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ORIGINAL PAPER

Projected climate change and limited dispersal potential threaten the seahorse species *Hippocampus hippocampus* and *Hippocampus guttulatus*

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Abstract

Climate change is predicted to drive species redistribution, altering the composition of marine communities and affecting ecosystem functioning. There is increasing evidence that fish distributions follow a trend of poleward expansion, while realised niches often decrease in range size. This study aimed to assess the influence of oceanographic connectivity and intrinsic dispersal mechanisms on changes in suitable habitats of the European seahorses (*Hippocampus hippocampus* and *Hippocampus guttulatus*) from the present (2010–2020) until the end of the century (2090–2100). Habitat suitability was assessed using Ensemble Species Distribution Modelling under two Shared Socio-Economic Pathways (SSP2 and SSP5) coupled with biophysical modelling to estimate oceanographic connectivity. The results show that intrinsic dispersal mechanisms and oceanographic connectivity limit the northward range expansion, while predicted habitat loss remained constant in all dispersal scenarios, with the highest habitat loss forecasted in the Mediterranean and northern Africa. Consequently, considering restricted dispersal, *H. guttulatus* was projected to experience a negative range change (or habitat contraction [-45% (SSP5)] as opposed to an expansion with unlimited dispersal (standard model) [+6% (SSP5)]. On the other hand, for *H. hippocampus*, a more limited range expansion [+8% (SSP5)] was forecasted compared to the standard model [+17% (SSP5)]. In addition, the lower emission scenario (SSP2) resulted in half of the habitat losses, while maintaining climate refugia for *H. guttulatus* populations in the north Mediterranean, Iberian Atlantic Coast, and Black Sea. This study highlights the importance of considering dispersal abilities when assessing climate change impacts on marine species distribution.

Keywords European seahorses · Species distribution modelling · Habitat loss · Climate refugia · Connectivity · Conservation

Introduction

Climate change is predicted to have profound impacts on marine organisms and trigger cascading effects on ecosystems (Parmesan 2006; Wernberg et al. 2016; Pecl et al. 2017; Pilotto et al. 2020). While projections vary depending on the species, spatial and temporal extent, most indicate significant biodiversity losses, raising concerns that, under worst-case scenarios, climate change could lead to a sixth mass extinction in Earth's history (Bellard et al. 2012; Penn and Deutsch 2022). Ocean warming can push coastal marine organisms beyond their thermal limits, disrupting vital physiological and ecological processes (Roessig et al. 2004; Pörtner 2010; Stuart-Smith et al. 2015). At their higher thermal limits, marine organisms are less resilient to additional climate-related stressors, such as ocean acidification and deoxygenation (Pörtner et al. 2005; Munday et al. 2009; Lima et al. 2024a, b) and non-climate stressors (e.g., overharvesting, reduced water quality, introduced species, habitat depletion) (Wernberg et al. 2011; Sinopoli et

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Extended author information available on the last page of the article al. 2019). Species may cope with climate change by tracking suitable habitats, leading to shifts in their geographic ranges (Anker-Nilssen et al. 2008; Chen et al. 2011; Lawlor et al. 2024). There is increasing evidence that fish distributions follow a consistent trend of a poleward movement in fish distribution, although the availability of thermal niches at higher latitudes is often limited by seasonal variability (Stuart-Smith et al. 2017; Hastings et al. 2020; Le Luherne et al. 2024). However, range shifts may vary according to the species' geographic range size, thermal niche width, and life-history traits (e.g., dispersal capacity) (Assis et al. 2017; Lima et al. 2022). Climate-induced range shifts can have negative impacts on ecosystem functioning and human well-being (Pecl et al. 2017), similar to those caused by introduced species (Sorte and Williams 2010). Furthermore, range shifts tend to occur faster in marine than terrestrial environments (Sorte and Williams 2010). These interrelations underline the importance of predictive forecasts of species redistributions for biodiversity conservation and management (Porfirio et al. 2014).

There is an increasing concern about the impact of climate change on seahorses, which belong to the Syngnathidae family and the genus *Hippocampus* and are characterised by their elongated bodies, prehensile tails and unique reproductive behaviour (i.e., males carry and give birth to the offspring) (Lourie et al. 2016). Seahorses are indicator species of their habitat status and important flagship species for conservation (Shokri et al. 2009). Experiments have shown that warming induces substantial changes in metabolic rates, growth, feeding, and activity levels, with more pronounced effects in juvenile than in adult seahorses (Aurélio et al. 2013; Faleiro et al. 2015; Costa et al. 2023). In the wild, the combined effects of warming, oxygen depletion, and acidification, as well as changes in hydrodynamics induced by increasing storms and sea level rise, may affect seahorses in unpredictable ways (Pearce and Selley 2024). Recent studies have discovered that thermal anomalies influence seahorse migratory behaviour along the Western Atlantic coast (Freret-Meurer et al. 2022) and that gradual warming causes the West African seahorse, *Hippocampus algiricus*, to expand its habitat northward to the Canary Islands (Otero-Ferrer et al. 2015). Although seahorses can adapt to unfavourable conditions by moving to more suitable areas, this may fragment local populations and impact reproductive success (Caldwell and Vincent 2012a; Correia et al. 2015). In addition, seahorses naturally have low density and low dispersal ability (Teske et al. 2007), which increases the risk of local extinction (Shaffer 1981; Pollom et al. 2021). Adult seahorses have small home ranges (Foster and Vincent 2004) and are therefore largely reliant on passive dispersal mechanisms for long-distance movement. This occurs primarily during the juvenile pelagic stage (Foster and Vincent 2004; Vandendriessche et al. 2005; Luzzatto et al. 2013; Wong and Teh 2017) or via rafting (juveniles or adults), while attached to seaweed, seagrass, or marine debris (Teske et al. 2007; Boehm et al. 2013; Li et al. 2021). The extent and duration of passive dispersal are shaped by the interaction between oceanographic patterns and a species' intrinsic dispersal potential (Treml et al. 2012). Oceanographic connectivity thus plays a key role in determining species distributions and can significantly influence climate-driven range shifts (Garciá Molinos et al. 2017). However, our understanding of how oceanographic connectivity and the dispersal capabilities of seahorses affect their potential to track suitable habitats in the face of climate change remains limited.

Here, we focused on two native European seahorses, *Hippocampus hippocampus* and *Hippocampus guttulatus*. Their geographic range stretches from the UK to Northern Africa (Lourie et al. 2016), exhibiting heterogeneous distribution and population densities that vary from rare sightings to locally established dense populations (Woodall et al. 2018; Pierri et al. 2022b; Bosso et al. 2024; Peiffer et al. 2024). According to the IUCN Red List, the two species are listed as Data Deficient in the Atlantic and Near Threatened in the Mediterranean (Pollom 2017; Woodall 2017). Recent population declines reported across Europe have raised concerns regarding their conservation (Caldwell and Vincent 2012b; Lazic et al. 2018; Pierri et al. 2021; Correia 2022). Thus, this study aimed to assess changes in the extent of suitable habitat for *H. guttul*atus and *H. hippocampus* until the end of this century by combining Ensemble Species Distribution Modelling with biophysical modelling as an estimate of connectivity. More specifically, the following key questions were investigated: (1) To what extent do patterns of habitat expansion and contraction differ between species, regions, and Shared Socioeconomic Pathway scenarios (SSP2 and SSP5)? and (2) How does the integration of ocean connectivity and intrinsic dispersal potential into ESDM influence projection outcomes compared to the standard model? This framework will be pivotal to understanding the effects of dispersal on species-specific redistribution driven by climate change.

Materials and methods

Study area

The study areas encompassed the native geographic ranges of both species, whose distribution ranges extend from the UK to the Black Sea for *H. guttulatus* and from the UK to Guinea for *H. hippocampus*, including the Mediterranean Sea (Lourie et al. 2016). The extent of the study area was expanded to allow the projection of habitats due to predicted range expansions [*H. guttulatus*: (12.1°W, 29.5°N, 45.1°E, 73.15°N); *H. hippocampus*: (37.4°W, 8.75°N, 44.65°E, 76.25°N)]. Although sympatric, these species show differences in micro-habitat preference and macro-habitat distribution (Curtis et al. 2007; Woodall et al. 2018; Correia et al. 2018): *H. guttulatus* is mainly found in confined waters, while *H. hippocampus* is found not only in confined, but also in marine shelf waters (Pierri et al. 2022b).

Species distribution data

Occurrence data of the two European *Hippocampus* species were compiled from various sources, including open-source databases, scientific surveys, and citizen science surveys (Supplementary Table 1). Duplicated data among different databases and spatial points on land, outside the known range, or with low coordinated accuracy were excluded from the datasets. Occurrence data on seahorses are limited (Pierri et al. 2022b); therefore, we prioritised data quantity over spatial data thinning given the importance of the number of occurrence points (Gaul et al. 2020). The final dataset consisted of 780 occurrence points for *H. hippocampus* and 571 points for *H. guttulatus*, spanning from the years 2000 to 2022 (Supplementary Figs. 1, 2) and allowing robust predictive performances (Wisz et al. 2008; Liu et al. 2019).

Environmental data

To extract the current and future environmental conditions for the two species, environmental raster layers were downloaded from Bio-Oracle (V 3.0) under the "present" (2010–2020) and for future climate scenarios (2090–2100) according to two distinct SSP scenarios (SSP2 and SSP5) (Assis et al. 2024). The raster files have a spatial resolution of 0.05° and a decadal temporal resolution from the present day to the end of the 21 st century (2000–2100). Raster layers were interpolated using inverse distance weighting with the "GDA" tool in QGIS to slightly extend the grid cells along coastal zones and estuarine habitats. Subsequently, the "fill no data" function was applied to replace missing values and ensure better coverage along the coastline. The variables were chosen based on their relevance to seahorses' habitat

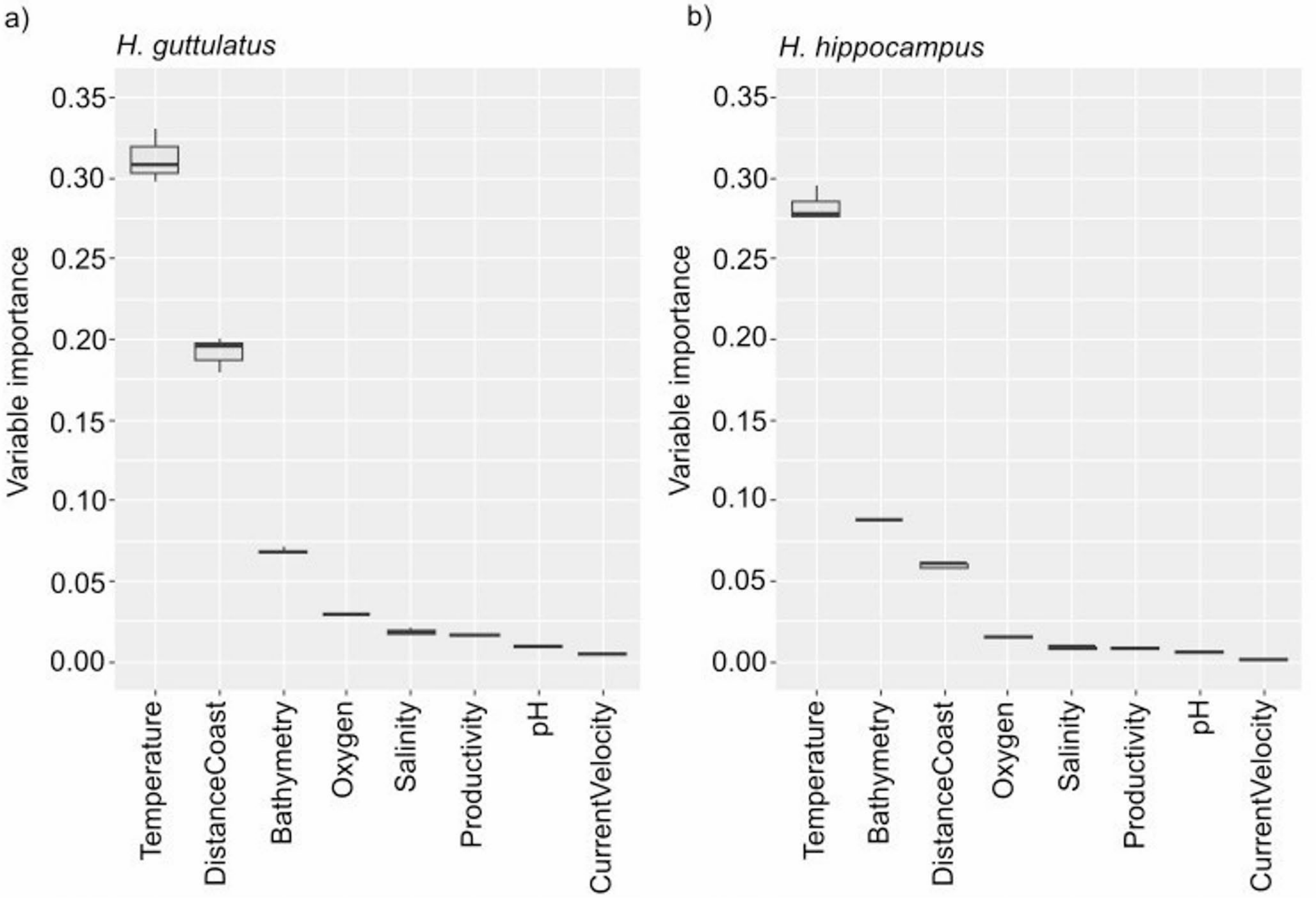


Fig. 1 Variable importance derived from the Ensemble Species Distribution Models of (**a**) *H. guttulatus* and (**b**) *H. hippocampus* ranked from the highest to the lowest relative importance

and survival requirements (i.e., bathymetry, temperature, salinity, oxygen, primary productivity, and current velocity) or on whether they could become relevant in the future (i.e., pH) (Foster and Vincent 2004; Faleiro et al. 2015; Zhang and Vincent 2018; Correia et al. 2018; Peiffer et al. 2024). Owing to the demersal and mostly shallow distribution of seahorses (Pierri et al. 2022b), we used environmental data at the minimum depth. Additionally, variables included in the models were selected based on their availability across both present-day and future scenarios (Supplementary Table 2). The Pearson correlation analysis was used to avoid using variables with a high correlation coefficient ($r > 0.7$) in the same model to improve the model performance (Ahmad et al. 2019).

Modelling approach

The Ensemble Species Distribution Modelling (ESDM) approach was used to identify suitable habitats in the present (2010–2020) and future (2090–2100). The models were trained using present-day climate conditions and projected onto future climate conditions under two different SSP scenarios: the "fossil-fuelled development" or highest emission scenario (SSP5) and the "Middle of the Road" scenario (SSP2) (Lee and Romero 2023). The ESDM approach was applied using the Biomod2 package in R (Thuiller 2024) to combine the outcomes of individual models of nine algorithms (Generalized Linear Models (GLM), Generalized Additive Models (GAM), Generalized Boosted Models (GBM), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Artificial Neural Networks (ANN), Maximum Entropy (MAXENT), Random Forest (RF), Surface Response Envelope (SRE). An equivalent number of pseudo-absences was randomly generated to match the number of presence points (Barbet-Massin et al. 2012). The models were built using 80% of the data to train the model and 20% of the data for evaluation of the model performance, and each model was generated three times. The accuracy of the model predictions was evaluated using two evaluation metrics: the Area Under the Curve (AUC) of Receiver Operating Characteristics (ROC) and the True Skills Statistics (TSS) (Allouche et al. 2006). Model algorithms that produced a TSS score of 0.7 or higher were included in the final ensemble model.

Variable importance

The variable's importance in predicting habitat suitability was calculated in three permutations with the function 'get_variables_importance' in the Biomod2 package (Thuiller 2024). Hereby, the importance of each variable was estimated by calculating the Pearson correlation between the original prediction and the predictions generated with the shuffled variable, while keeping the other variables constant (Thuiller 2024). The importance score was then computed as one minus the correlation score, resulting in a scale from 0 to 1, whereby a greater value indicates a higher influence of the variable on the model prediction (Elith et al. 2005). After multiple assessments of variable importance across different sets of uncorrelated variables, eight variables were selected for inclusion in the models: bathymetry, distance to the nearest coast, temperature, salinity, pH, dissolved oxygen, primary productivity, and current velocity (Supplementary Table 3).

Species range change

The predictive maps from the ESDM were reclassified into binary presence-absence maps based on habitat suitability, using a threshold that maximised the sum of sensitivity (i.e., true positive rate) and specificity (i.e., true negative rate), as determined by the TSS (Jiménez-Valverde and Lobo 2007; Liu et al. 2013). Thus, grid cells classified as 'presence' were interpreted as suitable habitat. To measure the gains, losses, and range change under future climatic conditions, we used the function 'BIOMOD_RangeSize' implemented in 'biomod2' (Thuiller 2024). This function calculates the number of grid cells representing habitat loss, stability, and gain, as well as their corresponding relative proportions (%) by comparing present and future binary projections from ESDMs (Thuiller 2024). The changes were estimated considering the geographic native range and the population structure of the two species individually (Woodall et al. 2011, 2015). Accordingly, *H. hippocampus* range change predictions were subdivided into UK/Bay of Biscay, Mediterranean Sea, Iberia, and West Africa (Woodall et al. 2011), while for *H. guttulatus*, the predictions were subdivided into the UK/Bay of Biscay, Iberia, Mediterranean Sea, and Black Sea (Woodall et al. 2015).

Connectivity

The influence of oceanographic connectivity and intrinsic dispersal mechanisms on potential range expansions under climate change was quantified by coupling the ensemble models with coastalNet, a biophysical model (BM) that simulates the influence of oceanographic currents and propagule durations (PD) on the connectivity of passively dispersed species (Assis et al. 2025). The coastalNet model has been validated against independent population genetics and demographic data (Assis et al. 2015; Klein et al.

2016; Gouvêa et al. 2023; Tavares et al. 2023; Abecasis et al. 2024). The model employs a forward-in-time Lagrangian simulation of passive dispersal, assimilating daily ocean current direction and intensity data from the Global Ocean Physics Reanalysis (EU Copernicus Marine Service product, ~9.2 km spatial resolution (Copernicus Marine Service 2024). This reanalysis product integrates satellite and in-situ observations and is forced by the ERA-Interim and ERA5 atmospheric reanalyses. The Lagrangian simulation used an Uber H3 grid system (Uber Technologies Inc. 2024) to define equal-area (~9.85 km resolution) source and sink hexagon sites. From these sites, particles were released daily over 21 years (2000–2020), totalling 7,670 particles per site and 12,617,150 particles overall. Particles were transported by ocean velocity fields for maximum durations of 14 and 100 days (see Dispersal Mechanisms below), and their positions were tracked hourly until reaching a sink site. Of the total particles released, 11,565,758 and 12,408,059 performed pairwise connectivity events for the 14-day and 100-day PDs, respectively. Connectivity matrices were generated by calculating pairwise connectivity, defined as the total number of particles exchanged between sites i and j, divided by the number of particles released from site i. Multigenerational dispersal estimates, accounting for cumulative stepping-stone connectivity pathways, were derived using a graph-theoretical approach. In this approach, graph nodes represented the sites, and edges represented the corresponding pairwise oceanographic connectivity. The Dijkstra algorithm was applied to find the shortest path between each pair of sites by minimising the sum of log-transformed distances. Multigenerational dispersal estimates were calculated by multiplying the probabilities along each shortest path (Assis et al. 2025). The binary maps from the standard ESDM were used to define target source and sink sites by linking the coordinates of raster grid cells classified as suitable habitat (value = 1) to the corresponding Hexagon IDs. After running the biophysical model, the Hexagon IDs were converted back into the spatial grid format of the original species distribution model. In this binary grid, successfully connected sites were assigned a value of 1 to indicate that a suitable habitat can be reached via passive dispersal. As mentioned above, the propagule duration (PD) during the connectivity event was determined by the species' dispersal mechanisms (Assis et al. 2025). The two main dispersal scenarios for seahorses were assessed: The first scenario is the pelagic drifting dispersal after juvenile seahorses are released from the brood pouch, which lasts about 14 days until their tails are developed enough to start the grasping behaviour (Otero-Ferrer et al. 2010; Novelli et al. 2017). The second scenario is a passive dispersal via rafting as adults or juveniles when seahorses are attached to algae, seaweed, seagrass, or marine debris (Teske et al. 2007; Luzzatto et al. 2013; Boehm et al. 2013). The duration of this type of dispersal can vary depending on environmental conditions, raft type, food supply, the biological traits of the rafter, and ecological interactions (Vandendriessche et al. 2006, 2007a, b). However, with increasing travel time, organisms experience bottlenecks, and on average, most organisms stay up to 100 days on the raft (Thiel and Gutow 2005). Therefore, we also ran one scenario with 100 days as an estimate for rafting time, hence PD time. The resulting binary maps of the dispersal models were used to calculate gains, losses and stability of suitable habitat in the same way as for the standard models. The standard ESDMs represented unrestricted dispersal, meaning that the seahorses can reach long-distance sites if sporadic long-distance dispersal events are not impaired by environmental conditions (Teske et al. 2007; Otero-Ferrer et al. 2017; Li et al. 2021).

Results

Evaluation of model metrics and the relative importance of environmental variables

The final ESDMs showed high predictive performance with both evaluation estimates, AUC and TSS, higher than 0.9 for both species (Supplementary Fig. 3). The most significant variables governing the habitat suitability of *H. guttulatus* and *H. hippocampus* were temperature, distance to the coast, and bathymetry (Fig. 1). However, distance to the coast was more important for the habitat suitability of *H. guttulatus* than for *H. hippocampus*. The relative importance of the other variables in contributing to the model's performance was below 0.1; however, the stepwise exclusion of the variables did not improve the evaluation score of the model, hence the variables were retained.

Present-day habitat suitability

The seahorse *H. guttulatus* favours sheltered coasts spanning from the Netherlands to Portugal, encompassing the southern shores of the UK and Ireland, the Western Mediterranean, and the northern Black Sea (Fig. 2a). In contrast, the *H. hippocampus* seahorse demonstrates a preference for the North Sea, the Bay of Biscay, the southern Mediterranean, the African Atlantic, Macaronesia, and the Canary Islands, while largely not present in the eastern Mediterranean and the Black Sea (Fig. 2b).

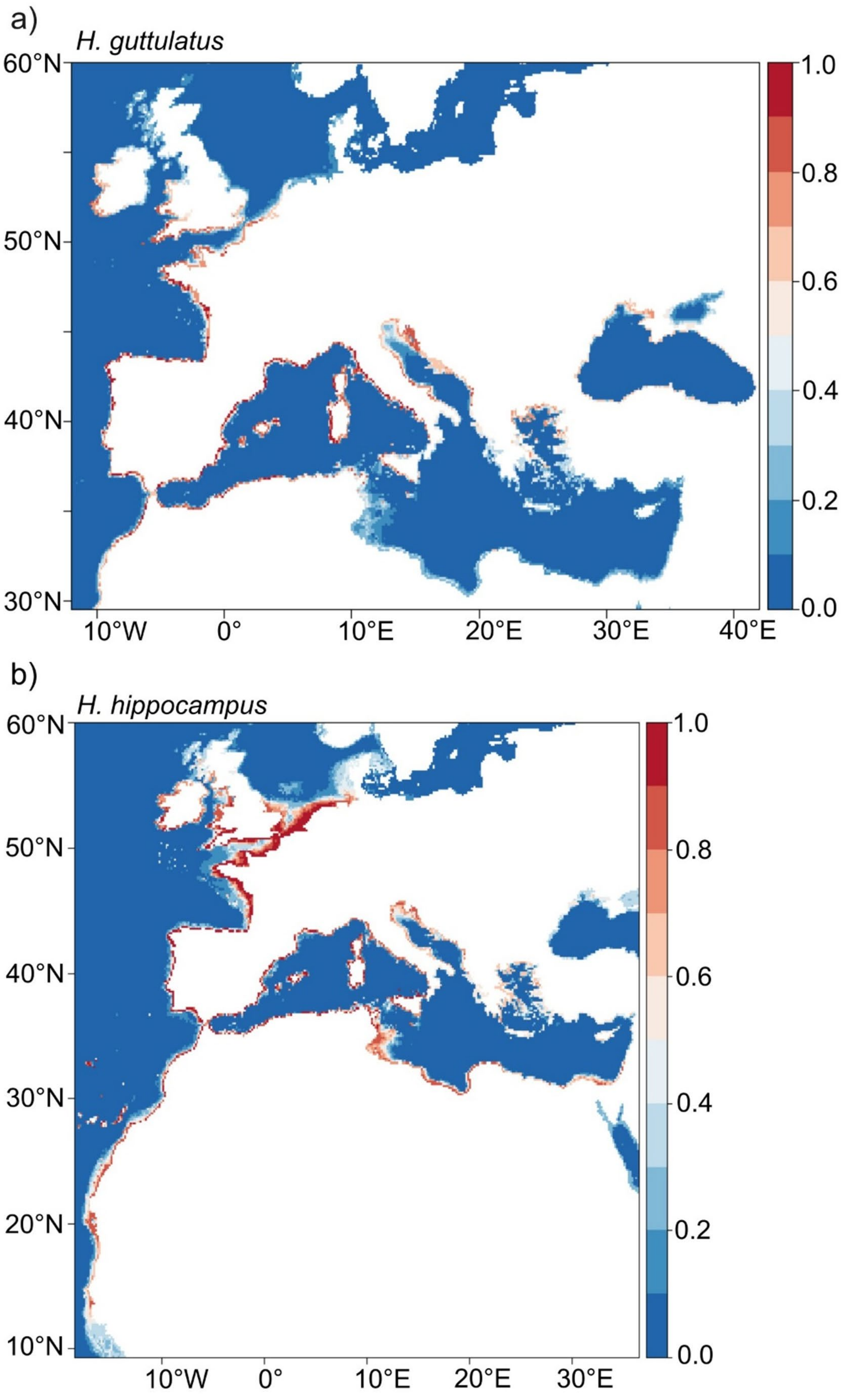

a)
H. guttulatus
60°N
50°N
40°N
30°N
10°W
0°
10°E
20°E
30°E
40°E
1.0
0.8
0.6
0.4
0.2
0.0
b)
H. hippocampus
60°N
50°N
40°N
30°N
20°N
10°N
10°W
0°
10°E
20°E
30°E
1.0
0.8
0.6
0.4
0.2
0.0

Fig. 2 Present-day habitat suitability maps of (**a**) *Hippocampus guttulatus* and (**b**) *Hippocampus hippocampus*

Connectivity influences on the distribution of seahorses

The predictions indicated that *H. hippocampus* and *H. guttulatus* will undergo significant range shifts under future climatic conditions, which differ by region, climate scenario, and dispersal mechanism (Figs. 3 and 4, Supplementary Figs. 8, 9). Our integrative connectivity approach, projected habitat suitability losses of ~34% under SSP2 and ~54% under SSP5 for *H. guttulatus* by the end of the century (Supplementary Fig. 4). For *H. hippocampus*, habitat suitability losses are generally lower, with projections showing losses of ~13% under SSP2 and ~26% under SSP5 (Supplementary Fig. 5). On the other hand, habitat suitability gain is higher for *H. hippocampus* even for the most restricted dispersal [22% (SSP2); 34% (SSP5)] than for *H. guttulatus* [7.5% (SSP2); 8.5% (SSP5)] (Supplementary Figs. 6, 7). The difference between shorter pelagic drifting dispersal (D14) and longer passive dispersal via rafting (D100) was small (<1%) for *H. guttulatus* (Supplementary Fig. 6), whereas for *H. hippocampus*, the gain of suitable habitat differed by 2% under SPP2 and 4% under SSP5 between dispersal scenarios (Supplementary Fig. 7). Notably, oceanic connectivity and dispersal abilities limit the northward expansion of suitable habitats compared with unlimited dispersal (i.e., the standard models) (Figs. 3 and 4, Supplementary Figs. 6, 7). Overall, the native distribution range was projected to experience overall contractions of suitable habitat for *H. guttulatus* (nearly −45% under both dispersal scenarios) and expansions for *H. hippocampus* [+8% (D14 pelagic scenario) and +12% (D100 rafting scenario)] under SSP5 (Supplementary Figs. 8, 9). For both species, distribution range contractions were predicted in the Mediterranean, Iberia, and Africa, whereas expansions were predicted in the North Sea and the UK/Bay of Biscay (Figs. 3 and 4, Supplementary Figs. 8, 9). However, some of the present-day suitable areas were projected to remain suitable under future climate conditions, primarily the North Sea, the Bay of Biscay, and the northern parts of the Iberian Atlantic coast (Figs. 3 and 4). The Mediterranean Sea exhibited the most severe loss of suitable habitats under SSP5, with 80% for *H. guttulatus* and 50% for *H. hippocampus* (Supplementary Figs. 4, 5). In contrast, merely half of the suitability losses were observed under the lower emission scenario (SSP2) (Supplementary, Figs. 4, 5, 10 and 11). Severe habitat losses were also projected for the Black Sea and Iberian populations of *H. guttulatus* under SSP5(Fig. 3; Supplementary Figs. 4, 10). Furthermore, losses of suitable habitats are predicted to occur for West African populations of *H. hippocampus* (Fig. 4; Supplementary Figs. 5,11).

Discussion

Our integrated assessment of *H. guttulatus* and *H. hippocampus* distributions under two climate change scenarios raised concerns about the future sustainability of the populations in the Mediterranean, North Africa, and southwestern Iberia. The projected northward expansion and anticipated range contractions across the southern regions, coupled with the stable habitat suitability in the Celtic-Bay of Biscay area, are aligned with existing projections on the effects of climate change along European coasts (Philippart et al. 2011; Monteiro et al. 2023). Although the poleward shift is one of the most documented consequences of climate change on species distribution (Hickling et al. 2006; Hastings et al. 2020), our integrated projections inform that the dispersal mechanisms influenced by ocean currents emerge as a crucial limiting factor to range expansions, especially under the "business as usual" SPP5-8.5 scenario.

The variable importance analysis shows that temperature plays a key role in the present-day species' distribution, raising concerns about the suitability of habitats under an expected warmer ocean (Garcia-Soto et al. 2021). Indeed, our projections showed that the species will experience significant habitat losses under future conditions. However, the impact of climate change is not uniformly distributed across the native ranges of the species. Therefore, the outcomes were further divided into sub-regions aligned to previously identified population units (Woodall et al. 2011, 2015). The most affected regions in terms of habitat loss were the Mediterranean and northern Africa, where declining trends of both species were identified in the IUCN Red List assessment in the Mediterranean (Pollom 2016a, b). Our results further show that in the Mediterranean, where *H. hippocampus* and *H. guttulatus* currently coexist, the loss of suitable habitats toward the future is likely to be higher for *H. guttulatus* than for *H. hippocampus*. Among others, it was predicted that *H. guttulatus* populations in Mar Menor and Mar Piccolo will suffer from a substantial loss of suitable habitat due to climate change in the future. Seahorse density declines are often associated with illegal fishing or habitat quality depletion, caused by destructive fishing activities, dredging and pollution, whose impact have caused declines of up to 90% in populations (Harasti 2016; Pierri et al. 2021; Correia 2022; Vivas et al. 2024). Nonetheless, negative correlations between *H. guttulatus* densities and temperature were detected in the Ria Formosa lagoon (Correia et al. 2018) and the Mar Piccolo of Taranto (Pierri et al. 2021). Furthermore, the reasons behind some of the declines of seahorse populations across the Mediterranean Sea remain uncertain. For instance, seahorses once reported in Stagnone di Marsala (Sicily), up until about 20 years ago, have now completely disappeared from the area (Pierri et

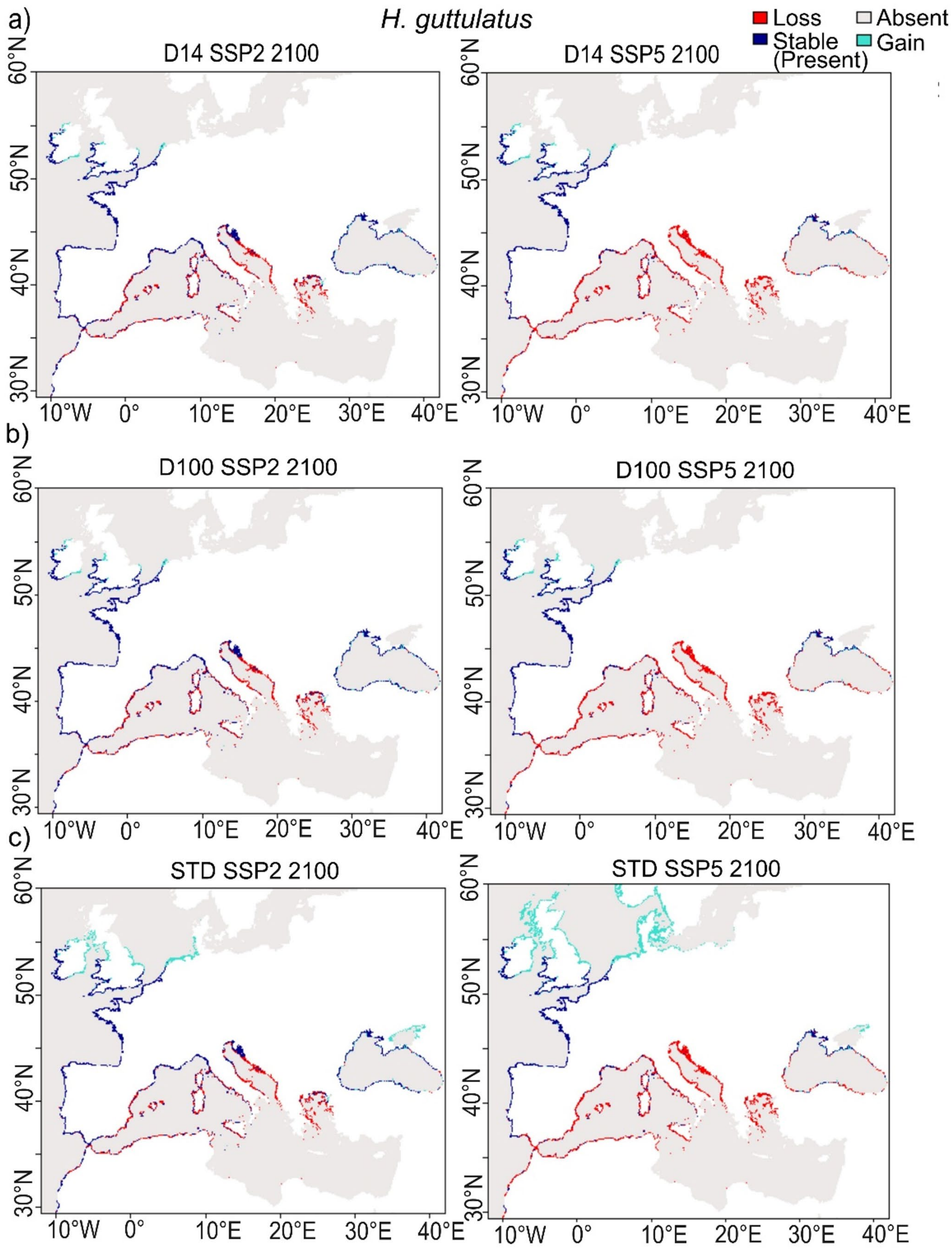
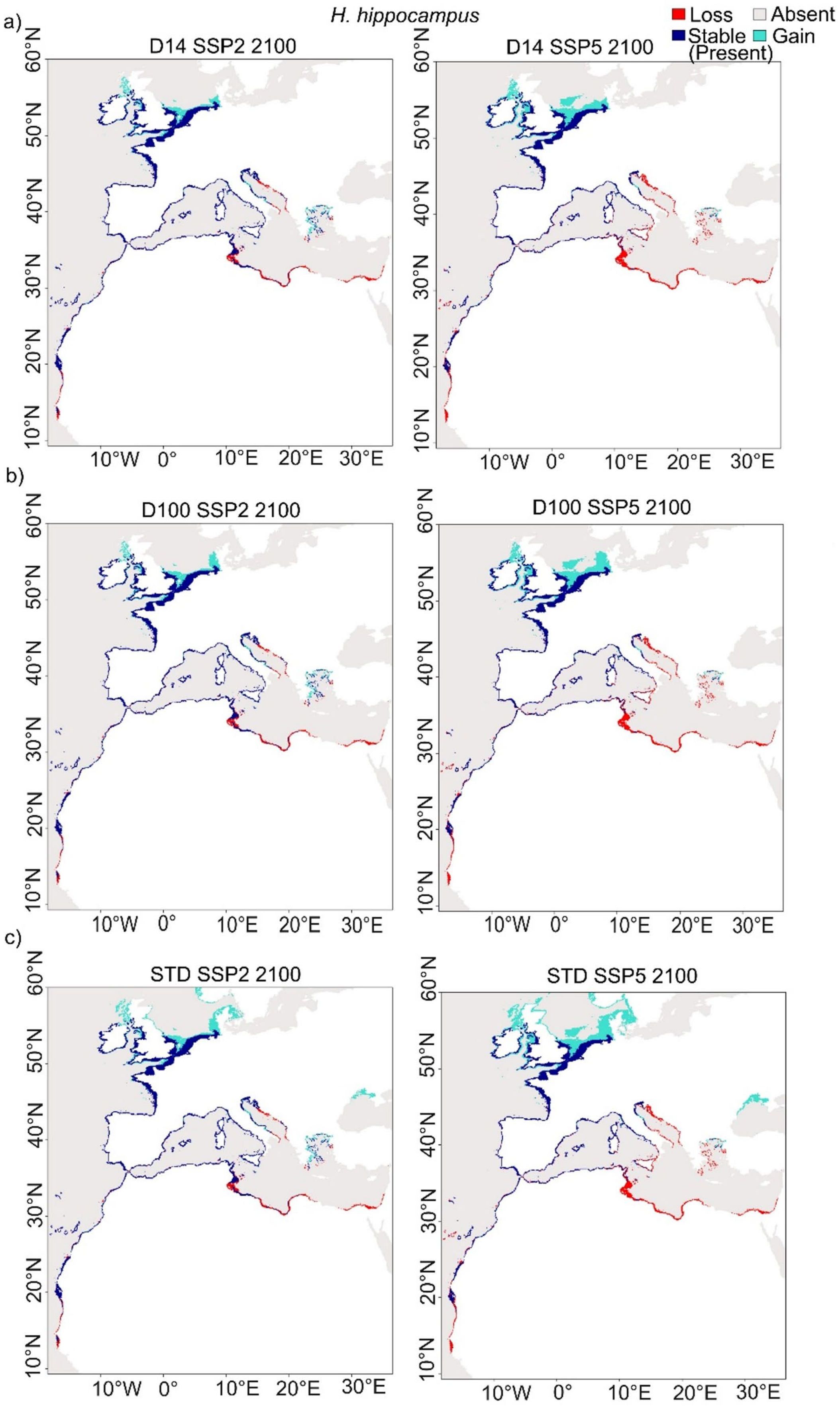

a)
H. guttulatus
Loss
Stable (Present)
Absent
Gain
D14 SSP2 2100
D14 SSP5 2100
b)
D100 SSP2 2100
D100 SSP5 2100
c)
STD SSP2 2100
STD SSP5 2100
60°N
50°N
40°N
30°N
10°W
0°
10°E
20°E
30°E
40°E

Fig. 3 Predicted gains (turquoise), losses (red), and stability (blue) of suitable habitat of *Hippocampus guttulatus* for (**a**) 14 days of pelagic drifting dispersal ("D14") (**b**) 100 days of passive dispersal via rafting ("D100") and (**c**) unlimited dispersal ("STD" - standard model) for SSP2 and SSP5 future climate scenarios until the year 2100. Grey represents the area where species were predicted to be absent in the present and future, while blue represents the area where species were predicted to be present in the present and future

al. 2022a). In the case of *H. hippocampus*, critical habitat losses are projected along the southern coastline of the Mediterranean, the coasts of Mauretania, Senegal, the Gambia, Guinea, and, to a lesser extent, the Canary Islands. Apart from climate change, West African populations of *H. hippocampus* and *H. algiricus* are threatened by illegal capture and trade for the Asian market (Cisneros-Montemayor et al. 2016; Foster et al. 2016). Based on genetic analysis, these populations of *H. hippocampus* are separated from those inhabiting the Mediterranean, Atlantic European coasts, and Macaronesia (Woodall et al. 2011). *H. hippocampus* used to be the only seahorse species reported in the Canary Islands (López et al. 2010; Lourie et al. 2016); however, recently, *H. algiricus* has been recorded at Gran Canaria, evidencing a northward expansion and a potential risk of hybridisation with *H. hippocampus* (Otero-Ferrer et al. 2015). Another case of interspecific interaction or hybridisation could occur in the Azores between the native *H. hippocampus* and the lined seahorse *H. erectus*, which likely reached the Azores via rafting (Woodall et al. 2011). According to the model results, the Iberian coast will remain stable and lose less than 10% of its suitable habitat under almost all scenarios because it is an upwelling centre that works as a refugia against warming sea temperatures (Lourenço et al. 2016). However, under the high emission scenario (SSP5), suitable habitats for *H. guttulatus* may decrease drastically (−30%) until the end of the century. This prompt decrease might be due to its preference for coastal lagoons and estuaries in this region (Pierri et al. 2022b), which tend to heat faster (Rodrigues et al. 2021). The contraction mostly affects the southern Portuguese and Spanish coasts, which harbour one of the largest populations of seahorses in Europe (Correia 2022). Thus, in the high-emission scenario, the Iberian region would lose the potential to become a climate refuge and corridor for the movement of Mediterranean population, should range shifts occur. In addition, a 40% decrease under the high-emission scenario was projected for *H. guttulatus* in the Black Sea. In contrast, under the low-emission scenario, the decrease may be smaller (3%). The habitat loss in this region can be attributed to its shallowness and the high stratification of the Black Sea, which results in rapid temperature increases and subsequent declines in oxygen levels (Capet et al. 2016; Sakalli et al. 2018; Korotaev et al. 2024). In the Mediterranean, the coastline of southern France and the northern Adriatic can hold suitable habitats and serve as refugia for *H. guttulatus* under lower emission scenarios, such as those recently detected by (Monteiro et al. 2023). On the other hand, the species is likely to disappear under the higher emission scenarios. The Thau Lagoon, in southern France, hosts one of the largest populations of *H. guttulatus*, which is considered an Evolutionarily Significant Unit (ESU) only found in Mediterranean lagoons (Riquet et al. 2019). This finding hints at the limited dispersal potential of this species in the region. If those regions become increasingly unsuitable, *H. guttulatus* will face limited opportunities for dispersal, significantly increasing the risk of substantial population declines. In the case of *H. hippocampus*, a lower emission scenario can halve the losses in the Mediterranean, especially in the Adriatic and Aegean Seas, where the presence of *H. hippocampus* is higher than that of *H. guttulatus* (Correia et al. 2020).

Several future climate projections predict the emergence of suitable habitats for Northeast Atlantic fish extending toward the North Pole (Philippart et al. 2011; Monteiro et al. 2023). Our models indicate that under restricted dispersal, *H. hippocampus* could gain up to 34% in suitable habitat by the end of the century, whereas gains for *H. guttulatus* remain below 9%. For both species, most of these shifts are concentrated in the northernmost parts of their native ranges (UK and Central North Sea). Under unlimited dispersal, gains in suitable habitats are substantially greater, reaching nearly 48% for *H. hippocampus* and 58% for *H. guttulatus*, and extending further north and toward Norway. Both approaches align with recent findings documenting an increasing presence of species with southern biogeographic affinities in the North Sea (Beare et al. 2004; Hiddink and ter Hofstede 2008). However, the contrasting results between dispersal scenarios highlight the importance of including dispersal into species distribution models, as it allows for a more mechanistic understanding of the constraints species face when shifting their ranges. While models assuming unlimited dispersal predict broad northward expansions, integrating dispersal limitations may reveal more realistic, spatially constrained outcomes.To date, the two seahorse species have been reported along the coasts of Belgium (Vandendriessche et al. 2005), the Netherlands (Nijssen and De Groot 1974), the south-western coasts of the UK and Ireland, and the English Channel (Garrick-Maidment and Newman 2011). Between 2001 and 2007, the first records of *H. hippocampus* in the Central North Sea (Dogger Bank) were recorded in the summer (Pinnegar et al. 2008). In 2023, dead individuals of *H. hippocampus* and *H. guttulatus* were recorded in Denmark (iNaturalist 2024), while in the same year, a seahorse was found alive in southern Sweden, which was assumed to be an *H. hippocampus* (https://www.gu.se/en/news/first-discovery-of-a-seahorse-in-sweden). However, it remains questionable whether these findings


H. hippocampus
🟥 Loss
▢ Absent
🟦 Stable (Present)
🟩 Gain
a)
D14 SSP2 2100
D14 SSP5 2100
b)
D100 SSP2 2100
D100 SSP5 2100
c)
STD SSP2 2100
STD SSP5 2100
60°N
50°N
40°N
30°N
20°N
10°N
10°W
0°
10°E
20°E
30°E

◀ **Fig. 4** Predicted gains (turquoise), losses (red), and stability (blue) of suitable habitat of *Hippocampus hippocampus* for (**a**) 14 days of pelagic drifting dispersal ("D14") (**b**) 100 days of passive dispersal via rafting ("D100") and (**c**) unlimited dispersal ("STD" - standard model) for SSP2 and SSP5 future climate scenarios until the year 2100. Grey represents the area where species were predicted to be absent in the present and future, while blue represents the area where species were predicted to be present in the present and future

point to viable seahorse populations or if they were isolated arrivals of drifted specimens. Moreover, it remains unclear if the reported increase in the occurrence of *H. hippocampus* in the North Sea is a result of ocean warming or changes in the Gulf Stream (Stebbing et al. 2002) or due to increased awareness and sampling efforts (Garrick-Maidment and Newman 2011).

Seahorses have small home ranges (Foster and Vincent 2004); thus, their potential for range expansions largely depends on passive dispersal, which is shaped by oceanographic connectivity (Boehm et al. 2013). There is a gap in knowledge about the extent to which pelagic juveniles contribute to the long-distance dispersal of seahorses; however, juveniles have been occasionally found drifting freely or attached to rafts (Vandendriessche et al. 2005; Luzzatto et al. 2013) whereas molecular evidences show that adults and subadults can raft for long distances hooked onto clumps of mobile macroalgae or debris (Teske et al. 2007). Thus, passive dispersal via rafting of a small number of individuals could lead to the foundation of new populations and could be a means of range expansion over longer distances (Teske et al. 2007; Boehm et al. 2013). Sporadic dispersal events could also explain the connection between the populations of *H. hippocampus* from Madeira, the Azores, and the Canary Islands (Otero-Ferrer et al. 2017). However, in some cases, sporadic dispersal may be limited by barriers or be insufficient to sustain genetic connectivity (Teske et al. 2007; Boehm et al. 2013). In this study, incorporating both dispersal and ocean connectivity limited the expansion of the distribution range, resulting in an overall loss of suitable habitat range for *H. guttulatus*. Habitat preferences for shallow coastal habitats may influence dispersal capabilities and restrict colonisation of new habitats, as was found for two seahorses in Southeast Asia (Lourie et al. 2005). Comparably, the preference of *H. guttulatus* for shallow inshore waters and coastal lagoons (Pierri et al. 2022b; Peiffer et al. 2024) might explain the reduced dispersal potential compared to *H. hippocampus*, which has been captured on offshore sandbanks and in deeper waters (Pinnegar et al. 2008; Garrick-Maidment and Newman 2011). Sheltered bay habitats are often disjoint, resulting in limited dispersal and population mixing, which is particularly concerning for *H. guttulatus* (Woodall et al. 2015). Species with restricted dispersal ability tend to form isolated populations, which limits the potential of connectivity between populations and can hinder the colonisation of new suitable areas (Lourie et al. 2005). Furthermore, pelagic juveniles of sedentary coastal fish (rocky reefs and estuaries) use a retention mechanism to maximise local recruitment close to the sheltered inshore habitats (Borges et al. 2007). Based on this knowledge of larval ecology in sedentary coastal fish species and their traits (i.e. parental care, number of offspring, low swimming ability, growth rate, and habitat specificity), seahorses are expected to show similar patterns. For instance, juveniles of *H. guttulatus* in the Ria Aveiro (Portugal) and of *H. patagonicus* in San Antonio Bay (Patagonia) were collected at the surface during high tides, and near the bottom during ebb tides, which suggests that juveniles undergo vertical migrations to be retained in estuaries and lagoons (Pires 2010; Luzzatto et al. 2013). This retention mechanism limits the pelagic dispersal of juveniles and might explain why *H. guttulatus* (and to some extent *H. hippocampus*) are mainly found in enclosed bays in the Atlantic (Pierri et al. 2022b). However, due to the coarse resolution of the climate projections, our models fail to capture near-shore processes. Therefore, finer-scale nearshore climate models are urged to improve model outcomes and to confirm this theory.

According to the IUCN assessment, the resident extent of *H. hippocampus* does not encompass the Black Sea (Woodall et al. 2011; Woodall 2017); however, some studies have reported the capture of *H. hippocampus* in the Eastern Black Sea (Uncumusaoğlu et al. 2012; Başusta et al. 2014; Taylan et al. 2020). Historically, the presence of *H. hippocampus* was reported in the Romanian Black Sea waters; however, in recent works, only *H. guttulatus* has been reported (Nenciu et al. 2018). Our predictive models with unlimited dispersal suggest increased habitat suitability for *H. hippocampus* in the northern Black Sea, whereas the model with restricted dispersal showed no response. Possibly, *H. hippocampus* has entered the Black Sea via passive dispersal on many occasions; however, it struggles to maintain a viable population, possibly due to the Bosporus Strait, which can act as a barrier to dispersal (Debes et al. 2008; Durand et al. 2013). This uncertainty about the *H. hippocampus* population in the Black Sea highlights a knowledge gap in the dispersal of this species.

The cumulative impacts of multiple stressors and high uncertainty in how the species will respond challenge the accurate assessment of climate change risk and the development of conservation planning (Pearce and Selley 2024). Marine protected area networks can mitigate the adverse effects of climate change and promote the stability of fish communities (Benedetti-Cecchi et al. 2024). However, the current MPA network throughout Europe provides minimal protection, e.g., allowing destructive fishing practices, dredging and anchoring (Assis et al. 2021; Monteiro et al. 2023; Aminian-Biquet et al. 2024; Bosso et al. 2024; Peiffer et al. 2024). For seahorses, marine protected areas are not always beneficial, as they can lead to increased predator biomass (Harasti et al. 2014), while other threats, such as pollution, persist outside the MPA and continue to impact habitat quality (Yasué et al. 2012). Thus, addressing local stressors (e.g., pollution, anchoring), restoring habitat or creating artificial habitat (Correia et al. 2013; Simpson et al. 2020), and limiting non-selective and illegal fishing practices in the area (Curtis et al. 2007) can be relevant protection measures. In the face of climate-induced range shifts, it is crucial to increase protection measures in climate refugia and establish a network of protected sites to enhance resilience and maintain gene flow between seahorse populations (Planes et al. 2009; Ashcroft 2010; Warren et al. 2013; Wilson et al. 2020). Additional measures, such as translocating individuals or introducing captive-bred individuals to suitable habitat areas, could enhance conservation efforts if other main threats have been resolved and habitat requirements have been fulfilled (Caldwell and Vincent 2012a; Harasti et al. 2022). Seahorses are an important umbrella and flagship species; thus, implementing adequate conservation strategies would certainly resonate with other species and ecosystems of conservation concern (Pollom et al. 2021).

In conclusion, our study revealed that seahorse populations tend to be displaced from south to north following a global trend, implying the reduction of suitable habitat in their southern range border and the potential colonisation of new territories in the north. On the other hand, it was found that the northward expansion can be limited by dispersal ability and oceanographic connectivity, resulting in overall range contractions for *H. guttulatus* and limited range expansions for *H. hippocampus*. Despite that, both species are likely to experience losses in suitable habitat along their southernmost distribution range. Nevertheless, the model is relatively optimistic regarding dispersal mechanisms, as it assumes annual dispersal and that individuals reaching a certain point can disperse again in the following year. This underscores the need for further investigation on dispersal mechanisms and connectivity in different life stages to propose more robust measures related to spatial planning for seahorse conservation. Special attention should be paid to climate refugia for isolated *H. guttulatus* populations in the Mediterranean (Thau Lagoon, Mar Menor) and the Black Sea. Regular monitoring of populations, identification of dispersal mechanisms, and efforts to mitigate stressors in target areas, including those pointed out as potential climate refugia, will be crucial to alleviate the impacts of climate change on seahorses.

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Author contributions FP, ARAL, SH, GJFS and EJG contributed to the study conception and design. Data was collected by all authors. Data analysis was performed by FP, ARAL and JA. The original draft of the manuscript was written by FP, and all authors reviewed and edited previous versions of the manuscript. Funding acquisition, resources and supervision were facilitated by GJFS and EJG.

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Data availability The datasets generated during and/or analysed during the current study are not publicly available due to sensitive data on endangered species but are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial interests to disclose. However, we would like to declare that one co-author of this manuscript, Dr. Filipe Martinho, is an Associate Editor of 'Marine Biology'.

Ethical approval This is a computer modelling study and no humans or animals were handled. No ethical approval is required.

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