018). Oceanic species prefer habitats defined by the physical and chemical characteristics of the water, which define water masses and current boundaries (Ballance, 2018). Some species inhabit cold currents or cool upwelling waters with high primary and secondary productivity (Scales et al., 2017). Others use thermocline depth, strength, and surface water chlorophyll content to delimitate their habitat (Ballance, 2018). However, prey generally drives the species-habitat relationships, not the physical variables typically used in habitat suitability analysis. Even the cosmopolitan distribution of the killer whale (*Orcinus orca*) can broadly be explained by its various prey (fishes, pinnipeds, and cetaceans), as well as the migration of baleen whales between feeding and breeding grounds (Ballance, 2018).

1.1.3 | Diet

All baleen whales use their mouth to collect water in the euphotic zone and filter out small zooplankton (copepods, euphausiids, mysids), fish or squid (Moore et al., 2019), except for grey whales that feed mainly on benthic organisms in shallow waters (Caraveo-Patiño & Soto, 2005; Trites & Spitz, 2018). In contrast, toothed whales prey on individual animals such as cephalopods, fish (Marçalo et al., 2018), pinnipeds, or even other toothed and baleen whales (Saulitis et al., 2000; Barrett-Lennard et al., 2011; Trites & Spitz, 2018). Cetacean dietary information primarily derives from stranded and bycaught individuals, which limits spatiotemporal coverage and may not represent the entire population (Trites & Spitz, 2018). In addition, diets can change with age and season, vary between regions and years, and shift with environmental changes (Trites & Spitz, 2018). Cetaceans play an essential role as ecosystem engineers through interaction with their prey.

1.1.4 | Ecological role

Cetaceans influence ecosystem structure and function through bottom-up and top-down control processes (Hunt, 2006; Roman et al., 2014; Ballance, 2018). Bottom-up control

occurs when the availability of food resources limits population growth, while top-down control restricts population growth through predation (Hunt, 2006). These processes are intertwined and complement one another (Roman & Estes, 2018). Cetaceans shape marine ecosystems through four ecological pathways (Roman et al., 2014):

- › *Consumers*. Predation influences prey populations' ecological and evolutionary dynamics, altering food webs and biogeochemical cycles (Berge et al., 2012; Roman et al., 2014; Ballance, 2018).
- › *Prey*. Due to their large size, abundance, and high energy density, great whales represent a source of energy and nutrients in scarce ocean environments (Roman et al., 2014; Roman & Estes, 2018). Commercial whaling affected these whales (Springer et al., 2003), creating a trophic cascade that diminished the number of many species, such as sea otters, kelp forests, fish nurseries, and birds of prey (Reisewitz et al., 2006; Roman et al., 2014; Springer et al., 2003; Wilmers et al., 2012).
- › *Nutrient vectors*. Cetaceans represent a vector of nutrient and material flux, contributing to primary production through vertical mixing, horizontal transfer, and recycling of Carbon and other nutrients in the ocean (Roman et al., 2014). Cetaceans mechanically mix the ocean waters when diving to feed, which is especially important in stratified conditions (Dewar et al., 2006). Whale pump delivers nutrients (e.g., Fe, N) to surface waters by releasing faecal plumes, urine, and placentas, which increases photosynthesis in biological hotspots (Roman & McCarthy, 2010; Lavery et al., 2010). Migrating cetaceans horizontally transfer nutrients from nutrient-rich temperate and subpolar areas to the oligotrophic breeding grounds (Roman et al., 2014).
- › *Detritus*. Typically, cetacean carcasses sink to the seafloor, enriching areas depleted of nutrients and energy (Roman et al., 2014). Whale falls alter local food availability, provide habitat structure and food resources for many species, and connect hydrothermal-vent and cold-seep communities in the deep sea. Stranded

carcasses can complement terrestrial food webs (Smith, 2006; Lundsten et al., 2010).

As top predators, cetaceans are surrogate species that represent other species in the community, helping to address conservation measures. They can be classified as (Caro & O'Doherty, 1999; Sergio et al., 2008; Brito & Sousa, 2011):

- › *Keystone species* – used to restore ecosystems within reintroduction projects and manage trophic cascades.
- › *Biodiversity indicator species* – used to assess anthropogenic impact, monitor population trends in other species, and locate high regional biodiversity areas needing protection.
- › *Umbrella species* – used to define the habitat for protection, including the requirements of less demanding species.
- › *Sentinel species* – used as early warning systems for human-induced alterations of the environment.
- › *Flagship species* – used to raise awareness among the public due to their charismatic appearance and behaviour.

1.2 | Importance for humans

Cetaceans show attractive behaviours when surfacing for air, such as speed movements in large groups, breaching, leaps, and breaths visible from afar. Due to their behaviour and characteristics, they were part of early human culture and economy, recorded through old maritime reports, natural history descriptions, sea-related stories, and legal documents (Brito & Sousa, 2011). The relationship between humans and cetaceans continues today through whaling, tourism, research, and conservation. Whale and dolphin watching is a global industry contributing to the economy with approximately US\$ 2.1 billion annually (O'Connor et al., 2009). It provides the basis for scientific and educational programs stimulating people's interest in preserving marine wildlife and habitats.

Cetaceans were among the first species to be protected by national and international laws (Roman et al., 2013). Current research and management projects sustain seasonal industries in many communities and fuel a culture of protests against anthropogenic activity through organisations such as Sea Shepherd, World Wild Fund, and Greenpeace (Roman et al., 2014).

1.3 | Management and conservation

1.3.1 | Worldwide

Humans have now reached every square kilometre of Earth's Ocean, affecting cetaceans around the world directly by hunting, bycatch in fishing gear, conflicts with fisheries, and ship-strikes, and indirectly through habitat destruction by fishing, construction, chemical and noise pollution, overexploitation of prey resources, and climate change (Harwood, 2001; Hammond et al., 2013). Out of 92 cetacean species evaluated, the IUCN Red List classifies 33 species as Near Threatened, Vulnerable, Endangered, or Critically Endangered (IUCN, 2022). In comparison, ten species are little known and have been classified as Data Deficient (IUCN, 2022). However, cetaceans are challenging to protect due to their mobility, disregard for political boundaries and susceptibility to threats.

Many countries worldwide strive to understand the severity of the anthropogenic impacts on cetaceans and to mitigate them through national legislation, together with several international organisations: European Union, International Council for the Exploitation of the Sea (ICES), International Whaling Commission, Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR), and United Nations Environment Programme Convention on Migratory Species (Hammond et al., 2013).

1.3.2 | Portugal

The Portuguese Economic Exclusive Zone (EEZ) is located in the northeast of the Canary Basin, in the NE Atlantic Ocean (Correia et al., 2015). This area is under the scope of the

European Union Habitats Directive, according to which Member States must maintain or restore natural habitats and wild fauna and flora species in need of protection (European Union Habitats Directive, 1992), monitoring them and reporting their conservation status (Hammond et al., 2013). The Portuguese EEZ has also been included in the Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic Area meant to reduce threats on cetaceans by improving knowledge on these animals (ACCOBAMS, 2022). In addition, Portuguese waters are also protected by other conservation agreements such as the Oslo and Paris Convention (OSPAR Commission, 2022), the International Council for the Exploration of the Sea (ICES, 2022), the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS, 2022), and Convention on Migratory Species (CMS, 2022).

Bycatch is the main threat to small cetaceans in European Atlantic waters, highly affecting the harbour porpoise (*Phocoena phocoena*) and the short-beaked common dolphin (*Delphinus delphis*) (Read et al., 2006; Hammond et al., 2013) which was assessed as *Unfavorable-Inadequate* for the European Marine Atlantic in 2013 (Murphy et al., 2021). Published data on cetaceans are restricted to a few regional hotspots in Portuguese waters (e.g., the Azores and Madeira archipelagos, Sado estuary) (Cartagena-Matos et al., 2021). Knowledge of habitat suitability is needed to implement current and future conservation measures for cetacean species. However, essential data is still lacking in the NE Atlantic Ocean in the Algarve region of Portugal, slowing down conservation and management strategies.

1.4 | Cetaceans in Portugal, NE Atlantic

1.4.1 | Habitat characteristics

The NE Atlantic is a topographically and oceanographically complex system. It includes the Portuguese EEZ, specifically located in the northeast of the Canary Basin (Correia et al., 2015). This region has several significant topographical features, such as the Madeira-

Tore Rise, the Horseshoe Seamount Chain, and the Mid-Atlantic Ridge. The latter particularly impacts the Azorean ecosystems (Mason, 2009). This Portuguese EEZ is characterised by eddies associated with topographic structures such as seamounts around the Azores archipelago (Morato et al., 2008) or numerous canyons, particularly off western Iberia (Mason, 2009). The Portimão Canyon, located in the Gulf of Cadiz, is a significant topographical feature that restricts the path of the Mediterranean undercurrent, which is known to play a role in forming Mediterranean eddies (Serra & Ambar, 2002). Northeasterly trade winds (NTW) are mainly responsible for the formation of upwelling systems along the African and Portuguese coasts, together interacting with a high-pressure atmospheric system (the Azores High) (Mason, 2009). Latitudinal changes in these features result in seasonal variation in mesoscale oceanic eddies (Mason, 2009). The North Atlantic current is a distinct western limit that follows a stable, but meandering course, transporting heat towards western Europe (Mason, 2009). Such dynamic environments favour ecosystem richness and cetacean diversity (Ballance et al., 2006).

1.4.2 | Cetacean diversity

The Iberian Atlantic coastal margin is characterised by a relatively narrow continental shelf with highly productive and resource-rich waters (Goetz et al., 2015). Mainland Portugal has a coastline of about 832 km with important oceanographic and topographic features (Brito et al., 2009), with 24 cetacean species, Mysticeti and Odontoceti, recorded alongside it (Morais et al., 2021). Among the most abundant cetacean species found in this area are the short-beaked common dolphin (*D. delphis*), common bottlenose dolphin (*Tursiops truncatus*), striped dolphin (*Stenella coeruleoalba*), fin whale (*Balaenoptera physalus*), and minke whale (*Balaenoptera acutorostrata*) (Figure 1.1) (Brito et al., 2009; O'Connor et al., 2009). Furthermore, as many as 28 cetacean species have been sighted in the Portuguese archipelago of Azores due to its mid-ocean location (Silva et al., 2014), and 28 species in the Madeira archipelago (Alves et al., 2018; Correia et al., 2020). In addition, many cetacean species can be found alongside various coasts in NE Atlantic: 17

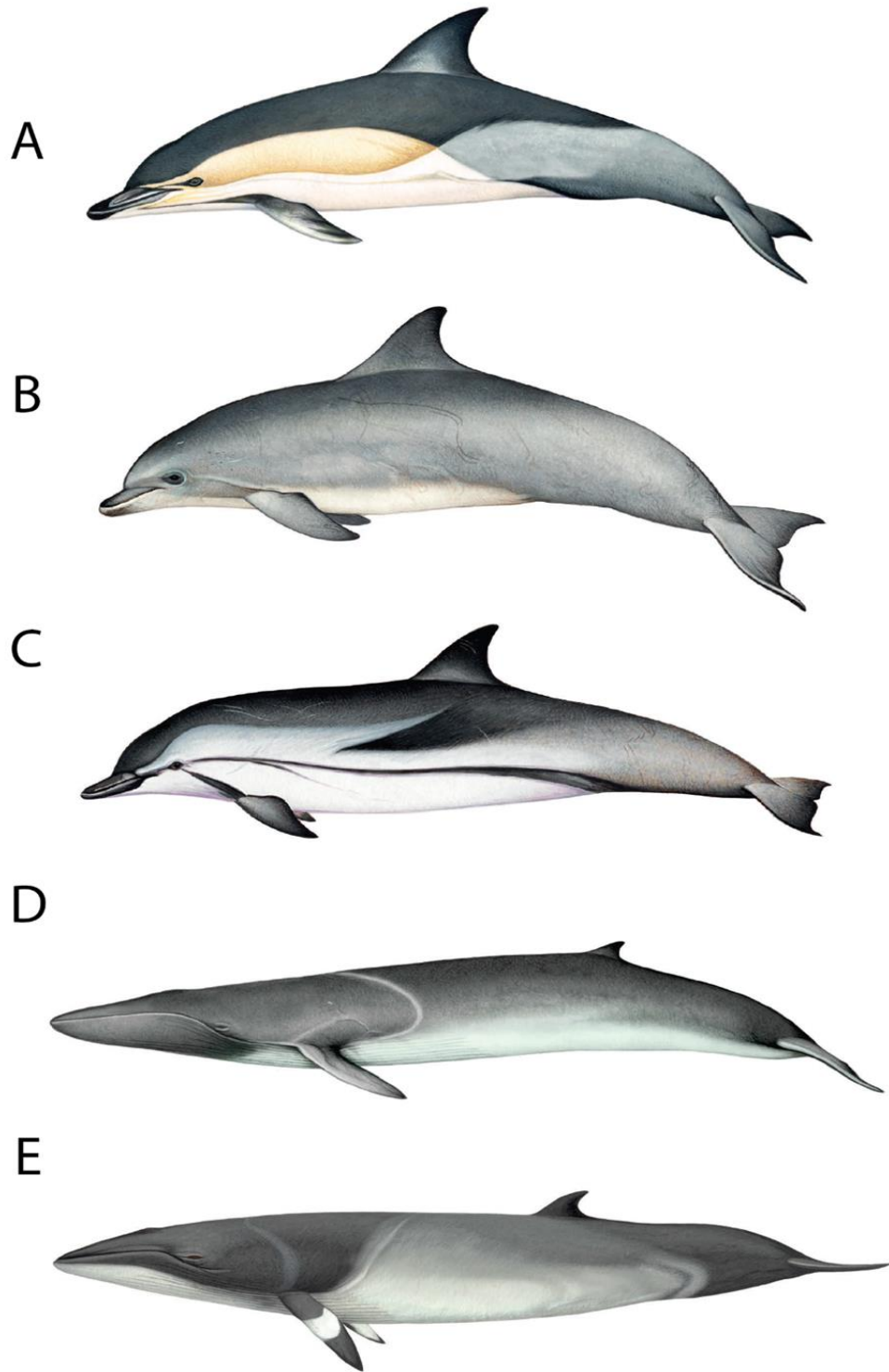


Figure 1.1 | Cetacean species present in the Iberian waters. A. *D. delphis*, B. *T. truncatus*, C. *S. coeruleoalba*, D. *B. physalus*, E. *B. acutorostrata*. (Illustrations by Martin Camm in *Handbook of Whales, Dolphins, and Porpoises*, 2019).

species in NW Spain, 28 in the Canary Islands, 24 in Cape Verde, and 36 in NW Africa (Correia et al., 2020).

Due to the wide latitudinal and longitudinal range of the NE Atlantic, cetaceans move and migrate boundlessly across the entire area (Alves et al., 2019). Thus, the cetacean community species vary in time and among sub-regions in the NE Atlantic (Correia et al., 2020). Therefore, a more intricate approach is needed to fully understand the habitat requirements of cetacean species in this area.

1.5 | Research gaps

Many cetacean studies have been conducted in the NE Atlantic in the past century on various topics, from genetics to ecology to human interactions (Cartagena-Matos et al., 2021). Within the area containing the Iberian Peninsula, NW African coast, and Macaronesia, 36 species of cetaceans have been recorded and studied, with representatives from all the main guilds of cetaceans: small dolphins (common dolphin), large dolphins (pilot whale), beaked whales (Cuvier's beaked whale), sperm whales, and baleen whales (minke whale) (Correia et al., 2020, 2021). In Portugal, ecological niche modelling studies on cetaceans increased and nowadays are present in a wide variety (Table 1.1). However, research is highly concentrated in Macaronesia, especially in the Azores archipelago (García et al., 2018; Valente et al., 2019; Fernandez et al., 2021, 2022).

Although research in this region has been increasing, there is a lack of distribution and habitat preferences studies in mainland Portugal, especially in the Algarve region, compared to the Azores archipelago, where the number of publications is much higher (Cartagena-Matos et al., 2021). Furthermore, as aquatic businesses such as dolphin and whale watching, sailing, diving, and recreational boating flourish in the Algarve region and put more pressure on the habitat, there is a need for cetacean distribution and habitat suitability studies which can play a relevant role in future conservation management.

Table 1.1 | A summary of recent worldwide studies (2018-2022) on ENMs of cetaceans. Models' abbreviations: MaxEnt (maximum entropy), GLM (generalised linear model), GAM (generalised additive models); multivariate adaptive splines (MARS), BRT (boosted regression trees, RF (random forests), SVM (support vector machines), DSM (density surface model), GBM (generalised boosted model), CTA (classification tree analysis).

Source	Location	Model type	Predictors	Main applications
Derville et al., 2018	South Western Pacific	GLM, GAM, BRT, MaxEnt, SVM	Temporal, topographic, oceanographic	Compare different model approaches
Fernandez et al., 2018	Eastern North Atlantic	MaxEnt	Spatio-temporal, topographic, oceanographic	Determine habitat suitability, test different predictors
García et al., 2018	Eastern North Atlantic	GAM	Spatio-temporal, topographic, oceanographic	Determine habitat preferences and temporal distribution
Giménez et al., 2018	Alboran Sea	DSM	Spatio-temporal, topographic, oceanographic	Investigate niche partitioning, determine spatial abundance
Passadore et al., 2018	Coffin Bay	MaxEnt, GAM, GBM, CTA, RF	Topographic, oceanographic, anthropogenic	Determine spatio-temporal distribution
Storrie et al., 2018	Northeast Atlantic	MaxEnt	Spatio-temporal, topographic, oceanographic	Determine spatio-temporal distribution
Barragán-Barrera et al., 2019	Caribbean Basin	MaxEnt	Topographic, oceanographic	Estimate potential distribution
García Barón et al., 2019	Eastern North Atlantic	GAM	Topographic, oceanographic	Determine relative abundance, test different predictors, identify critical areas for protection
Correa et al., 2019	Eastern Tropical Pacific	MaxEnt	Topographic, oceanographic	Determine habitat suitability
Correia et al., 2019	Eastern North Atlantic	GAM	Spatio-temporal, topographic, oceanographic	Determine spatio-temporal distribution, test different predictors
Valente et al., 2019	Northeast Atlantic	GAM	Spatio-temporal	Identify distribution patterns
Correia et al., 2020	Eastern North Atlantic	GAM	Spatio-temporal, topographic	Determine spatio-temporal distribution
Figueiredo et al., 2020	Western South Atlantic	not mentioned	Topographic, oceanographic	Determine geographical, fundamental and realized niches
Melo-Merino et al., 2020	World-wide	MaxEnt, GAM, GLM, and others	Detectability, spatio-temporal, topographic, oceanographic	ENMs and SDMs review
Putra & Mustika, 2020	Savu Sea	MaxEnt	Spatio-temporal, topographic, oceanographic	Describe habitat preference and distribution
Stephenson et al., 2020	South Pacific	RES, BRT	Spatio-temporal, topographic, oceanographic	Determine spatial distribution
Correia et al., 2021	Eastern North Atlantic	GAM, MaxEnt	Detectability, spatio-temporal, topographic, oceanographic	Relate habitat characteristics to distribution
Fernandez et al., 2021	Eastern North Atlantic	MaxEnt	Spatio-temporal, topographic, oceanographic	Determine spatio-temporal distribution
Ramírez-León et al., 2021	Gulf of Mexico	MaxEnt	Spatio-temporal, topographic, oceanographic	Determine habitat suitability
Fernandez et al., 2022	Eastern North Atlantic	GLM, GAM, MaxEnt	Topographic, oceanographic	Determine the role of absences in ENMs
Natoli et al., 2022	Persian Gulf	MaxEnt	Topographic, oceanographic	Determine distribution patterns and habitat preferences
Senigaglia et al., 2022	Bohol Sea	MaxEnt, GLM	Spatio-temporal, topographic, oceanographic	Determine species richness, distribution, habitat use, and interspecific associations

1.6 | Ecological niche modelling

The relationship between species diversity and distribution is essential for ecosystem management and conservation (Hooper et al., 2005), which requires high-resolution species distribution data (Tobeña et al., 2016). Unfortunately, such data is difficult to obtain due to the dynamic nature of cetaceans and the oceanographic processes of a

boundless marine ecosystem (Tobeña et al., 2016; Alves et al., 2018). Nevertheless, ecological niche models (ENMs) can be used to address this information gap.

ENMs are widely used to predict cetaceans' habitat suitability based on the environmental preferences of the species (Gregr et al., 2013; Melo-Merino et al., 2020), as well as to assess areas in need of conservation and research on human-wildlife interactions (Bailey & Thompson, 2009) (Table 1.1).

1.6.1 | Types of models

ENMs can be built with various statistical algorithms (Derville et al., 2018), such as:

- › Profile models: ecological niche factor analysis (ENFA),
- › Regression models: generalized linear models (GLMs), generalised additive models (GAMs), multivariate adaptive splines (MARS),
- › Machine learning: maximum entropy (MaxEnt), boosted regression trees (BRTs), random forests (RFs), support vector machines (SVMs),
- › Bayesian approaches: occupancy models.

MAxEnt and GAM are two of the most often used models in cetacean studies. The maximum entropy algorithm (MaxEnt) is a method used to predict the potential distribution of a species based on its ecological requirements and the environmental conditions of a particular region. It is based on the principle of maximum entropy, which states that, given a set of constraints or requirements, the probability distribution that best represents the current state of knowledge is the one with the highest entropy (i.e., the one that is the most uncertain or random) (Correa et al., 2019). MaxEnt has been applied successfully on species with limited data, including cetaceans (Derville et al., 2018; Barragán-Barrera et al., 2019). It has been used in various studies to predict the potential distribution of cetaceans such as *Stenella* genus species in the Western South Atlantic (do Amaral et al., 2015), *T. truncatus* in the Eastern Tropical Pacific (Correa et al., 2019), and broad group of cetaceans in Northeastern Atlantic (Correia et al., 2015). GAMs are statistical models that analyse the relationship between a response variable and one or

more predictor variables while allowing for non-linear relationships. They have been successfully applied to many cetacean species, such as *Baleanoptera musculus* (Redfern et al., 2017).

1.6.2 | Predictors

The predictors frequently used in cetacean ENMs are static habitat variables (e.g., topographic: depth, seabed slope, substrate type), as they are easier to quantify to use in management plans, being relevant to cetacean habitat preference (Correia et al., 2021). Dynamic habitat variables (e.g., oceanographic: sea surface temperature (SST), sea level, Chlorophyll-a concentration) are also considered for cetacean distribution modelling, as their effects determine physiological limits and prey availability (Lambert et al., 2014; Correia et al., 2021). The spatial and temporal scales of each variable can also influence the model results and application. For example, SST may be relevant to cetacean distribution at several scales. At larger scales, meaning lower spatial resolution, SST can help define the thermal niches of cetaceans and their prey at different life stages and the locations of water masses and current systems (Fernandez et al., 2018; Correia et al., 2021). At smaller scales, meaning higher spatial resolution, SST can be used to determine the occurrence of mesoscale oceanographic features associated with prey aggregations (Fernandez et al., 2018; Correia et al., 2021). Therefore, the model approach and methodology for determining cetacean distribution must be used regarding available data, sampled area and the model's aims whilst accounting for the species' biology (Redfern et al., 2006).

1.6.3 | Observation platforms of opportunity

For wide-ranging species, collecting data on their occurrence and defining their habitat use requirements is challenging due to their complex and expensive logistics (Moura et al., 2012; Alves et al., 2018). Nowadays, observation platforms of opportunity (OPOs) increasingly receive more attention, providing long-term fine-scale data that can be used in ecological niche modelling analysis to determine the cetacean distribution and its

relationship with habitat characteristics (Tobeña et al., 2016; Alves et al., 2018; Correia et al., 2021). The scientific data are mainly collected from three types of OPOs (Alves et al., 2018): ferries or cargo ships with specific regular routes, fishing vessels with non-regular routes, and whale-watching boats with targeted observational efforts. All OPOs are suboptimal and have procedural limitations (Moura et al., 2012). Still, they can provide large data sets in areas that would otherwise be neglected (Alves et al., 2018). The whale-watching industry is growing worldwide, with more qualified staff onboard (i.e., biologists), generally allowing for better data collection (Alves et al., 2018). However, data can be impaired by spatial and temporal coverage biases, time spent with a cetacean group of interest, and data quality (Alves et al., 2018).

1.6.4 | Citizen science

Combining data from multiple sources can overcome difficulties in collecting marine data. Thus, citizen science could aid in increasing the quantity and spatial extent of cetacean observation for habitat modelling purposes (Tiago et al., 2017). Citizen science is defined as ‘the engagement of non-professionals in scientific research’ (Miller-Rushing et al., 2012), from trained volunteers to fishing operators, whale-watching companies, and the general public (Derville et al., 2018). However, using such data comes with statistical challenges, as it is difficult to determine if a higher encounter rate at a site is caused by high habitat suitability or by higher observer effort (Bird et al., 2014). Therefore, statistical tools should be used to handle errors and biases common to citizen science data (Bird et al., 2014).

1.7 | Objectives

In this study, we used niche-based models to provide details of how cetacean species use coastal habitats in the Algarve region of South Portugal, NE Atlantic Ocean, describing the factors that influence their distribution in the study area and identify the habitats in need of urgent management and conservation measures. The main objectives were to:

- › Provide data on the most sighted cetacean species in the Algarve region,
- › Identify the spatial and temporal patterns of cetacean distribution,
- › Perform ENM techniques to characterise habitat preferences and produce habitat suitability maps,
- › Address future research questions, conservation measures, and cultural and economic implications.

The obtained results are expected to help identify potential cetacean hotspots in the southern coastal waters of Portugal's mainland. Thus, protecting these areas and the surrounding waters is crucial for maintaining the area's biodiversity and cultural and economic benefits.

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Cetacean distribution and habitat modelling in the NE Atlantic Ocean

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Abstract

The world's ocean, central to life on our planet, is rapidly deteriorating due to human activities. Cetaceans, many of which hold the position of apex predators, play a pivotal role in upholding the integrity of marine ecosystems, serving as indicators of ecosystem health and productivity. However, the conservation of these species is hindered by the scarcity of available data concerning their occurrence and distribution patterns. Ecological niche models are useful in studying habitat suitability concerning the environmental preferences of the species. Combining data from platforms of opportunity and citizen science can overcome difficulties in collecting marine data. This study aimed to model habitat suitability for the most sighted cetacean species: the short-beaked common dolphin (*Delphinus delphis*), common bottlenose dolphin (*Tursiops truncatus*), fin whale (*Balaenoptera physalus*), and minke whale (*Balaenoptera acutorostrata*) in the Algarve region, South Portugal. Seasonal habitat preference for the target species was investigated using the Maximum Entropy Model for the period 2019-2022. The results show that cetaceans are highly dependent on the coastal habitats of the Algarve, likely due to upwelling events and notable topographic features such as capes, that lead to resource-rich waters. For the short-beaked common dolphin, chlorophyll-a concentration was a key predictor, reflecting prey availability. Models revealed distribution differences between inshore and offshore populations of the common bottlenose dolphin. Fin whales use this area as a migratory corridor, moving between high latitude feeding grounds and low latitude breeding grounds. Minke whales are considered residents in Portuguese waters, present year-round but more reported in spring and summer. Given the great importance of cetaceans for the planet's well-being and the rapid increase in economic activities in the Algarve, these findings should influence future marine protected area plans to preserve the biodiversity and associated cultural and economic benefits.

Keywords: cetaceans, ecological niche modelling, MaxEnt, habitat suitability, Portugal, NE Atlantic.

2.1 | Introduction

Humans have now reached every square kilometre of Earth's Ocean. Marine ecosystems are rapidly deteriorating due to global climate change and increased anthropogenic activities (McCauley et al., 2015; Worm et al., 2006). Thus, marine ecosystems could reach a level of instability that would lead to regime shifts, affecting natural communities and the valuable ecosystem services that benefit human society (Möllmann et al., 2015; Worm et al., 2006). To prevent such changes, management and conservation policies must be based on the most current science on species ecology (Soulé et al., 2005).

Cetaceans, including whales, dolphins, and porpoises, are the largest group of marine mammals (Hoyt, 2011). Most species are top predators, contributing to the integrity of marine ecosystems, indicating ecosystem health and productivity (Roman et al., 2014). Due to their large size and abundance, they represent a high energy source, and their carcasses are a source of detritus for nutrient-depleted environments (Roman et al., 2014; Roman & Estes, 2018). They also contribute to primary production through vertical mixing, horizontal transfer, and recycling of Carbon and other nutrients (Roman et al., 2014). Despite their obvious benefits to our oceans, cetaceans around the world are directly affected by humans through hunting, bycatch in fishing gear, conflicts with fisheries, and ship strikes, and indirectly through habitat destruction caused by fishing, construction, chemical and noise pollution, overexploitation of prey resources, and climate change (Hammond et al., 2013; Harwood, 2001).

In the marine environment, human activities have the greatest impact on coastal ecosystems (Halpern et al., 2008; Passadore et al., 2018). Marine apex predators like whales and dolphins, are especially vulnerable to human-induced stressors due to their life-history traits, such as late maturity, low reproductive rate, and long-life span (Passadore et al., 2018; Reeves et al., 2003). This susceptibility is especially notable in coastal regions where some of the most endangered species are found (Passadore et al., 2018). Various coastal dolphin populations, especially those with strong site fidelity and limited range movement, are threatened by factors like habitat degradation, by-catch,

prey depletion, tourism, and pollution (Atkins et al., 2016; Currey et al., 2007; Monk et al., 2014; Rojas-Bracho et al., 2006). Identifying suitable habitats with high species abundance can revert the decline in dolphin populations caused by humans (Guerra & Dawson, 2016).

The ocean is a complex environment, characterised by constant change and a lack of clear boundaries, making it difficult to monitor and administrate (Evans et al., 2012). To address this challenge, many studies focus on the ecology and conservation status of top predators because they often serve as flagship species, attracting funds due to public interest; as umbrella species, defining protected areas that benefit other species; as keystone species, influencing ecosystem structure; and as biodiversity indicator species, reflecting ecosystem health (Brito & Sousa, 2011; Caro & O'Doherty, 1999; Sergio et al., 2008). Evidence supports that managing protected areas based on top predator distribution can enhance biodiversity and ecosystem benefits (Sergio et al., 2006, 2008). Thus, prioritizing the protection of cetaceans and their habitats contributes to overall marine management, as these measures often extend to other marine areas (Hooker et al., 2011; Sergio et al., 2006, 2008). However, essential data is still scarce in the NE Atlantic Ocean in the Algarve region of Portugal, slowing down conservation strategies.

The Iberian Atlantic coastal region has a relatively narrow continental shelf with highly productive and resource-rich waters (Goetz et al., 2015). The coastline of mainland Portugal stretches for approximately 832 km and is surrounded by significant oceanographic and topographic attributes (Brito et al., 2009). In this area, 24 cetacean species have been sighted, including both Mysticeti and Odontoceti (Morais et al., 2021). Among the most prevalent cetacean species identified are the short-beaked common dolphin (*Delphinus delphis*), common bottlenose dolphin (*Tursiops truncatus*), fin whale (*Balaenoptera physalus*), minke whale (*Balaenoptera acutorostrata*) and other toothed and baleen whales (Brito et al., 2009; O'Connor et al., 2009).

Over the past century, numerous cetacean studies have been conducted in the NE Atlantic, encompassing diverse topics such as genetics, ecology, and human interactions

(Cartagena-Matos et al., 2021). Despite the growing research efforts, there is a lack of distribution and habitat preference studies in mainland Portugal, particularly in the Algarve region, in contrast to the Macaronesia region, especially the Azores archipelago, where publications are more abundant (Cartagena-Matos et al., 2021; Silva et al., 2014; Tobeña et al., 2016). Furthermore, given the continuous rise of aquatic activities over the last two decades, such as whale watching, sailing, diving, and recreational boating in the Algarve, which impose pressures on the habitat, there is a need for ecology studies on cetaceans that could contribute to future conservation management efforts.

Species distribution studies offer valuable insights into their ecological behaviours (Guisan & Zimmermann, 2000). Ecological niche modelling (ENM) is an effective tool for predicting species movement patterns, identifying habitat preferences, and understanding ecological barriers to species dispersal (Isari et al., 2007; Moura et al., 2012; Ravago-Gotanco et al., 2007; Skov et al., 2008). ENM is especially valuable when studying species with vast distribution ranges, and low sighting records (Guisan et al., 2006). Obtaining high-resolution data and understanding the habitat preferences of highly mobile species proves difficult due to complex and costly logistics (Alves et al., 2018). Nowadays, observation platforms of opportunity (OPOs) such as commercial whale-watching vessels offer detailed long-term data due to increased activity and better-qualified staff onboard (Alves et al., 2018). Combining information from multiple sources can effectively overcome challenges in marine data collection. Thus, using citizen science, defined as ‘the engagement of non-professionals in scientific research’ (Miller-Rushing et al., 2012), can increase the quality and spatial extent of cetacean records for habitat modelling studies (Tiago et al., 2017).

This study analyses four years of cetacean sighting data from commercial whale-watching vessels and citizen science in the Algarve region, South Portugal. Using niche-based models, we aimed to understand how cetaceans use coastal habitats and describe the factors influencing their distribution in the Algarve region, identifying habitats needing urgent management and conservation. The main objectives were to (1) gather data on the most frequently observed cetacean species in the Algarve, (2) identify patterns of

spatial and temporal cetacean distribution, (3) use ENM techniques to characterise habitat preferences and create suitability maps, and (4) address future research questions and conservation guidelines. The results are expected to assist in identifying potential cetacean hotspots in the southern coastal waters of mainland Portugal, emphasising the importance of protecting these areas and adjacent waters to preserve biodiversity and associated cultural and economic benefits.

2.2 | Methods

2.2.1 | Study area

Data were collected in the Algarve region, South Portugal, between 36.709° -7.250° and 37.230° -9.210° (Figure 2.1). This Algarve Basin is located in the Gulf of Cadiz, along the southwestern margin of the Iberian Peninsula and stretches from São Vicente Cape (W) to the Guadiana River (E). The area is characterised by different water depths ranging from less than 1 m up to more than 1200 m, comprising coastal, open sea (Levin & Sibuet, 2011) and deep-sea areas (Metaxas & Snelgrove, 2019). The Algarve continental shelf has an average of 17 km, features a gradual slope with an inclination of 0.40° and breaks

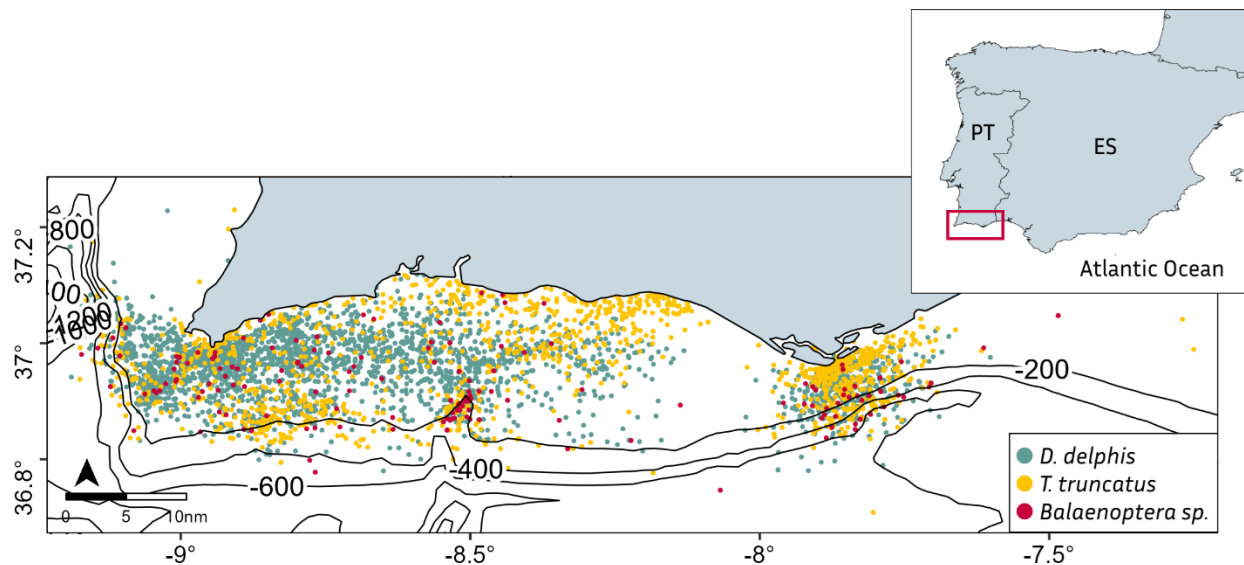


Figure 2.1 | Distribution of occurrences (2019-2022) in Algarve of *D. delphis* (green), *T. truncatus* (yellow), and *Balaenoptera sp.* (red).

at c. 110-150 m water depths (Lopes & Cunha, 2010; Roque et al., 2010). The continental slope has a steeper inclination, with steps of 700-800 m in depth, separated by canyon heads or ditches (Moita, 1986) such as the Faro-Albufeira contourite drift, and Faro, Portimão, Lagos, Sagres and São Vicente submarine canyons with steep margins and erosive floors (Hernández-Molina et al., 2006). Various ocean current systems affect the water dynamics and biodiversity in the Algarve. The equatorward flowing Portugal current is a geostrophic eastern part of the North Atlantic Subtropical Gyre, which is influenced by upwelling along the western Portuguese coastline (Barton, 2001), as well as by other factors such as freshwater discharge and bathymetry (Bellanova et al., 2022). The Atlantic Surface Water (ASW) and the Mediterranean Outflow Water (MOW) Currents influence the oceanic circulation dynamics of this area, mainly driven by density differences between the water masses of Atlantic and Mediterranean origin (Roque et al., 2010).

2.2.2 | Data collection

To address the goals proposed in this study, occurrences of short-beaked common dolphin (*D. delphis*), common bottlenose dolphin (*T. truncatus*), fin whale (*B. physalus*) and minke whale (*B. acutorostrata*) were obtained from observation platforms of opportunity (OPOs), land surveys and citizen science platforms.

During their regular tourist trips, data were collected during the daytime between 2019 and 2022 by four commercial whale-watching companies operating in Sagres, Portimão, Vilamoura, and Faro areas. Over four years, three companies operated year-round, with varying levels of effort: 641 days in Sagres, 456 days in Faro, and 343 days in Portimão. However, their activity was interrupted between March and June 2020 by the COVID-19 pandemic. In contrast, Vilamoura data was collected only for two years (2021-2022), and records from scoping land surveys from a coastal high vantage point were also obtained. Most sightings were recorded during summer as companies operate more during the tourist season. The trips followed a random and opportunistic sampling protocol, covering different distances and depths. At the same time, an experienced observer scanned the area aided by binoculars, searching for cetaceans without targeting a specific species.

The sighting data included species identified to the lowest taxonomic level possible, coordinates recorded with a Global Positioning System (GPS), date, time, behaviour, and the possibility of repeated sightings. Cetacean occurrences corresponded to the boat's location at the sighting. Crowdsourced sightings of the four species of interest were also collected from the Global Biodiversity Information Facility (GBIF) platform from 2019 to 2022 for the entire study area. They amounted to a total of 197 days of effort. The citizen science dataset included information on species, coordinates, and time. Fin and minke whale records were grouped under the *Balaenoptera sp.* (baleen whales) category due to the low number of occurrences. The collected data were logged into an Excel database and prepared for further analysis.

2.2.3 | Environmental variables

A set of environmental variables (Table 2.1) were selected based on data availability and ecological relevance for cetaceans from previous studies (Correia et al., 2015, 2019; Moura et al., 2012; Pennino et al., 2017; Prieto et al., 2017; Ramesh et al., 2021; Scales et al., 2017). Latitude and longitude were recorded with a GPS during the sea-surveys, while seasonality was derived from the sighting date. Due to the availability of the cetacean occurrence, which was recorded from January to December of each year, for this study, seasons comprised of the following months: winter (win) from January to March, spring (spr) from April to June, summer (sum) from July to September, and autumn (aut) from October to December. The topographic variables used included bathymetry, bathymetric slope, and distance to the shore. The bathymetry raster was retrieved from NOAA National Centers for Environmental Information with an original resolution of 15 arc-seconds (NOAA National Centers for Environmental Information, 2022). Bathymetric slope and distance to the shore rasters were obtained from MARSPEC, a high-resolution GIS database of ocean climate layers (Sbrocco & Barber, 2013).

Oceanographic variables were also included in the model, as they are reliable indicators of productive areas and, thus, act as proxies for species distribution in marine habitats (Correia et al., 2015). In addition, habitat models combining static and dynamic variables

prove more efficient (Ballance et al., 2006; Correia et al., 2015). Two oceanographic variables were obtained from E.U. Copernicus Marine Service Information (CMEMS). Remotely sensed monthly sea surface temperature (*sst*) had an original spatial resolution of 0.05° (Donlon et al., 2012; Good et al., 2020; Stark et al., 2007), while remotely sensed monthly Chlorophyll-a concentration (*chl_a*) had an original spatial resolution of 0.083° for the period of January 2019 to November 2021 (Aznar et al., 2016), and 0.028° from December 2021 to December 2022 (Gutknecht et al., 2019). These variables were chosen as they are excellent proxies for identifying productive areas associated with upwelling phenomena, known for their cooler and nutrient-rich waters (Robinson, 2010). Layers with seasonal means of monthly *sst* and *chl_a* were created altogether for the four years of the study as the model's accuracy can decline significantly due to data loss from cloud interference (Prieto et al., 2017).

Table 2.1 | Characteristics of the spatiotemporal and environmental variables used as predictors for ecological niche models.

Variable	Code	Unit	Spatial resolution	Temporal resolution	Source	Reference
Latitude	lat	Decimal degrees	-	-	Sea-surveys (GPS)	-
Longitude	lon	Decimal degrees	-	-	Sea-surveys (GPS)	-
Season	win/spr/sum/aut	-	-	Monthly	Month of survey	-
Sea surface foundation temperature	sst	K	0.05°	Monthly	Copernicus	Good et al., 2020; Donlon et al., 2012; Stark et al., 2007
Mass concentration of chlorophyll a in sea water	chl _a	mg/m ³	0.083°/ 0.028°	Monthly	Copernicus	Aznar et al., 2016/ Gutknecht et al., 2019
Bathymetry	bathymetry	m	15 arc-second	-	NOAA	NOAA National Centers for Environmental Information, 2022
Bathymetric slope	slope	°	30 arc-second	-	MARSPEC	Sbrocco & Barber, 2013
Distance to shore	dist_shore	nm	30 arc-second	-	MARSPEC	Sbrocco & Barber, 2013

All layers were cropped to include the study area and adjusted to a standard resolution of 0.002° per grid cell using the raster package (Hijmans, 2023) in R (R Core Team, 2022). The correlation among the layers was explored by calculating the variance inflation factor (VIF) using the usdm package (Naimi et al., 2014). A VIF greater than ten signals that the model has a collinearity problem (Naimi et al., 2014).

2.2.4 | Environmental niche models

Habitat preference for the target species was initially investigated using three different niche modelling techniques: Generalized Linear Model (GLM), Boosted Regression Tree Model (BRT), and Maximum Entropy Model (MaxEnt). Although non-systematic cetacean surveys do not typically record presence-absence data, records of other sighted species, such as other cetaceans, fish, reptiles, or birds, were used as absences to fit GLM and

BRT models. For these two approaches, 10,000 pseudo-absences were also created to model habitat suitability for each species (Barbet-Massin et al., 2012). However, after analysing the models' performance, MaxEnt outperformed the others. MaxEnt is a machine learning technique that models species distribution based on presence-only data and environmental variables (background) (Prieto et al., 2017). Its predictive performance has consistently proven to be competitive with other well-established methods, even those using presence-absence data (Aguirre-Gutiérrez et al., 2013; Elith & Graham, 2009; Prieto et al., 2017; Ren-Yan et al., 2014). MaxEnt has proved consistent across different sample sizes, even with less than ten occurrences (Aguirre-Gutiérrez et al., 2013). Still, the optimal performance is obtained when 20 or more occurrences are used in the model (Prieto et al., 2017; Shcheglovitova & Anderson, 2013). Thus, MaxEnt proved to be the best modelling approach for this study.

To build MaxEnt species distribution models for all four seasons, only sightings correctly identified at the species level were included as presence. Using the SDMtune package (Vignali, Barras, & Braunisch, 2022; Vignali, Barras, Arlettaz, et al., 2022), data were then scrutinised and filtered, duplicated records were removed, as well as records outside of the study area or erroneously marked on land. The records for all species were divided into smaller datasets corresponding to each season. The presence-only dataset was split into a testing subset (20%) and a training subset (80%) for each species to evaluate the fitness of the model and its predictive power (Barragán-Barrera et al., 2019). For each species, 10,000 background sample points were generated (Vignali, Barras, & Braunisch, 2022; Vignali, Barras, Arlettaz, et al., 2022). Duplicated grid records were removed to reduce replication (Assis et al., 2017) using the environmental variables' 0.002° spatial resolution grids.

Preliminary models for all four seasons were built for each species using all five environmental variables. The relative importance of each variable was determined using the permutation importance (PI) parameter. By randomly permuting one variable at a time, using both training and background datasets, and then calculating the decrease in training area under the receiver-operator (ROC) curve (AUC), the PI measures the contribution

(%) of each variable to the final model (Prieto et al., 2017). Variables with a PI value < 5 were considered to have little predictive significance and were excluded from the set (Merow et al., 2013; Prieto et al., 2017). The process was repeated until no more variables with a PI value < 5 were detected, thus creating the final model. To evaluate the model's accuracy, the AUC parameter was used as an indicator of the predictive skill of the model (Phillips et al., 2004), where the AUC value varies between 0.5 (random performance) and 1 (outstanding performance) (Correa et al., 2019; Hosmer & Lemeshow, 1989).

2.3 | Results

2.3.1 | Environmental niche models

After excluding sightings with incomplete information, as well as duplicated grid records, a total of 2139 *D. delphis*, 1087 *T. truncatus*, and 128 *B. physalus* and *B. acutorostrata* sightings were used for the seasonal models (Table 2.2). Most sightings were recorded during summer and spring for all species of interest. The sample size for baleen whales was limited, especially during winter and autumn, with less than 20 occurrences. However, previous studies indicated that MaxEnt was a fit modelling technique for small sample sizes (Pearson et al., 2007; Prieto et al., 2017; Shcheglovitova & Anderson, 2013).

Table 2.2 | Number of sightings used in the MaxEnt models for each season for *D. delphis*, *T. truncatus*, and *Balaenoptera sp.* Mean area under the receiver operating characteristic curve (AUC) was calculated for the models of each season for all species, with respective standard deviations (SD).

Season	Number of sightings used in the model		
	<i>D. delphis</i>	<i>T. truncatus</i>	<i>Balaenoptera sp.</i>
Winter	50	27	5
Spring	348	254	39
Summer	1359	622	65
Autumn	381	184	19
Total	2138	1087	128
Mean AUC ± SD	0.931 ± 0.012	0.907 ± 0.030	0.908 ± 0.035

None of the predictive variables revealed strong collinearity according to the VIF factor (VIF < 10 for all variables). Thus, models were initially run with all five predictors, gradually reducing the number of variables based on their relative contribution to the models, as indicated by the PI values (Table 2.3). Variables used for each seasonal model varied only slightly. In general, the *slope* was the least used variable, while baleen whale models were fitted with fewer predictors overall, as several of them had a PI < 5.

Table 2.3 | Permutation importance (PI) (%) for the environmental variables used in the MaxEnt models for each season for *D. delphis*, *T. truncatus*, and *Balaenoptera sp.* – marks variables not used in the models, with a PI < 5.

Species	Season	Permutation importance (PI)				
		chl _a	sst	bathymetry	dist_shore	slope
<i>D. delphis</i>	Winter	23.2	19.1	7.4	39.9	10.4
	Spring	7.5	16.9	41.3	34.3	-
	Summer	20.0	22.9	23.1	27.6	6.4
	Autumn	20.0	22.4	23.3	27.9	6.4
<i>T. truncatus</i>	Winter	13.9	10.8	14.0	39.3	22.0
	Spring	10.2	19.1	25.0	45.7	-
	Summer	17.4	12.6	28.7	35.5	5.8
	Autumn	13.5	13.0	39.1	34.4	-
<i>Balaenoptera sp.</i>	Winter	-	21.7	-	63.8	14.4
	Spring	-	-	20.8	23.9	55.3
	Summer	56.5	7.8	5.6	21.6	8.5
	Autumn	19.4	16.4	-	-	64.2

Based on the mean AUC, all the seasonal models of each species reported an outstanding predictive performance (AUC > 0.9) (Hosmer & Lemeshow, 1989). The models for the short-beaked common dolphin had the best performance with an AUC > 0.93.

2.3.2 | *Delphinus delphis*

The mean AUC for the short-beaked common dolphin models was the highest (0.931), indicating a very strong model performance in assessing presence and background points (Table 2.2) (Prieto et al., 2017).

Overall, predictor *dist_shore* contributed the most to the seasonal models (Table 2.3). Bathymetry showed significant input as well, except during winter. Mean *chl_a* moderately contributed to the models, with low information content during spring. The *slope* had a negligible impact on the models and, based on the PI, was removed from the spring model.

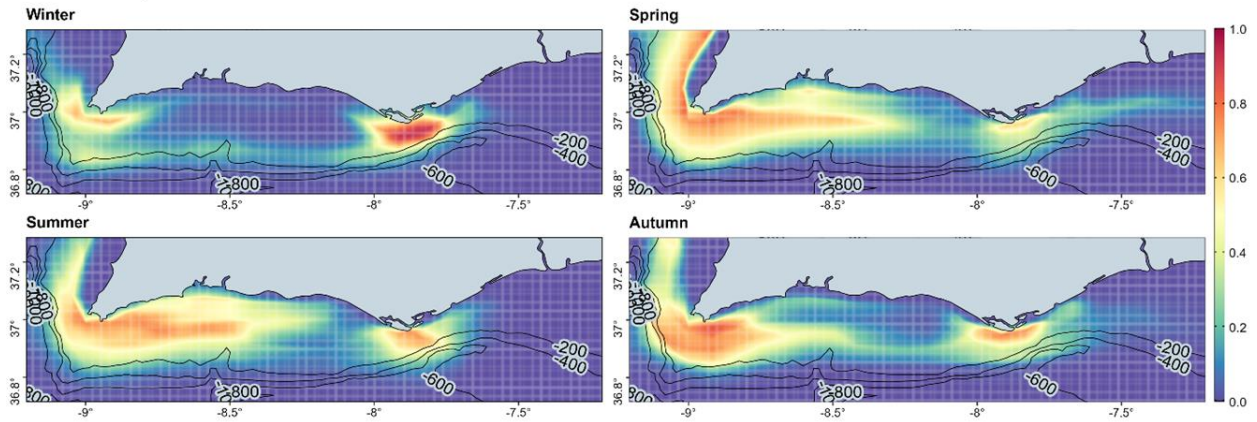
Habitat suitability for *D. delphis* (Figure 2.2.A) is exceptionally strong (≈ 1) during winter around Faro until the edge of the continental slope. During spring, it shifts towards the SW coast of the Algarve and mildly extends eastward. Sagres area becomes highly suitable in summer and around Portimão, peaking in autumn, while Faro waters regain more robust suitability. Faro and Sagres areas generally have the best habitat conditions, while far eastern waters are unsuitable.

2.3.3 | *Tursiops truncatus*

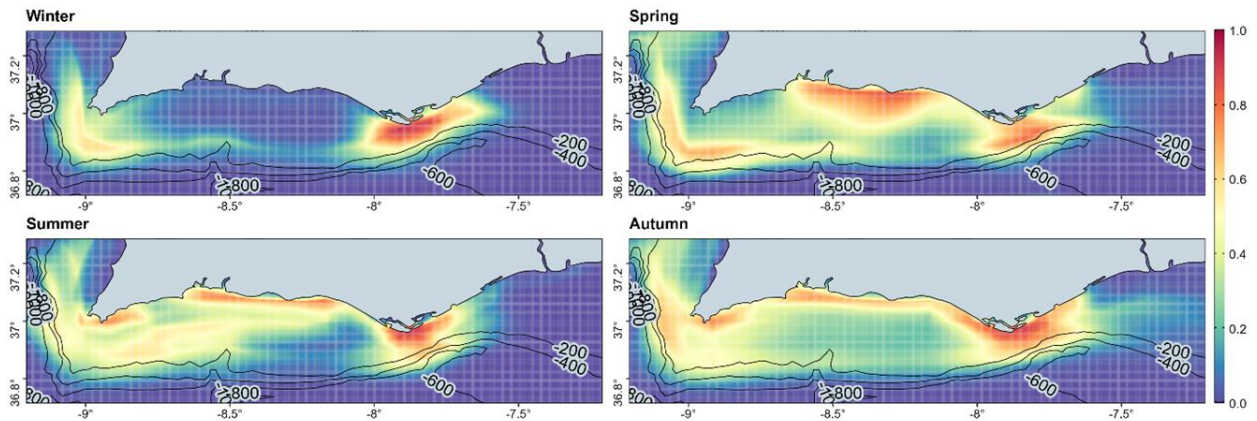
The mean AUC for common bottlenose dolphin models is slightly less (0.907) than the one of the short-beaked common dolphins, but still with a relevant predictive performance, on the verge between excellent and outstanding (Table 2.2) (Hosmer & Lemeshow, 1989). The most substantial contribution to the models was *dist_shore* (Table 2.3). Mean *chl_a* and *sst* revealed similar but lower contributions. The less significant input came from the *slope* predictor, which was removed from two seasonal models (spring and autumn) based on the PI values.

The predictive models for *T. truncatus* (Figure 2.2.B) show similar habitat suitability with *D. delphis* (Figure 2.2.A) during winter but with a shifted suitability closer to the continental shelf edge around Sagres. The spring model reveals apparent suitability alongside Vilamoura - Portimão coast and in Faro and Sagres waters along the 200 m isobath. In summer, the suitability hotspots (≈ 1) move towards the coast, with Faro waters displaying excellent habitat conditions. The autumn model is comparable to the summer model with the summer one and has the most eastern predictions.

A. *D. delphis*



B. *T. truncatus*



C. *Balaenoptera sp.*

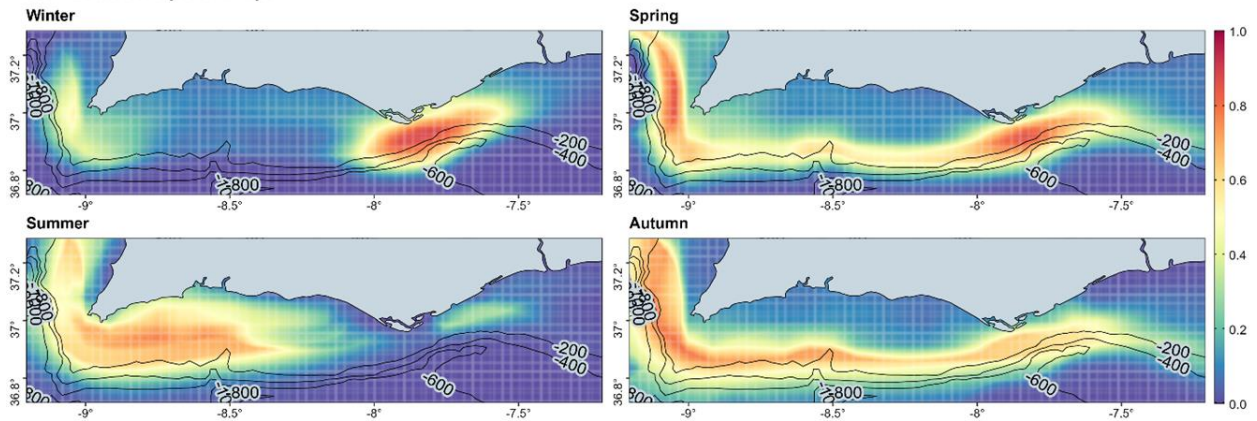


Figure 2.2 | MaxEnt habitat suitability maps for *D. delphis* (A), *T. truncatus* (B), and *Balaenoptera sp.* (C) in the Algarve region, South Portugal. Habitat suitability is represented by colour shade: reds correspond to higher suitability, yellows, to average, while blues, to lower suitability.

2.3.4 | *Balaenoptera sp.*

The baleen whale models had an excellent overall performance based on the mean AUC value (0.908), almost identical to the one of the short-beaked common dolphins (Table 2.2).

Contrary to the previous species, the *slope* predictor had a significant input in all seasonal models (Table 2.3). *Dist_shore* had a high contribution, as well as mean *chl*_a, despite being removed from the winter and spring models due to low PI. Only the summer model was built based on all five environmental variables.

The predicted potential distribution map for *Balaenoptera sp.* (Figure 2.2.C) in winter resembles the ones of the other two species of interest; however, it extends past the 600 m isobath in the Faro hotspot (≈ 1). Spring and autumn models display similar strong suitability patterns around the 200 m isobath, parallel to the edge of the continental shelf. In summer, habitat suitability almost completely shifts towards the central-west side of the Algarve. Overall, the suitability extends more eastwards compared to the other two species.

2.4 | Discussion

This study defined ecological niche models for the short-beaked common dolphin, common bottlenose dolphin, and two baleen whales (fin and minke whales) in the North Atlantic. These models were used to assess the seasonal distribution patterns of the target species and characterise their environmental niches in the coastal waters of South Portugal. To the best of our knowledge, this is the first study incorporating habitat modelling of baleen whales in this area.

2.4.1 | Caveats

There are two main caveats in this study, the use of presence-only records and the opportunistic nature of the data collected, which impacts both the seasonality and the

geographic coverage of the data. The use of a presence-only dataset limits this study. Presence-absence models estimate the occupied niche, leading to better estimates of the actual distribution of the species of interest, while presence-background algorithms such as MaxEnt restrict the potential inferences that can be drawn, delivering results similar to the realised niche (Correa et al., 2019; Soberón & Nakamura, 2009). Nonetheless, due to the oceanic environment's dynamic nature and cetaceans' mobility, recording true absences can be an unattainable objective (Correa et al., 2019). Furthermore, using pseudo-absences, false absences generated due to the lack of records in habitat modelling, can cause inaccurate distribution patterns (Lobo et al., 2010). Thus, presence-absence algorithms could be unsuitable for cetaceans and should be used for studies focused on a small area, thoroughly sampled, with complete data on all the environmental conditions present (Correa et al., 2019). Opportunistic datasets can provide crucial insight into cetacean distribution in such a dynamic environment and can potentially overcome the shortcomings of a MaxEnt modelling approach due to frequent sampling in a relatively small area (Correa et al., 2019; Fernandez et al., 2018).

Opportunistic datasets, such as the ones collected from OPOs or citizen science platforms, have some explicit constraints. The data used for this study are limited to coastal areas where whale-watching companies operate. Correia et al., 2015 recorded numerous offshore sightings of cetaceans with relatively little effort in the Portuguese Economic Exclusive Zone (PEEZ). They identified several species-specific potential suitable habitats, which might be based on different environmental interactions. Thus, the study highlighted the importance of an exhaustive sampling approach covering offshore waters. The inshore bias of our dataset limited relevant environmental and spatial inputs for the target species, affecting the predictive performance of the models outside the study area (Fernandez et al., 2018; Owens et al., 2013). Nonetheless, our models' performance proved to be, on average, above excellent (mean AUC > 0.9) and accurately characterised the temporal and spatial dimensions of the environmental niche.

Sampling efforts peaked during the summer season for touristic operations, but the COVID-19 pandemic halted data collection during the spring and summer of 2020.

Overall, the low number of records used might influence winter and autumn models for baleen whales because of the uneven sampling effort, the COVID-19 pandemic, and the difficulty in spotting baleen whales. However, trips occur year-round, which can reveal temporal patterns of cetacean distribution (Fernandez et al., 2018). In addition, few records were collected from the southeastern waters of the Algarve, which might have affected the predictability of the models for habitat suitability in this area for the target species.

Data collected from OPOs and citizen science platforms could have a lower quality (e.g. misidentified species, incorrect GPS positions, and other errors) when compared to records from dedicated research trips. On the other hand, whale watching is a growing industry, employing more qualified staff members to collect data that would otherwise be unfeasible from research vessels (Alves et al., 2018). It is important to note that the quality of this type of data differs from each OPO and region, but it is nonetheless an asset in habitat modelling studies (Alves et al., 2018).

2.4.2 | *Delphinus delphis*

The short-beaked common dolphin emerges as the prevailing cetacean species in Portuguese waters (Goetz et al., 2015; Hammond et al., 2013), consistently noted as one of the most abundant inhabitants. Although the majority of research efforts have concentrated on the archipelago habitats (Alves et al., 2018; Fernandez et al., 2021; Silva et al., 2014; Tobeña et al., 2016), it is worth noting that the Algarve coast has been somewhat overlooked in these studies. This oversight is concerning, given the region's susceptibility to heightened anthropogenic activity. The need for enhanced management strategies becomes evident, as the Algarve coast faces significant challenges arising from human impact. While the short-beaked common dolphin takes the spotlight due to its frequent appearances, addressing the ecological well-being of the entire marine ecosystem along the Algarve coast warrants greater attention to ensure its preservation amid ongoing anthropogenic pressures (Bellanova et al., 2022).

Dolphins' ecological niches seem to be defined by variables that influence the distribution and abundance of prey (Baumgartner et al., 2001; MacLeod et al., 2008). The distribution of common dolphins within the study area was influenced by chlorophyll concentration, especially during winter, summer, and autumn. While chlorophyll itself doesn't directly determine dolphin distribution, it acts as a proxy for other underlying biological factors (Moura et al., 2012), such as a higher presence of pelagic schooling fish (Ware & Thomson, 2005; Zainuddin et al., 2006). Previous research has highlighted that common dolphins prey on such species (Meynier et al., 2008; Pusineri et al., 2007). Along the Portuguese coast, sardines (*Sardinia pilchardus*) were the primary prey item found in the stomach content of common dolphins (Marçalo et al., 2018; Silva, 1999) and were also reported as the most abundant pelagic schooling fish (Marques et al., 2003). Although the common dolphin is described as an opportunistic feeder (Meynier et al., 2008), it appears to be ecologically specialised in small pelagic schooling fish (Marçalo et al., 2018; Moura et al., 2012). This specialisation is unique to common dolphins and not observed in other dolphin species (Moura et al., 2012).

Chlorophyll concentration had a low input into the spring model of the common dolphin. The phytoplankton spring bloom is an essential biological event in the North Atlantic Ocean, followed by zooplankton development with a time lag of several weeks to months (Longhurst, 2007). Thus, common dolphin's prey, such as sardines that feed on zooplankton, are more abundant during late summer (Bandarra et al., 1997). Time-lagged chlorophyll concentration for several weeks before the sighting date of the target species could better define the relationship between chlorophyll and cetacean habitat suitability (Prieto et al., 2017).

From spring to autumn, habitat suitability is high around Sagres, possibly due to more productive waters caused by more vigorous upwelling. Upwelling events occur from July to September on the west coast of Portugal and are sporadic and less intense during December and January (Fiuza et al., 1982). On the south coast, the upwelling effects are reduced, caused by locally westerly winds or upwelled waters intruding from the west coast (Relvas & Barton, 2002). Similar studies elsewhere also associated common dolphin

distribution with high chlorophyll concentration (Cañadas & Hammond, 2008) or upwelling regions (Jefferson et al., 2009).

Habitat preference for common dolphins shifted around Santa Maria Cape during wintertime, probably due to higher prey availability. Less upwelling events (Fiuza et al., 1982) and lower chlorophyll concentrations (Longhurst, 2007) during these months could result in less prolific waters in Sagres. Water temperature is also an essential factor that defines the ecological habitats of cetaceans (MacLeod, 2009). Water temperature is higher in Faro than in Sagres during winter. Previous studies reported that common dolphins preferred warmer waters (Correia et al., 2015; Fernández et al., 2013), possibly explaining the high habitat suitability in Faro during winter.

2.4.3 | *Tursiops truncatus*

The results support the distribution differences between inshore and offshore populations of the common bottlenose dolphin. The inshore population appears to have stronger habitat suitability during spring months, where the variables *dist_shore* and water depth strongly contributed to the models. The offshore population is mildly represented all-year round along the 200 m isobath, which has previously been proven to influence their ecological niche (Correa et al., 2019). However, the effort was mainly focused closer to the shore due to the nature of the OPOs' activity, resulting in a model that preferentially displays the inshore population niche. Bathymetry and distance to the coast have been used to identify boundaries between bottlenose dolphin ecotypes in other locations (Correa et al., 2019; Hale et al., 2000; Segura et al., 2006). Despite the differences in habitat preferences, the two ecotypes have been sighted together (Correa et al., 2019).

The distance to the shore best predicted all four seasonal models. Coastal marine ecosystems such as wetlands and seagrass beds contribute to high productivity and biodiversity providing food resources for local and oceanic organisms (Barragán-Barrera et al., 2019). The coastal waters of Santa Maria Cape display high suitability for this species year-round, which could result from the high biodiversity and productivity caused by the Ria Formosa lagoon. This species is known to inhabit shallow coastal waters and

enter estuaries and lagoons in search of fish and cephalopods (Goetz et al., 2015; Pennino et al., 2017; Pierce et al., 2010; Santos et al., 2007). Having a distribution closer to the shore can also be related to predator avoidance (Blasi & Boitani, 2012).

The habitat of São Vicente Cape stands out as a year-round environment with consistent suitability for the targeted species, owing to the persistent occurrence of robust upwelling events. These events play a pivotal role in influencing the availability of prey, mirroring the distribution pattern observed in common dolphins. Additionally, the area's exceptional suitability for the species might also be attributed to the presence of significant geographical features, such as the Portimão Canyon. This submarine canyon holds a vital connection to the region's highly productive waters, providing an ideal habitat for various cetacean species. As noted by Moors-Murphy in 2014, the proximity of São Vicente Cape to this canyon contributes to the overall attractiveness of the area for cetaceans. The combination of strong upwelling events, favourable prey availability, and the presence of submarine canyons underscores the significance of São Vicente Cape as a habitat that offers optimal conditions for sustaining diverse cetacean populations.

The bottlenose habitat range complemented the one of common dolphins during the months of spring, summer, and autumn. Common and bottlenose dolphins can cohabit coastal waters but have separate trophic niches (Giménez et al., 2018). Bottlenose dolphins have diverse food preferences and are considered generalist predators feeding on various fish, cephalopods, and small crustaceans (Blanco et al., 2001; Santos et al., 2007; M. B. Santos et al., 2007), while common dolphins are ecological specialists restricted to small pelagic schooling fish in South Portugal (Moura et al., 2012). A study by Correia et al., 2015 described distinct differences in habitat preferences for bottlenose and common dolphins, despite reported mixed sightings. Bottlenose dolphins prefer habitats with warmer waters closer to the coast and broader ranges of slope inclination, depth, and distance to the coast, being also sighted on high seas (Correia et al., 2015, 2020).

2.4.4 | *Balaenoptera sp.*

The migration of baleen whales is described as wide-range seasonal movement between high latitude feeding grounds and low latitude breeding grounds, exposing them to the effects of climate change and human activity (Lascelles et al., 2014). In contrast with the other target species, the northeastern North Atlantic fin whale population migrates from the eastern North Atlantic (summer feeding ground) to the Mediterranean Sea (winter breeding ground) and back (Castellote et al., 2012). According to spring and autumn models, Algarve waters represent a migratory corridor between the Atlantic Ocean and the Mediterranean Sea, being a highly suitable habitat alongside the continental shelf. A study by Gauffier et al., 2018 reported a two-way migration of a small community of fin whales through the Strait of Gibraltar, with a main flow towards the Atlantic Ocean in late spring – early summer and towards the Mediterranean in late autumn. These findings support the habitat suitability pattern found in our models. Furthermore, the spring model was created based only on topographic predictors suggesting that the corridor along the 200 m isobath is mainly used for movement rather than foraging. Nonetheless, the highly suitable areas around the capes of São Vicente and Santa Maria could be attractive areas for baleen whales due to prey-abundant waters, though a more in-depth analysis is needed. The *slope* best predicted the autumn model, which indicates a strong correlation between the high habitat suitability of baleen whales and the continental shelf edge used as a passing corridor.

Migrating baleen whales use feeding stop-over sites to restore energy reserves before reaching highly productive feeding grounds in northern latitudes (Silva et al., 2013). The seasonal models do not account for the behaviour of baleen whales in the study area, making it difficult to differentiate between habitats used for foraging, migration, or resting. However, some conclusions can be drawn about habitat use by analysing model outcomes alongside the most predictive environmental factors influencing each model (Prieto et al., 2017). During summer, the coastal waters around São Vicente Cape are highly suitable for baleen whales. The model is best predicted by mean chlorophyll concentration. Fin whales might use this region as a foraging stop-over ground on their

way to higher latitudes. The area could be abundant in prey due to the spring bloom (Longhurst, 2007) and strong summer upwelling along the west coast compared to the south coast (Fiuza et al., 1982), stimulating plankton development.

Minke whales were the most sighted baleen species within the four years of the study. Compared to the fin whale, minke whales are considered residents in Portuguese waters (Laborde et al., 2015; Waerebeek et al., 1999). Waerebeek et al., 1999 reported cases of this species feeding at lower latitudes, suggesting that their need to migrate for feeding diminishes in regions with rich biological productivity. Despite being present year-round, they were mainly reported during spring and summer (Valente et al., 2019; Waerebeek et al., 1999). According to Correia et al., 2020, minke whales prefer deeper waters distant from the coast, which can be observed in our spring and autumn models, where high suitability is found at the edge of the continental shelf. The autumn model was mildly predicted by chlorophyll concentration, suggesting that the region around São Vicente Cape and along the continental shelf edge can be suitable for foraging, possibly caused by westerly upwelled waters in late autumn (Fiuza et al., 1982). During winter, habitat suitability is extremely high around Santa Maria Cape. The distance to the coast and sea surface temperature strongly influenced the model. Despite no chlorophyll concentration input, this area appears to be a suitable habitat, likely due to warmer waters and prey availability influenced by the Ria Formosa lagoon, as was the case for the *Delphinidae* species.

2.4.5 | Management and conservation issues

Identifying areas of particular importance for cetaceans can aid in addressing management and conservation issues. Coastal marine ecosystems are highly affected by anthropogenic activity. The Algarve coast hosts several economic activities such as fishery (Bueno-Pardo et al., 2017), agriculture, paper industry (Díez et al., 2005), and tourism (including whale-watching, sailing, and water sports), while the offshore shelf is an essential maritime route connection between the North Atlantic Ocean and the Mediterranean Sea (Monteiro, 2016; Pandolfi et al., 2011). Thus, wildlife managers should

consider these findings in future marine protected area plans to protect cetacean species in Portugal.

2.5 | Concluding remarks

The results of this study show a high dependency of cetacean species on the coastal habitats of the Algarve region, defined by great upwelling events and notable topographic features that lead to resource-rich waters. Despite their limitations, OPOs such as whale-watching vessels and citizen science can provide detailed information on cetacean occurrence. Increasingly overexploited and in constant decline, this aquatic ecosystem, together with its transient and resident species, should receive more attention to preserve the biodiversity and associated cultural and economic benefits. To implement effective conservation measures, additional research is necessary to gain a deeper understanding of the distribution-environment relationship of cetaceans, as well as to regulate human activities in coastal waters inhabited by these species.

2.6 | Acknowledgements

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2.7 | References

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