



Habitat suitability of two flagship species, *Hippocampus hippocampus* and *Hippocampus guttulatus*, in the Atlantic coast of the Iberian Peninsula - implications for conservation

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ABSTRACT

Anthropogenic pressures on marine ecosystems are increasing worldwide, causing loss of biodiversity and ecosystem functioning, and driving species towards risk of extinction. To protect vulnerable species and habitats, Marine Protected Areas (MPAs) are increasingly established worldwide as conservation measures. Seahorses act as flagship species for coastal ecosystem conservation due to their charismatic appearance and high vulnerability to habitat degradation. Here, the habitat suitability of the two European seahorse species, *Hippocampus hippocampus* and *Hippocampus guttulatus*, was assessed along the western Iberian Peninsula, using an ensemble species distribution modelling approach. Furthermore, the coverage of their core habitat (relative habitat suitability (HS) ≥ 0.5) with MPAs was estimated. The results show that the main drivers for habitat suitability were distance to the coast, aspect of the seafloor, tidal amplitude, and temperature. However, the importance differed between the two species. The suitable habitat of *H. hippocampus* extended to higher distances to the coast, while *H. guttulatus* were mostly restricted to areas in the vicinity of the coast and facing away from the open sea (i.e., the westerly aspect of the seafloor). Furthermore, temperature contributes more to the variation in habitat suitability in *H. hippocampus* than in *H. guttulatus*. The areas with the highest habitat suitability are estuarine or inlet waters and sheltered coasts in northwestern Spain, central and south of Portugal. Both species' core habitats are covered by about 19–20 % with implemented protected areas in Portugal. In comparison, there is less coverage for both species in Spain, with 12 % for *H. guttulatus* and 6 % for *H. hippocampus*. Besides, zones of full protection cover less than 0.5 % of

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the core habitat while the rest of the protected areas provide only moderate to low restrictions and do not specifically address the protection of seahorses in their management plans. The results provide useful information on the distribution and the different habitat preferences of the two species, indications for further monitoring of populations, and recommendations for efficient spatial conservation areas that can protect the species and other associated vulnerable species and habitats.

1. Introduction

Anthropogenic pressures on marine ecosystems worldwide are increasing and have caused extensive degradation of marine habitats and promoted local species depletion (Barnosky et al., 2011; Dulvy et al., 2021; O'Hara et al., 2019). Overexploitation and destructive fishing practices, coastal development and pollution, the introduction of invasive species, and climate change are threatening the biodiversity and integrity of coastal ecosystems worldwide (Halpern et al., 2007; Pilotto et al., 2020). However, not all ecosystems and latitudes are equally affected by those threats (Halpern et al., 2007; Stratoudakis et al., 2019). For instance, it was found that in higher latitudes more vulnerable species are associated with estuarine habitats that have high connectivity with the marine ecosystem (Vasconcelos et al., 2017). Consequently, the vulnerability of marine species to human impacts is not only determined by their life history traits but also by spatial traits such as home ranges and preferred habitats (Butt et al., 2022; de Juan et al., 2020; Pearson et al., 2014).

To protect vulnerable species and habitats, in line with global targets agreed upon under the Convention on Biological Diversity, Marine Protected Areas (MPAs) are increasingly established worldwide to mitigate the impact of anthropogenic stressors and to sustainably manage marine resources (Edgar et al., 2014; Gaines et al., 2010; Grorud-Colvert et al., 2021; Palumbi, 2002). Spatial assessment of habitat suitability for marine species at risk inside and outside an area of protection can provide a better understanding of the true potential of MPAs and MPA networks in effectively protecting marine species and the need for future conservation measures (Abecasis et al., 2014; O'Hara et al., 2019). Often charismatic species, also referred to as flagship species, are used as a tool to raise awareness and get stakeholder engagement to protect their habitats and constituent species (Zacharias and Roff, 2001). Recently the International Union for Conservation of Nature (IUCN) resolution 95/2020 encouraged the use of iconic Syngnathides as flagship species to promote the protection and restoration of transitional and coastal habitats important for Syngnathides species while urging governments to enforce regulations on fisheries, area-based management, and habitat protection (IUCN World Conservation Congress, 2020).

Seahorses belong to the Syngnathidae family and are considered particularly sensitive to human pressures, due to their low dispersal, small home ranges, and complex reproduction strategies (i.e., low fecundity, seasonal breeding, and mate fidelity) (Foster and Vincent, 2004). Particularly habitat degradation and fragmentation caused by coastal development, aquaculture, dredging activities, and destructive fishing practices (e.g., bottom trawling), pose a threat to seahorse populations (Caldwell and Vincent, 2012a; Curtis et al., 2007; Guimarães et al., 2011; Pollom et al., 2021). Furthermore, marine traffic can harm seahorses through anchoring, noise pollution, and a decrease in the water quality (Palma et al., 2019). Although seahorses are known to be sedentary, they can adapt to progressive habitat changes by moving to more suitable areas or occupying alternative habitats, like artificial structures (e.g., trash, mooring lines, lost fishing gear) (Correia et al., 2018, 2015b; Masonjones et al., 2010). Nevertheless, forced dispersal through habitat destruction might fragment local populations and directly impact reproductive success (Caldwell and Vincent, 2012b). Another threat to seahorses is the use of non-selective fishing gear which can promote accidental bycatch (Curtis et al., 2007; Vasconcelos et al., 2019). In some locations, seahorses are also targeted by illegal fishing for the Chinese medicine market and ornamental trade (Correia, 2021; Foster et al., 2016; Pierri et al., 2021). Other than that, the impact of climate change could be manifold in the future, either indirectly by changes in the hydrodynamics and morphology of the habitat due to increasing storms and sea level rise, or directly by increasing water temperatures resulting in physiological impairments (Aurélio et al., 2013; Costa et al., 2023). However, the intensity of the impact of the various factors is likely to vary depending on the seahorse species and location.

This study focuses on two sympatric European seahorses, the short-snouted seahorse (*Hippocampus hippocampus* Linnaeus 1758) and the long-snouted seahorse (*Hippocampus guttulatus* Cuvier 1829). Both species are listed as Data Deficient in the IUCN Red List for the Atlantic and as Near threatened for the Mediterranean (Pollom, 2017; Woodall, 2017). Efforts have been made to increase the protection of these species, such as the inclusion in Appendix II of the Bern Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the IUCN resolution WCC-2020-Res-095, as well as the inclusion of these species on the OSPAR List of threatened and/or declining species and habitats (OSPAR Commission, 2013a, 2013b) and the protection by law in Portugal (Decree Law 38/2021) and Spain (Royal Decree 139/2011). The two species have a wide geographic range extending across most of Europe and northern Africa, including the Atlantic Ocean, Mediterranean Sea, and Black Sea (Lourie et al., 2016). However, their ecological distribution is not continuous and population densities fluctuate from rare to locally abundant across the species' range (Pierri et al., 2022; Woodall et al., 2018). Our research effort was focused on the Atlantic coast of the Iberian Peninsula based on previous knowledge of the genetic population structure and special habitat preferences of the two seahorses in this location (Pierri et al., 2022; Woodall et al., 2015, 2011). Furthermore, the Iberian Atlantic coast is important for conservation since it is a recognized transition zone between warm-water species and cold-water species, thus highly susceptible to range changes due to climate change (Pinho et al., 2016; Tuya et al., 2012). Additionally, it was considered to host the largest European seahorse population in the world, which suffered from drastic declines of 70 %- 90 % of the population (Caldwell and Vincent, 2012a; Curtis and Vincent, 2006). However, besides

dedicated studies in the Ria Formosa lagoon, only a few studies focused on seahorses within the study area (e.g., (Planas et al., 2021)). The information is limited to seahorse occurrences in grey literature, or as part of marine faunal assemblage assessments (Guerreiro et al., 2021; Leitão et al., 2007; Pombo and Rebelo, 2002; Serrano Gordo and Nogueira Cabral, 2001; Valladares et al., 2014). Nonetheless, population declines reported in the Ria Formosa, and other places in Europe, have raised concern about the conservation of the species (Caldwell and Vincent, 2012a; Correia, 2021; Lazic et al., 2018; Pierri et al., 2021).

In this context, this study aims to assess and predict the habitat suitability of the seahorse species *H. hippocampus* and *H. guttulatus* to improve efficient spatial conservation. The specific objectives were to use Ensemble Species Distribution Modelling to 1) identify the most important variables governing the species' habitat suitability, 2) to predict the core habitats (i.e., relative habitat suitability ≥ 0.5) and 3) to assess whether core habitats are covered by MPAs.

2. Material and methods

2.1. Study area

The study area of the model lies inside the temperate Large Marine Ecosystem (LME) "Iberian Coastal" which extends along the western coast of the Iberian Peninsula (-12.6°W , -5.1°W , 34.38°N , 45°N) (Fig. 1). LMEs represent multi-country, ecosystem-based



Fig. 1. Study area including the outlines of the designated MPAs in blue.

management units that are characterized by their unique undersea topography, current and water mass structure, marine productivity, and food chain interactions (Sherman, 2001). The study area includes important estuarine waters and salty lagoon areas such as the Rias Baixas in the north of Spain, and the main estuaries and coastal lagoons in Portugal (Vasconcelos et al., 2017). Due to limited genetic connectivity between ecoregions and strong population structure across the geographic range in the case of seahorses (Pierri et al., 2022; Woodall et al., 2015, 2011), the research was focused on this study area to increase resolution and targeted conservation efforts. The western coast of the Iberian Peninsula is the northern zone of the Canary Upwelling System, one of the four major coastal upwelling regions in the world (Patti et al., 2008), resulting in high primary productivity (which occurs mainly during the spring-summer season) and biodiversity (Alvarez et al., 2008; Herrera et al., 2008). In this region, the swell predominantly comes from the west, i.e., the open Atlantic Ocean, thus the coastlines facing the west are the most exposed to strong waves and currents, particularly in winter (Hernández-Urcera et al., 2021; Planas, 2022). The seabed varies between sandy bottom and hard substrates on the coast, and muddy to fine sand substrates in the estuaries and coastal lagoons (Vasquez et al., 2021).

2.2. Species data

As seahorses are cryptic and rare species, geo-referenced occurrence data of the seahorse species are scarce. Therefore, data was compiled from a variety of sources including several databases and scientific surveys from projects of various institutes which included dedicated surveys as well as opportunistic sightings in various environments (Supplementary, Table 1). Additionally, an independent citizen science survey was conducted between July and September 2022 among dive centers in the study area. It was a call to report seahorse sightings with date, location, habitat, and photos whenever available. Duplicated data in date and location among different databases and spatial points located on land or outside the known range were excluded from the datasets. The final dataset included a total of 155 occurrence points for *H. hippocampus* and 115 points for *H. guttulatus* for the time range between the years 1990 and 2022 (Supplementary, Fig. 1), which conformed to the minimum required number for robust predictions (Liu et al., 2019; Wisz et al., 2008). While there might be a sample bias that could decrease prediction performance, it was decided that occurrence points were not filtered to increase sample size, since sample size and the choice of modelling method are more important than spatial bias (Gaul et al., 2020).

2.3. Environmental predictor

A total of 18 biotic, climate, and geophysical variables which were available and assumed to be relevant, were tested to define the present-day habitat suitability of the two seahorse species (Supplementary, Table 2). Data of the variables was downloaded from different web sources (Supplementary, Table 2) and transformed into raster layers with a common spatial resolution of 0.0083° (about 1 km) and cropped to the extent of the study area by using the `resample` function in the raster package in R software 4.2.3 (Maintainer and Hesterberg, 2015; R Core Team, 2023). To increase coverage along the coast, raster layers were interpolated in the spatial analysis tool QGIS using the process tool 'GDA' and the function 'Fill no data'. The function fills raster cells with no data values by interpolation from nearby cells, using inverse distance weighting. In this study, phytoplankton biomass, which supports planktonic crustaceans which are the main food source of seahorses, was used as a proxy for food availability (Gurkan et al., 2011). Furthermore, the constant supply of prey to the sessile seahorses is facilitated by the exchange of water determined by the average maximum tidal amplitude (Cereja et al., 2021; Lopes and Dias, 2014; Silva and Duck, 2001). Exposure to waves and currents was represented by current velocity and the east-west aspect of the seafloor. The east-west aspect of the seafloor is the horizontal orientation of the seafloor and gives information on which direction the seafloor is facing. The reasoning behind including this variable is, that in the study region, the west-facing coastline is the most exposed to waves and currents. Furthermore, a raster of substrate types was created by rasterizing the EUSeaMap (2021) (Vasquez et al., 2021). In the process of rasterizing, the occurring substrate types were assigned category numbers ranging from 1 (small grain size) to 9 (big grain size) according to the hierarchy of the Folk 7 classification system (Kaskela et al., 2019) (Supplementary, Table 3). In this region, the substrate layer does not include biological habitats, such as seagrass and seaweed since no consistent data layers were available. The correlation among all layers was tested by Pearson's correlation matrix and to avoid multicollinearity only layers with a correlation below 0.7 were included in the same set of environmental predictors (Dormann et al., 2013). Since there was a correlation between ecologically relevant variables (e.g., temperature, salinity, and depth), it was necessary to run several models with different sets of environmental variables (Čengić et al., 2020). The relative contribution of each variable in determining the habitat suitability for *Hippocampus* spp. was calculated in three permutations with the function 'get_variables_importance' in the Biomod2 package (Thuiller, 2023). On a scale from 0 to 1, the higher the value, the more influence the variable has on the ensemble model. Additionally, response curves were commuted which showed the variability of habitat suitability relative to each explanatory variable, while the other variables were fixed as constant (Elith et al., 2005). The final model setup for assessing the habitat suitability of *H. hippocampus* and *H. guttulatus* was decided based on evaluation metrics, variable importance, response curves, as well as the predictive performance of the models.

2.4. Model selection, calibration, and evaluation

To predict the present-day habitat suitability of the two Iberian seahorses *Hippocampus* spp., occurrence data was modelled as a function of topographic, biological, and oceanographic variables, using an ensemble modelling approach in the Biomod2 package (Thuiller, 2023) in R (version 4.2.1). Ensemble modelling combines predictive outputs from several different algorithms into a unique ensemble model to achieve a more robust predictive performance (Araújo and New, 2007). The model algorithms used to build the ensemble model included the Generalized Linear Model (GLM), Generalized Additive Model (GAM), Artificial Neural Network (ANN),

Flexible Discriminant Analysis (FDA), Generalized Boosting Model (GBM), Maximum Entropy (MAXENT), Random Forest (RF), Classification Tree Analysis (CTA), Surface Response Envelope (SRE) and Multiple Adaptive Regression Splines (MARS). Since there were no true absence points available, pseudo-absences had to be generated randomly using the same number of pseudo-absences as available presences and with equal weighted sums of presence and absence (Barbet-Massin et al., 2012; Liu et al., 2019; Thuiller, 2023). This framework provides reliable predictions for rare species' distribution with a low number of presence points and pseudo-absences (Breiner et al., 2015; Hernández-Urcera et al., 2021; Liu et al., 2019). For model validation, the presence and pseudo-absence data were partitioned randomly into 80 % for calibration and 20 % for testing in each model run (Guisan and Zimmermann, 2000). Two metrics were used to evaluate the predictive performance of the algorithms: the True Skill Statistic (TSS) (Allouche et al., 2006) and the Area Under the receiver-operating characteristic Curve (AUC or ROC; (Fielding and Bell 1997). Predictive performance of algorithms is considered good ($AUC \geq 0.9$; $TSS \geq 0.6$), moderate ($0.7 \leq AUC \leq 0.9$; $0.2 \leq TSS \leq 0.6$), or poor ($AUC \leq 0.7$; $TSS \leq 0.2$) (Landis and Koch, 1977; Pearce and Ferrier, 2000), but only algorithms with a TSS of ≥ 0.7 were combined to run the Ensemble Models. The evaluation metric TSS was chosen as the primary criterion for selecting models for ensemble forecasting as this metric is more closely related to the accuracy of predictions and has a higher variability among models (Allouche et al., 2006). The predictive performance of the model was also assessed by checking the plausibility of the fitted species-environment relationship by assessing the variable importance and visual inspection of response curves. The ensemble forecast provides the prediction as an estimated species probability of occurrence translated into relative habitat suitability (HS) of each grid cell, where 0 represents the lowest suitability and 1 indicates the greatest suitability. Relative suitability above 0.25 indicates a suitable habitat. Core habitat is defined as cells having an $HS \geq 0.5$ which is considered moderate to high suitability. Hotspots were defined as areas with suitability higher than 0.75 (Ahmad et al., 2019; Garzon et al., 2020).

2.5. Coverage with existing protected areas

To assess the coverage of the core habitats by MPAs, the overlap of the surface area of the core habitat ($HS \geq 0.5$) with protected areas of different designation types and the actual habitat suitability within each MPA was calculated with the vector overlap and zonal statistics tool in QGIS. The list of MPAs and their designation types were sourced from the Protected Planet database for Portugal and Spain (Protected Planet, 2023). To further assess the effectiveness of protection, information on dredging activities and levels of fishing protection were extracted from Protected Seas Navigator (ProtectedSeas, 2023), Marine Protection Atlas (Marine Conservation Institute, 2023), and the European Marine Observation and Data Network (EMODnet) (European Commission, 2023). Unimplemented MPAs and protected areas that do not serve the protection of the seahorse species, such as the NATURA 2000 sites under the Birds Directive and RAMSAR wetland sites, were excluded from the analysis to avoid a false sense of protection (Horta e Costa et al., 2019; Trochet and Schmeller, 2013). Additionally, the coverage of the core habitat with zones of full protection / no-take zones (Prof Luiz Saldanha Marine Park) and designated seahorse refuge areas (Ria Formosa) was calculated.

3. Results

3.1. Model performance

The ensemble models for *H. guttulatus* and *H. hippocampus* achieved an AUC of 1.00 and a TSS of 0.98, respectively (Supplementary,

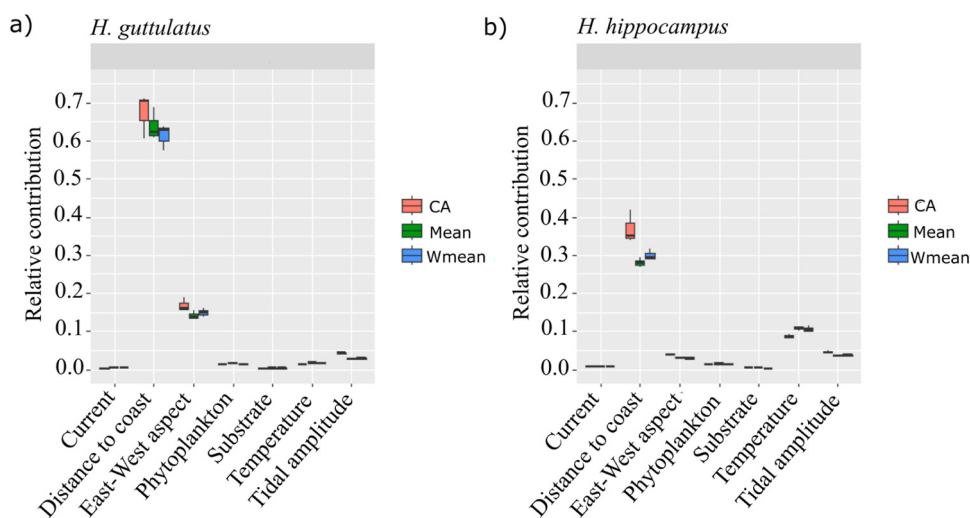


Fig. 2. Relative contribution of the seven predictors in the habitat suitability derived from the Ensemble Model of a) *H. guttulatus* and b) *H. hippocampus* based on the Ensemble models' community averaging (CA), mean (mean) and weighted mean (wmean).

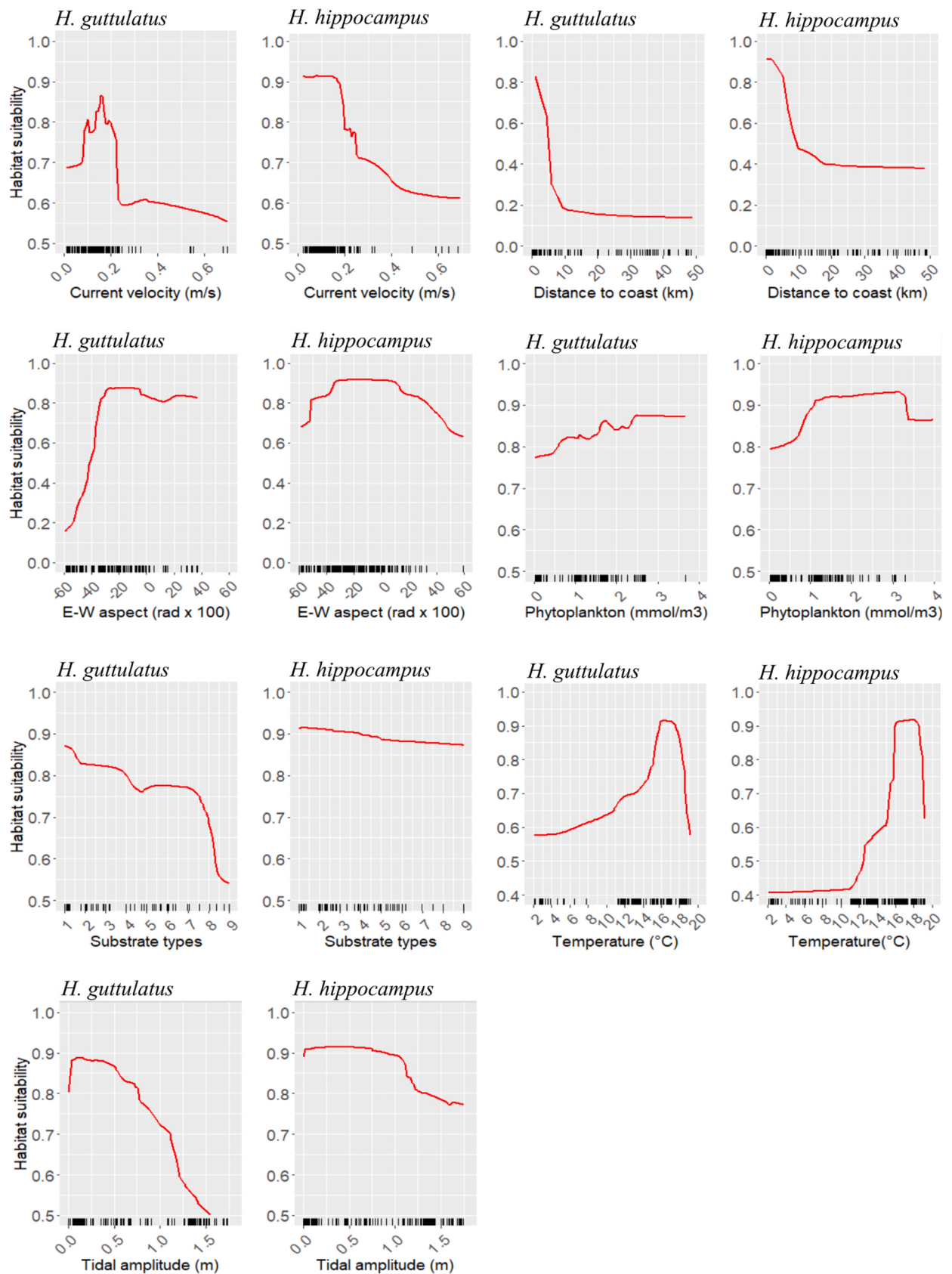


Fig. 3. Response curves of the ensemble mean of each variable for both species when the median is used as a fixed constant for the remaining variables.

Fig. 2). The scores indicate that the model had predicted the distribution of both species with high accuracy (Pearce and Ferrier, 2000). The predictive accuracy of the individual algorithms used in the ensemble model was good but varied between algorithms, with RF, MAXENT, and MARS performing the best (Supplementary, Fig. 3). However, all models reached the threshold to be included in the Ensemble Model (Supplementary, Fig. 3).

3.2. Importance of predictors

The final run of the *H. guttulatus* and *H. hippocampus* ensemble models included seven out of the eighteen variables tested: distance to coast, temperature, east-west aspect, current velocity, phytoplankton, substrate, and tidal amplitude (Supplementary, Table 4). The most significant predictors out of the tested predictors in the model governing the habitat suitability of *H. guttulatus* were the distance to the coast and the east-west aspect of the seafloor (Fig. 2a), while the most significant variables governing the distribution of *H. hippocampus* were distance to coast and temperature (Fig. 2b). The rest of the variables had relatively low contributions, but the model did not improve when excluding the variables (Fig. 2a, b).

The response curves (Fig. 3) showed that the habitat suitability decreases with distance to the coast, with an optimum of less than 5 km for *H. guttulatus* and less than 10 km for *H. hippocampus*. The orientation of the seafloor towards the west decreases the habitat suitability of *H. guttulatus* more than of *H. hippocampus*, while for *H. hippocampus* the habitat suitability also decreases slightly with increasing aspect (i.e., orientation) towards the east. Habitat suitability first increases with increasing mean temperature for both species but decreases again after 17.5 °C for *H. guttulatus* and after 18.5 °C for *H. hippocampus*. In the case of phytoplankton, the habitat suitability for both species increases with increasing phytoplankton biomass and stays high throughout the whole range. Tidal amplitude does not have a great effect on the habitat suitability of *H. hippocampus* but decreases for *H. guttulatus* after 0.5 m. In the case of current velocity, for both species, habitat suitability is high up to 0.2 m/s and after decreases, with a steeper decrease for *H. guttulatus*. Concerning substrate, the type of substrate does not affect the habitat suitability for *H. hippocampus*. Still, for *H. guttulatus* it is highest in sandy and muddy substrates and decreases with coarse sediment and hard substrata.

3.3. Predictive maps of habitat suitability

The predictive maps of the final ensemble models revealed that presently, the hotspots (habitat suitability ≥ 0.75) of *H. hippocampus* and *H. guttulatus* are concentrated in the estuarine and coastal lagoon waters of central and south Portugal, and for *H. guttulatus* also in the northwestern Spain (Fig. 4). Furthermore, the habitat suitability is generally lower for *H. hippocampus* than for *H. guttulatus* in northern Spain. Additionally, sheltered, and shallow coastal areas such as Arrábida and the south coast of Portugal (Algarve) showed higher habitat suitability for both species (habitat suitability ≥ 0.5). In the south of Spain, the habitat suitability is highest (habitat suitability ≥ 0.5) in the estuaries of Rio Tinto and Guadiana, and around Barbate. Additionally, the core habitat (habitat suitability ≥ 0.5) of *H. hippocampus* also stretches along the coast of Sintra/Cascais, Berlengas, Costa Vicentina, and the Bay of Cadiz.

3.4. MPA coverage

Both species' core habitat is covered by about 19–20 % with implemented protected areas in Portugal. In comparison, there is less coverage for both species in Spain with 12 % for *H. guttulatus* and 6 % for *H. hippocampus*. All implemented areas (i.e., operational with concomitant management in place that aims to ensure compliance and enforcement) are considered as “low” protected (i.e., areas that afford some protection but allow moderate to extensive extraction and associated impacts) (Marine Conservation Institute, 2023). Zones of full protection cover less than 0.5 % of the core habitat. In Portugal, the protected areas with the highest mean, maximum, and majority of habitat suitability for both species were Arrábida (Nature Park /OSPAR), Sudoeste Alentejano e Costa Vicentina (Nature Park/OSPAR), Ria Formosa (Nature Park) and the Sado estuary (Nature Reserve) (Supplementary, Fig. 4, 5, 6). In Spain, the protected areas with the highest mean, maximum, and majority of habitat suitability were Marítimo-Terrestre de las Islas Atlánticas de Galicia and Rio Guadiana (Natura 2000) for *H. guttulatus* and Rio Guadiana and Cabo Busto-Luanco (Natura 2000) for *H. hippocampus* (Supplementary, Fig. 7, 8, 9). According to the ProtectedSeas Navigator, the most restrictive areas in terms of fishing and coastal development are Berlengas, Sado estuary, Sudoeste Alentejano and Ria Formosa in Portugal and Bahía de Cádiz, Estrecho, Marismas del Barbate and Marítimo-Terrestre de las Islas Atlánticas de Galicia in Spain (ProtectedSeas, 2023).

4. Discussion

This is the first study to assess the degree of protection of the data-deficient flagship species, *H. hippocampus* and *H. guttulatus*, through the estimation of habitat suitability and the overlap between MPAs and species' core habitat, across the Atlantic Coast of the Iberian Peninsula. The results indicate that the protection of the two species is low considering that the species are vulnerable to noise caused by ship traffic (Palma et al., 2019) and to destructive fishing practices (Correia, 2021), and the coverage with full protection/no-take areas was less than 0.5 %, while all other implemented areas allow moderate to extensive extraction and associated

impacts (Marine Conservation Institute, 2023). Furthermore, our findings revealed new insights into the differences in habitat preferences between the two *Hippocampus* species and provided reliable information for spatial conservation due to its high resolution and assessment of protected area coverage. The extent and resolution of the model considered the population structure of the species which was decisive in identifying special habitat characteristics and the core habitat in the Iberian Atlantic population. Due to their cryptic nature and rareness, the collection of a large sample size of occurrence points without sample bias is difficult to achieve and poses a challenge to modelling their habitat suitability. The sample sizes of our models were relatively small, however considering the nature of the species and the extent of the study, the sample size was large enough and sufficiently representative of the species since occurrence data was collected from various sources (Bosso et al., 2024; Camins et al., 2024; Wisz et al., 2008; Zhang and Vincent, 2018, 2017). Furthermore, pseudo-absences had to be commuted, thus the ultimate strength of the model may be affected, however, previous studies confirmed that SDMs based on small sample sizes and using pseudo-absences can provide useful predictions (Patrão et al., 2015; Pearson et al., 2007; Stirling et al., 2016).

4.1. Importance of environmental drivers

Our results show that the distribution of both *H. hippocampus* and *H. guttulatus* are mostly influenced by a few environmental factors, and the relative importance of these factors in determining habitat suitability varies between species. For instance, distance to the nearest coast was the most important predictor for both species, but the relative importance was higher for *H. guttulatus* than for *H. hippocampus*. Furthermore, the second most important predictor for *H. guttulatus* was the east-west aspect of the seafloor, while for *H. hippocampus* it was temperature. The decrease in habitat suitability with an increasing aspect of the seafloor towards the west is more pronounced in *H. guttulatus*, which indicates that *H. guttulatus* prefers habitats that face away from exposure to waves and currents. These findings are supported by field observations which found *H. guttulatus* more associated with confined water habitats,

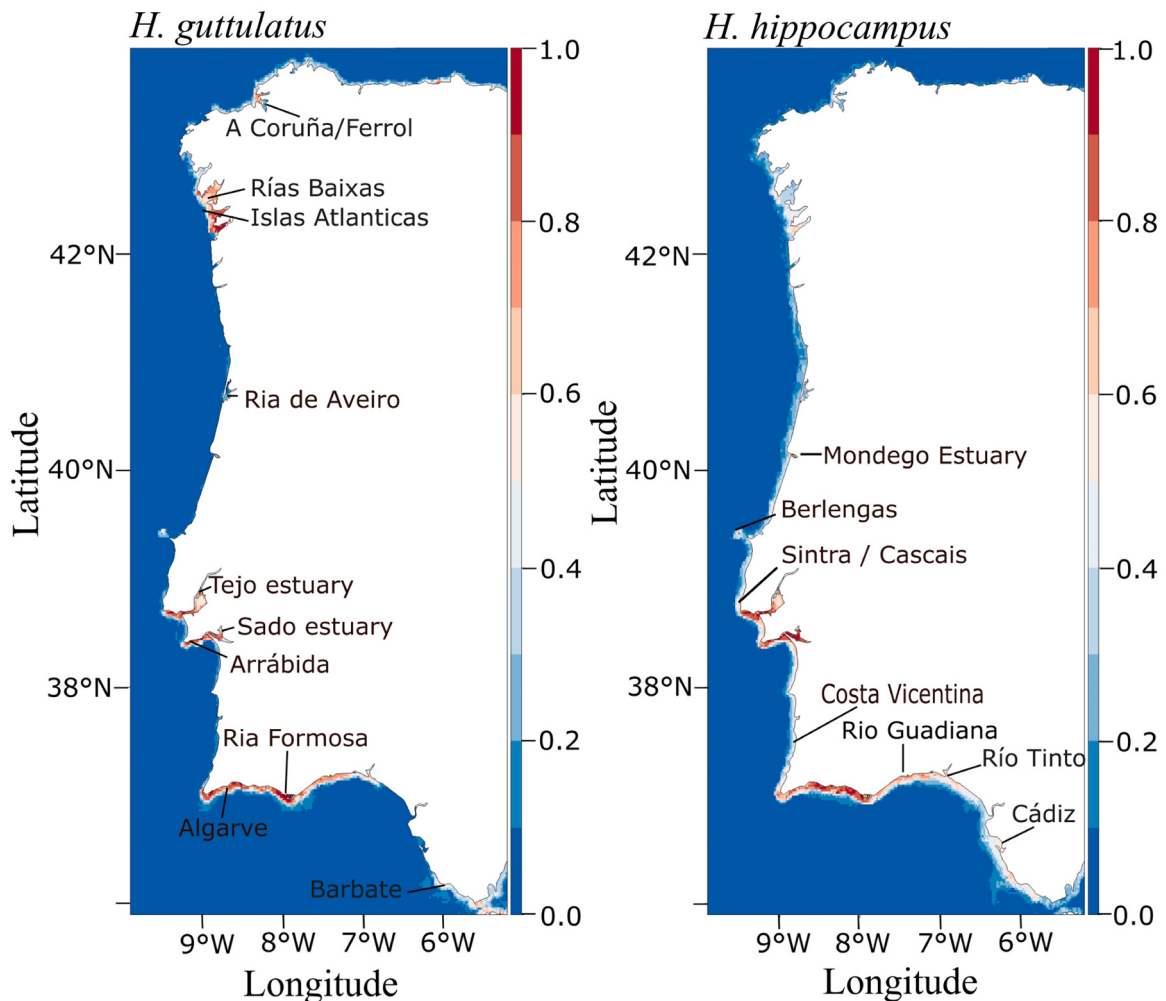


Fig. 4. Current habitat suitability of *H. guttulatus* and *H. hippocampus* based on the Ensemble Species Distribution Model with the variables distance to coast, temperature, east-west aspect of the seafloor, current velocity, phytoplankton, substrate, and tidal amplitude.

while *H. hippocampus*, has been found more frequently in marine shelf areas and habitats with comparably higher current velocities (Caldwell and Vincent, 2012a; Pierri et al., 2022; Woodall et al., 2018). In places where *H. guttulatus* and *H. hippocampus* occur in sympatry, *H. hippocampus* tends to have lower population densities than *H. guttulatus* (Woodall et al., 2018), suggesting that the species require different habitat conditions to thrive according to the co-occurrence theory of species (Sfenthourakis et al., 2006). Furthermore, an increased density of *H. guttulatus* and artificial habitat negatively correlated with the activity of *H. hippocampus* (Spatafora et al., 2023). Temperature was a more important predictor for the habitat suitability of *H. hippocampus* than for *H. guttulatus* which suggests that predicted temperature changes could affect the habitat suitability of *H. hippocampus* more strongly. So far it is known that the distribution of Syngnathidae species is expected to continue shifting poleward with progressing climate change (Monteiro et al., 2023). Furthermore, temperatures above 24 °C cause physiological stress in *H. guttulatus* (Costa et al., 2023). In the field, temperatures above 17 °C were negatively correlated with the abundance of *H. guttulatus* (Correia et al., 2018) which confirms the result of the response curve. The response of *H. hippocampus* is less known, however, the resident extent of *H. hippocampus* reaches further south (Woodall, 2017), and its temperature range is wider than that for *H. guttulatus* (Froese, 2020). The maximum tidal amplitude, which is decisive for the exchange of sediment and food particles between the estuary and the ocean (Cereja et al., 2021; Lopes and Dias, 2014; Silva and Duck, 2001), contributed a fair amount to the habitat suitability. Higher tidal amplitudes generally correspond to stronger tidal currents, which bring food but can also cause seahorses to become dislodged from their preferred habitat. These two causalities are reflected in the response curves of the species which show an increase in habitat suitability up to a certain point and then a decrease with increasing tidal amplitude, which is more pronounced in *H. guttulatus* which prefers habitats with less current. Dredging of navigation channels, coastal development and rising sea levels influence the tidal amplitude and may lead to an increase in the tidal current or an increase of sedimentation which can make the seahorse habitat unsuitable (Woodall et al., 2015, 2011). The substrate type was a less decisive predictor, although the response curve showed a decrease towards hard substrate for *H. guttulatus*. Here, it needs to be considered that the substrate type alone does not provide information on the holdfast availability. Particularly for *H. guttulatus* positive correlations between the population densities and natural complex holdfast availability have been observed (Correia et al., 2015a). Thus, the result is not surprising since *in situ* studies showed that both seahorse species occupy all sediment types (Woodall et al., 2018), and hard substrate with less vegetation is most often found at exposed sites (Hernández-Urcera et al., 2021). However, seahorses rely on holdfast availability to grasp with their tail which can range from low complexity (e.g., shells, sponges, tunicates, tube-dwelling polychaetes (*Sabella* sp.) to complex macrophyte communities (Correia et al., 2018; Curtis and Vincent, 2005; Foster and Vincent, 2004). Across the native range with several interspecific differences, seagrasses were the most used holdfasts of both species (Pierri et al., 2022). We tested the importance of seagrass by including proximity to seagrass as a predictor in one of the model set-ups, which showed high importance (Supplementary Fig. 10). However, proximity to seagrass is highly correlated with distance to the coast and thus proximity to other algae and invertebrate communities as well as a higher density of artificial structures. It has been shown that whenever seagrass is not present or has disappeared over time, both species used other objects as holdfasts including intentionally placed artificial structures or simply trash, i.e., in the form of ropes, abandoned traps, and nets (Correia et al., 2015b; Woodall et al., 2018).

4.2. Predictive habitat suitability maps

Both seahorse species have a wide geographic range that extends across most of Europe, including the Atlantic Ocean, Mediterranean Sea, and Black Sea (Pierri et al., 2022), however, *H. hippocampus* is resident in the north of Africa (Woodall, 2017), while the Iberian region is the southernmost limit of the resident extent of *H. guttulatus* on the Atlantic Coast (Pollom, 2017). Our study showed that the north of Iberia provides a higher habitat suitability for *H. guttulatus* than for *H. hippocampus*, while the south of Spain seems to be more suitable for *H. hippocampus*. The western Iberian coast is interlinked with a diversity of shallow ecosystems, from coastal habitats to lagoons and estuaries, which are influenced by complex hydrodynamic factors such as tidal ranges and upwelling events (Relvas et al., 2007). According to literature, in the eastern Atlantic Ocean, both species are mainly present in confined areas (lagoons, estuaries, or semi-enclosed bays), while in other seas both species are most frequently found in marine shelf areas (Pierri et al., 2022). This difference in habitat use is also reflected in our models since the predictive maps showed higher habitat suitability in both species on the Iberian coast for wide estuarine waters, which also provide suitable habitat for a high diversity of other fish, birds, and invertebrate species. For instance, the Rias Baixas and Tagus estuary are confirmed Key Biodiversity Areas of international significance (KBAs) (Key Biodiversity Areas, 2023). In northern Portugal, the habitat suitability was low, and the confirmation of the occurrence of live seahorses in the wild could not be confirmed either by scientific surveys or citizen science. However, while recent scientific surveys in Ria de Aveiro did not find seahorses, there were several recent sightings of washed-up *H. hippocampus* in the Ria Aveiro lagoon ((ii)Naturalist, 2023; Nuno Monteiro personal communication 2023) and an older sighting from literature (Pombo and Rebelo, 2002). Nevertheless, in the Mondego estuary, *H. hippocampus* observations in scientific surveys have become more frequent over the last decade (Guerreiro et al., 2021; Martinho et al., 2015), which could be related to the observed increase in the abundance of marine fish in higher latitudes due to climate change (Hastings et al., 2020), thus, it should be monitored and taken into consideration when planning conservation measures.

4.3. Implications for conservation

The coverage of the core habitat of *H. guttulatus* and *H. hippocampus* with protected areas was estimated to be between 6 % and 20 %, with higher protection in Portugal than in Spain. These numbers are lower than recently reported for seahorse populations in Italy (Bosso et al., 2024). Furthermore, there is concern about the effectiveness of MPAs when they are not properly implemented or do

not have strict protection measures in place (Gorud-Colvert et al., 2021; Horta e Costa et al., 2016; Roessger et al., 2022), such as is the case for most of the protected areas in Portugal and Spain (Marine Conservation Institute, 2023). These areas provide little or no additional protection compared to outside areas (Horta e Costa et al., 2019). Only in a few of the protected areas management plans are implemented, and both bottom trawling and dredging are restricted or prohibited (e.g., Arrábida, Berlengas, Sado estuary, Sudoeste Alentejo and the Ria Formosa), which can serve as important refuges for seahorses. Natura 2000 sites were found to be less effective for marine fish and mammal species (Fortuna et al., 2018; Guidetti et al., 2019; Trochet and Schmeller, 2013), allowing the main threats known to affect these species in this region (i.e., fishery bycatch, bottom trawling, and dredging). In line with this, studies confirming the effectiveness of MPAs in protecting seahorses are still lacking, while some studies show either no effect or a potentially negative impact due to increased predator abundance (Harasti et al., 2014; Martin-Smith and Vincent, 2005; Yasué et al., 2012). Seahorses face multiple threats that can also originate from outside the MPAs and are often more affected by habitat degradation than direct exploitation (Martin-Smith and Vincent, 2005). That is why careful planning when designing an MPA and proper management is important to avoid negative impacts on seahorse populations by accounting for increased predator abundance (Harasti et al., 2014); key habitat requirements (Zhang and Vincent, 2018); and adaptations to climate change (Monteiro et al., 2023). Nonetheless, predictive maps of habitat suitability are a useful tool to inform on management and conservation of seahorses (Bosso et al., 2024; Zhang and Vincent, 2018). In our case, the extent and resolution of the predictive maps were appropriate in indicating specific locations for further research and highlighting areas where more conservation efforts need to be invested. As both *H. guttulatus* and *H. hippocampus* are currently classified as Data Deficient at the global scale and as Near Threatened for the Mediterranean region (Pollom, 2017; Woodall, 2017), population presences and trends are unknown in many locations, therefore conservation measures should include monitoring activities. Based on the maps, recommended regions for further research and population assessment are, from north to south, the coast between Ribadeo and Cabo Pena, Ria da Coruña and Ferrol, Cascais/Sintra, Sudoeste Alentejo, and the region of Cadiz, Barbate, and Estrecho (Tarifa). Furthermore, regions recommended for increased protection are the Tagus and Mondego estuaries and the south coast of Portugal (Algarve) between the protected areas of Sudoeste Alentejo and Ria Formosa. Furthermore, it is recommended to do more research on the potential presence of populations around Porto, Berlengas, Ria Aveiro, and Lagoa de Óbidos where seahorses have been sighted historically or otherwise irregularly in bycatch or washed up on the shore (Almeida et al., 2018; Pombo and Rebelo, 2002). Besides, bycatch data and interviews with fishermen can also be important initial indications for the presence/absence of the two species (Aylesworth et al., 2017). Another important aspect to consider is the difference in their habitat suitability since *H. hippocampus* has a wider spatial habitat suitability and occurs further away from shore while *H. guttulatus*' habitat suitability is more concentrated in less exposed inshore areas such as estuaries and coastal lagoons. It has been shown in previous studies that *H. guttulatus* benefits more than *H. hippocampus* from habitat restoration or enhancement of habitat complexity through artificial structures, as well as the protection from indirect effects of destructive bottom-touching fishing gears on benthic habitats (Correia et al., 2015b; Curtis et al., 2007; Spatafora et al., 2023). *H. hippocampus* on the other hand is more often directly affected by fishing practices as accidental bycatch with different fishing métiers in coastal shallow sandy areas (Almeida et al., 2018; Cabral et al., 2003; Vasconcelos et al., 2019). Thus, an increase in conservation efforts in inner-shelf soft-sediment, low-complexity habitats, and outside of MPAs, would not only be beneficial to *H. hippocampus* but also to other endangered demersal species such as *Rostroraja alba* and *Raja undulata* (Sousa et al., 2018; Stratoudakis et al., 2019). The best conservation measure for both species is to create fully protected areas with a total ban on destructive fishing practices, dredging and boat activities, covering areas of both high and low-complexity habitats and with appropriate extents for both species. Furthermore, as charismatic fish, seahorses can function as flagship species to engage the public and policymakers (Zacharias and Roff, 2001), who can serve as active conservation agents by denouncing illegal fishing activities and promoting the reduction of pollution in the local communities.

5. Conclusion

To conclude, the final predictive maps reflect well the habitat suitability of the two species and can be used as a tool to inform where to invest more research and conservation efforts. For instance, our findings highlight a lack of spatial protection of the Iberian population and the importance of conserving highly vulnerable habitats such as estuaries and coastal lagoons as well as inner-shelf soft sediment habitats. The mere designation of protected areas is not sufficient for seahorse protection, instead in the future, it is recommended to involve stakeholders in decision-making and implement specific measures such as the prohibition of fishing and dredging in essential fish habitats, the restoration of habitats (e.g., seagrass meadows) as well as monitoring of the existing populations. Furthermore, the results suggested that there are differences in habitat preferences of the two species, thus a potential niche partitioning in the congeneric species which must be considered when monitoring and discussing protective measures and assessing the conservation status of the two species since the conservation measures can affect the two species differently.

CRediT authorship contribution statement

Miguel Correia: Writing – review & editing, Data curation, Conceptualization. **Gonçalo Jorge Franco Silva:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Friederike Peiffer:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Data curation, Conceptualization. **Sofia Henriques:** Writing – review & editing, Supervision, Formal analysis, Data curation, Conceptualization. **André Ricardo Araújo Lima:** Writing – review & editing, Supervision, Software, Methodology. **Filipe Martinho:** Writing – review & editing, Data curation. **Miguel A. Pardal:** Writing – review & editing, Data curation. **Emanuel Gonçalves:** Supervision, Funding acquisition, Conceptualization. **Jorge M. S. Gonçalves:** Writing – review & editing, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e02993](https://doi.org/10.1016/j.gecco.2024.e02993).

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