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Future distribution of demersal species in a warming Mediterranean sub-basin

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Predicting range shifts of marine species under different CO2 emission scenarios is of paramount importance to understand spatial potential changes in a context of climate change and to ensure appropriate management, in particular in areas where resources are critical to fisheries. Important tools which use environmental variables to infer range limits and species habitat suitability are the species distribution models or SDMs. In this work, we develop an ensemble species distribution model (e-SDM) to assess past, present and future distributions under Representative Concentration Pathway (RCP) 8.5 of nine demersal species and hotspot areas for their two life stages (adult and juvenile) in the Adriatic and Western Ionian Seas in four time windows (1999-2003, 2014-2018, 2031-2035 and 2046-2050). The e-SDM has been developed using three different models (and sub-models), i.e. (i) generalized additive models (GAM), (ii) generalized linear mixed model (GLMM), (iii) gradient boosting machine (GBM), through the combination of density data in terms of numbers of individuals km^2 and environmental variables. Then, we have determined the changes in the aggregation hotspots and distributions. Finally, we assess gains and losses areas (i.e. occupation area) in the future climate change scenario as new potential range shifts for the nine species and their life stages. The results show that densities of some key commercial species, such as *Merluccius merluccius* (European hake), *Mullus barbatus* (red mullet), and *Lophius budegassa* (anglerfish) will be shifting northwards.

KEYWORDS

marine species distribution, ensemble model, climate change, fisheries management, Adriatic and Ionian Seas

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1 Introduction

Ocean is warming and observations confirm that sea temperature accelerated rapidly in recent decades (Cheng et al., 2019; IPCC, 2022). Temperature increase and consequential oceanographic changes are impacting marine life in several ways, including massive displacement of species from their historical areas (Kleisner et al., 2016; Baudron et al., 2020). The poleward shift of the marine species, for instance, is among the cause of current changes in the regional biodiversity (Román-Palacios and Wiens, 2020).

Such shifts in distribution also affect commercially exploited species, whose displacement may cause changes in fishing grounds that can result in social and economic costs and further complicate fisheries management (Olafsdottir et al., 2019). Assessing the vulnerability and geographical changes of different exploited resources is essential for management plans and sustainable resource use (Hidalgo et al., 2022). In particular, understanding future changes in the spatial distribution of marine species helps to define strategies to cope with seemingly inevitable changes and to prepare adaptive solutions in fisheries management (Bahri et al., 2021). In this context, semi-enclosed basins such as the Mediterranean Sea are particularly vulnerable to climate change (MedECC, 2020; IPCC, 2022) where reduced migration opportunities for certain species are exacerbating competitions and local extinction can be induced by climate change (Hoegh-Guldberg et al., 2014).

The Mediterranean Sea is a biodiversity hotspot with more than 650 fish species (Coll et al., 2010), and the impacts of climate change are already substantial (Darmaraki et al., 2019), leading for example to significant changes in population dynamics (Moullec et al., 2016), loss of genes (Chefaoui et al., 2018), and invasion of species (Azzurro et al., 2019).

Climate projections for the Mediterranean basin show an overall warming of seawater along with general acidification, oxygen depletion, and a decrease in plankton biomasses and nutrients in the water column (Soto-Navarro et al., 2020; Reale et al., 2022; Solidoro et al., 2022). In addition, increases in the frequency and intensity of marine heat waves (Frölicher and Laufkötter, 2018; Darmaraki et al., 2019) are impacting the marine ecosystem and biodiversity (Smale et al., 2019; Dayan et al., 2023). The modification of species ranges in the Mediterranean sea is already occurring (Baudron et al., 2020) with significant effects on the economies and communities of all countries surrounding the basin (Blasiak et al., 2017; FAO, 2022; Farahmand et al., 2023). Although, the fisheries economic sectors in the developing countries in the southern part of the basin might appear more vulnerable (Pita et al, 2021), it is expected that larger potential socio-economic impacts will also affect the northern part of the basin, where fisheries capacities, infrastructure and economies are well established (FAO, 2023).

In particular, the Adriatic and Ionian region (Figure 1), is important for fisheries in Mediterranean sea and climate change is expected to bring significant oceanographic and biological changes in both basins, such as an increasing northward shift of thermophilic species (Dulčić and Grbec, 2000; Dulčić et al., 2011) as well as the rarefaction or disappearance of cold-water species especially in the Adriatic (Boero and Bonsdorff, 2007; Templado, 2014), whose further northward migration of the species is prevented due to its dead-end nature (Ben Rais Lasram et al., 2010). Future climate change would favor an increase in invasive species such as *Siganus luridus* or *Lagocephalus sceleratus* (Carbonara et al., 2017; D'Amen and Azzurro, 2020) in these two sub-basins, that could dramatically affect the dynamics of the local food web (Occhipinti-Ambrogi, 2007) and eventually promote a further displacement of resident species.

Intensive commercial fishing in the Adriatic and Western Ionian Sea, has led to the overfishing of stocks such as *Merluccius merluccius* (European hake) and *Parapenaues longirostris* (deep-water rose shrimp), while the situation is fairly better for other stocks such as *Nephrops norvegicus* (Norway lobster), *Mullus barbatus* (red mullet) and *Sole solea* (common sole) (GFCM-FAO, 2018a, b; Russo et al., 2019; GFCM-FAO, 2021a, b). Thanks to important management efforts, however, the status of the fisheries resources in the region is currently improving (FAO, 2023). These efforts are based on a Multi Annual Management Plan (MAP; GFCM-FAO, 2019; GFCM-FAO, 2022a, b) that include temporal or spatial closures (Scarcella et al., 2014; Bellido et al., 2020), such as the Fisheries Restricted Area (hereafter FRA) (Cardinale et al., 2017), in the Pomo/Jabuka Pit and Bari Canyon (GFCM-FAO, 2017).

While temporal and spatial closure of demersal fisheries had been key for improving the sustainable exploitation of commercial species in the area, maintaining their efficacy also under climatic-induced modifications is critical (FAO, 2022). In general, predicting future spatial shift of commercial species could help to optimize spatial fisheries management tools (Pinsky et al., 2013; Melo-Merino et al., 2020).

However, the dynamic distribution of marine species is the result of a complex set of interconnected factors that might be difficult to be considered explicitly (Nagelkerken and Munday, 2016). Such factors include for example physiological responses, behavior, feeding and habitat preferences, as well as avoidance of disturbances and predators that might be implicitly considered using statistical approaches. Species distribution models (SDMs) are correlative empirical approaches that can be trained over past data integrating species density (number of individuals per unit of surface) and oceanographic variables and than used to predict species distributions in response to climatic oceanographic changes (e.g. Kearney and Porter, 2009). SDMs relate occurrence (presence/absence) or biomass/density data to environmental variables (Thorson et al., 2015; Lauria et al., 2017; Brodie et al., 2020) and are used to extrapolate future distribution considering different species-specific scenarios (e.g. Robinson et al., 2017; Moullec et al., 2019).

The objective of the study is to explore the potential displacement of the main commercial species in the Adriatic and Ionian Sea in two future time windows, namely 2035 and 2050. The study implements an ensemble of species distribution models (hereafter e-SDM) developed previously (Panzeri et al., 2023) to derive the best estimate of future distributions and hotspot for 9 demersal of commercial interest species on the basis of essential

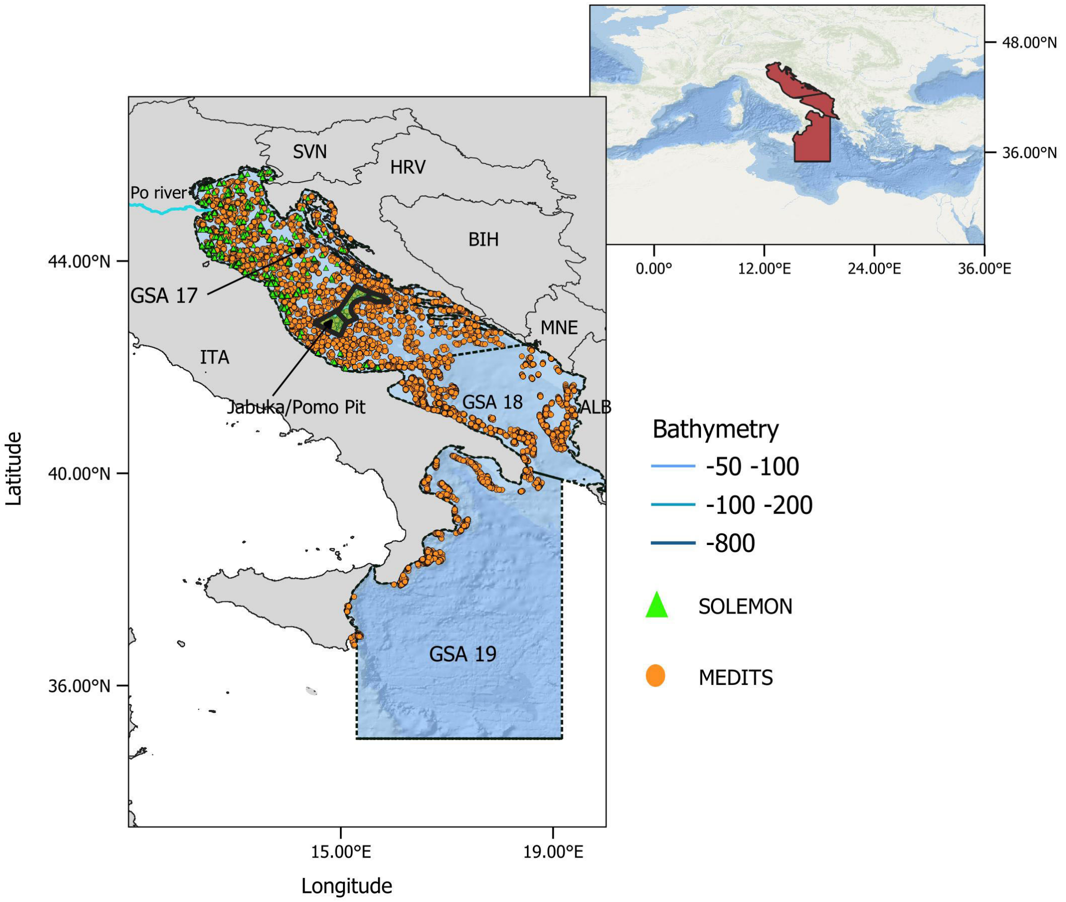

FIGURE 1
Map of the study area, northern and central Mediterranean (red area, in box at top right). The Adriatic and western Ionian Seas (focal area) comprise GSA 17-18-19 (delineated by black dashed lines) with bathymetric layers down to 1000 m depth (see legend). The orange dots show the position of MEDITS hauls during 1999-2018, and the green triangles show the position of SOLEMON hauls during 2005-2018. ITA, Italy; SVN, Slovenia; HRV, Croatia; BIH, Bosnia-Herzegovina; MNE, Montenegro; ALB, Albania. Jabuka/Pomo Pit Fisheries Restricted Area (FRA) is shown in the center of the basin (green area).

ocean variables (EOVs) derived from a physical-biogeochemical 3D model under emission scenario RCP 8.5.

The work aims at identifying future regional anomalies in species distribution to assess changes in future fishing opportunities in the basin. Furthermore, by identifying future changes in the hot spots of aggregation for juvenile and adults of the 9 demersal species the work set the basis for understanding efficacy of current spatial management areas and indications for future plans.

2 Material & methods

2.1 Study area

FAO-GFCM (General Fisheries Commission for the Mediterranean) designates the northern, southern Adriatic Sea, and the Ionian Sea as Geographical Subareas (GSA) 17, 18, and 19, respectively (Figure 1).

The northern Adriatic Sea (GSA 17) is a relatively shallow basin (maximum depth 273m), where the general circulation is driven by runoff and wind stress (Giani et al., 2012). The southern Adriatic Sea (SAS, GSA 18; Figure 1) is characterized by complex topography with steep continental slopes reaching depth of 1250 m, and the presence of muddy bottoms, relict sands, rocky bottoms (Alfirević, 1981), canyons and cold-water coral mega habitats (D'Onghia et al., 2012; Carbonara et al., 2020). In the central of GSA 17 there is a deep depression called Jabuka-Pomo Pit area (depth 200-260m), which is subject to restrictions and recommendations for fishing (GFCM-FAO, 2017).

The Adriatic Sea is heavily impacted by fisheries, with trawlers and beam trawls (Colloca et al., 2013, 2017). In the Jabuka-Pomo Pit area, the situation has evolved positively since 2017, but several demersal species such as European hake (*Merluccius merluccius*) and Norway lobster (*Nephrops norvegicus*) are still overfished (FAO, 2023).

2.2 Input data

2.2.1 Trawl survey data

Sampling data for 1999-2018 are based on the MEDITS dataset (Mediterranean International Trawl Survey; Spedicato et al., 2019), based on averages 326 sampling sites per year in the three GSAs and bathymetric range between 10 and 800 m, and SOLEMON (Sole Monitoring; Scarcella et al., 2011; Grati et al., 2013), based on average of 70 sampling sites per year in GSA 17 from 2005 to 2018, and bathymetric range between 10 and 100 m.

Density indices per haul for demersal species (number of individuals per km^{-2}, hereafter N/km^{2}) were retrieved from the MEDITS dataset for four bony fish species: (i) European hake (*Merluccius merluccius*), (ii) red mullet (*Mullus barbatus*), (iii) anglerfish (*Lophius budegassa*), (iv) European horse mackerel (*Trachurus trachurus*). In addition, one crustacean species (v), Norway lobster (*Nephrops norvegicus*), and one cephalopod (vi), broadtail shortfin squid (*Illex coindetii*), were included.

From the SOLEMON dataset, one fish, one crustacean, and one cephalopod species were included: (i) common sole (*Solea solea*), (ii) mantis shrimp (*Squilla mantis*), and (iii) cuttlefish (*Sepia officinalis*) respectively.

These 9 species are among the most important commercially exploited by otter and beam trawl in the Adriatic and western Ionian Seas (UNEP-MAP-RAC/SPA, 2015; FAO, 2022) and account for ~60% of the total demersal fish landings of the Adriatic and Ionian Sea.

We then subdivided the data into two classes, namely adults and juveniles fishes, based on a species-specific size threshold (total length) of 24 cm, 9 cm, 33 cm, 14 cm, and 19 cm for European hake, red mullet, anglerfish, European horse mackerel, and sole, respectively; the carapace length thresholds were 2.5 cm for Norway lobster and mantis shrimp and 15 cm and 10 cm for broadtail shortfin squid and cuttlefish, respectively (Supplementary Table S2).

2.2.2 Temporal evolution of thermohaline and biogeochemical properties in the Adriatic and Ionian Sea

Marine physical and biogeochemical data for the Adriatic and Ionian Sea have been extracted from the reanalysis and climate projections data available for the Mediterranean region that have been produced using the OGSTM-BFM modelling system (Lazzari et al., 2012, 2016). Past physical and biogeochemical data are from reanalysis datasets, available from the Copernicus Marine Service (CMS, https://marine.copernicus.eu/), covering the period 1999-2019 with a spatial resolution of 1/16° and 72 unevenly vertical levels (Simoncelli et al., 2019; Teruzzi et al., 2019). On the other hand, physical and biogeochemical projections under emission scenario RCP8.5 cover the period 2005-2100 with a spatial resolution of 1/16° and 70 unevenly vertical levels (Reale et al., 2022; available at https://dds.cmcc.it/, last access 21/06/2023).

The reanalysis datasets have been used to provide an estimation of thermohaline and biogeochemical properties of the domain under investigation in two 5-year time windows: (i) 1999-2003 (hereafter "past") and (ii) 2014-2018 (hereafter "present"). The climate projections have been used to provide an assessment of the same variables under the RCP8.5 emission scenario in two future time windows: (iii) 2031-2035 (hereafter '2035') and (iv) 2046-2050 (hereafter '2050'). Although being built with the same modelling system, the two datasets have been produced by using different numerical setups and boundary conditions and some adjustments for accounting of model spurious trends in the climate projections has been done (see Reale et al., 2022).

The explanatory variables i.e. both geoposition (in UTM, northing and easting, hereafter Y.utm and X.utm respectively) and Essential Oceanographic variables, were preliminarily selected using the VIF approach (Variance Inflation Factor; Sheather, 2009) with a threshold of VIF< 5 (Supplementary Table S3) to avoid collinearity (Sion et al., 2019). The Essential Ocean Variables (EOVs) considered in this work were: average salinity in the water column (hereafter 'sal'), bottom temperature (hereafter 'TMP_bot', °C), average nitrate (hereafter 'nit') and phosphate (hereafter 'pho') concentrations in the water column (mmol m-3), and particulate organic carbon at the bottom (hereafter 'poc', mg m-3).

Furthermore, the granulometry (hereafter 'grain') variable with the 1/16° of resolution was only available for the northern Adriatic (GSA 17) trough SOLEMON survey. For this reason, it was used only for species living in close contact with benthic sediment, within the bathymetric range 10-100 and recorded by SOLEMON sampling (Scarcella et al., 2011). In addition, we also assessed the correlation between the variables using Pearson's test (Supplementary Figure S1).

These variables were selected because of their known relevance to the selected demersal species for their general ecological importance (Carlucci et al., 2018; Bitetto et al., 2019; Panzeri et al., 2023), their effects on physiological processes (e.g., 'TMP_bot'), their use as proxies for favorable coastal conditions for juvenile fish (e.g., 'nit', 'pho'), and for feeding areas also for adult fish ('poc').

2.3 The species distribution models

We implemented an ensemble of species distribution models (e-SDM) that combine multiple individuals model to create a single model result (Nisbet et al. (2009). The individual model used are:

1) Delta - Generalized Additive Models (hereafter 'D-GAM') (Hastie and Tibshirani, 1986);
2) Delta - Generalized Linear Mixed Model with sdmTMB (hereafter 'D-GLMM', Anderson et al., 2022);
3) GAM with Tweedie family distribution with log link function (hereafter 'TW-GAM'; see *mgcv* R package, Wood, 2017).
4) Generalized Boosted Regression Model (hereafter 'GBM'; Schapire, 2003).

For 1) and 2), a delta model (Cragg, 1971; Maunder and Punt, 2004) was implemented in two steps: i) a binomial occurrence model that fits presence/absence data (logit link function of the binomial family error distribution), ii) a Gaussian distribution model with log link function fits the density presence-only data for D-GAM (Grüss et al., 2014; Lauria et al., 2017), and a Gamma function with log link that fits the density presence-only data for D-GLMM. The final spatial distribution of species abundances (N/

km^2) is obtained by multiplying the binomial models and the distribution model predictions in each grid point of the domain (Grüss et al., 2014; Lauria et al., 2017).

For all GAM models (1 & 3), we chose a knot number of 5 for all covariates except coordinates, after trying different knot combinations for determining the best significance and variance, but also relying on literature references (Wood, 2001; Nie and Racine, 2012) and the ecological sense of splines. The final formula of variables used for each model can be found in Supplementary Table S4 (knots are implicit, Supplementary Material).

Finally, for 4) we used 5000 trees with a shrinkage of 0.01 (gbm package R, https://github.com/gbm-developers/gbm, Greenwell et al., 2022).

For each species and type of model (D-GAM, TW-GAM, D-GLMM, and GBM), a stepwise approach was used. The approach consisted of increasing the number of explanatory variables by successively adding to the simplest model (given by the minimum spatiotemporal explanatory variables) those with higher F-statistics until the model with all explanatory variables was reached. This approach led to a series of models with different combinations of explanatory variables to obtain the response variable (N/km^2 or presence/absence).

Each model was subjected to a k-fold cross validation process; thus it was fitted on a spatial training dataset made by randomly choosing 70% of the data. The remaining 30% of records were used for testing the best-fitting of the model (Panzeri et al., 2021a, 2023). The training and testing were repeated using 5 spatial folds each selecting randomly without replacement data from squared blocks using the BlockCV package (Valavi et al., 2019; Panzeri et al., 2021a, 2023). Blocks were defined having side of approximately 36 km, equal to 6 cells of the 1/16° grid, as the best solution to reduce autocorrelation of the data and assure good spatial coverage (function *cv_block_size*, Valavi et al., 2019).

The best model was then selected based on metrics of model performance such as explained deviation (% ED) and prediction error (AIC, Akaike Information Criterion) of the training datasets and mean absolute error (MAE) of model predictions in the test dataset. In addition, the validation process includes a prediction of the best model on the training data set and an evaluation of the correlation with the test data using the coefficient of determination r^2 (Lewis-Beck and Lewis-Beck, 2015; Table 1). For each individual model, the best model (derived from training and test routine) was shown to be able to capture spatial patterns. Therefore, the best distribution was considered as e-SDM, i.e., the weighted average of the distributions obtained with the 4 individual models, and the r^2 (Table 1) derived from the validation process was considered as a weighting factor (Pearman et al., 2020; Panzeri et al., 2021a) as expressed in Equation 1.

We also assessed the normal distribution of the residuals derived from each fitted model with the Kolmogorov-Smirnov test (for samples of more than 5000 data) using *ks.test* (see results in Supplementary Table S5). In addition, we compared the median and standard deviation of the final prediction results of each model (including e-SDM) and observed data to evaluate the main pattern and see how each model can capture the median of the observed data (Supplementary Figure S4).

All analyses were coded with the software R (4.3.3, windows version) and the results were plotted with ggplot2 (version 3.5.0, Wickham, 2016).

2.4 Ensemble modelling

After running the best model resulting from the training and testing routine for the period (1999-2018), we used the fitted model to simulate the density of demersal species on a regular UTM grid on the basis of the temporal evolution of the environmental variables in four time windows ('past', 'present', '2035' and '2050'). To develop an e-SDM, we calculated, for each model, an average density index (N/km^2) for each time window and developed the final ensemble model by weighting the density obtained from the 4 models (Equation 1) by the corresponding r^2 (Table 1). The distribution for each species results in density maps for the 'present' period (Figure 2).

TABLE 1 Results of the r^2 from the validation process for adults and juveniles of the species studied (common name).

	Adults				Juveniles			
	D-GAM	TW-GAM	D-GLMM	GBM	D-GAM	TW-GAM	D-GLMM	GBM
European hake	0.70	0.51	0.68	0.63	0.77	0.59	0.76	0.68
red mullet	0.62	0.48	0.68	0.60	0.70	0.51	0.60	0.60
Norway lobster	0.58	0.41	0.48	0.43	0.61	0.45	0.45	0.41
anglerfish	.48	0.21	0.35	0.24	0.58	0.33	0.40	0.37
broadtail shortfin squid	0.51	0.47	0.60	0.53	0.67	0.47	0.62	0.58
European horse mackerel	0.51	0.47	0.58	0.51	0.46	0.46	0.55	0.54
cuttlefish	0.75	0.55	0.65	0.78	0.73	0.53	0.66	0.76
mantis shrimp	0.78	0.76	0.74	0.79	0.82	0.75	0.69	0.77
common sole	0.55	0.55	0.73	0.81	0.60	0.41	0.55	0.76

These values are used for the weighted e-SDM. (See 'The SDM ensemble' section in Materials and Methods). Orange indicates values below 0.5 (default values that do not represent a strong correlation), green values above 0.6 (good correlation), and yellow between 0.5 and 0.6 (moderate correlation).

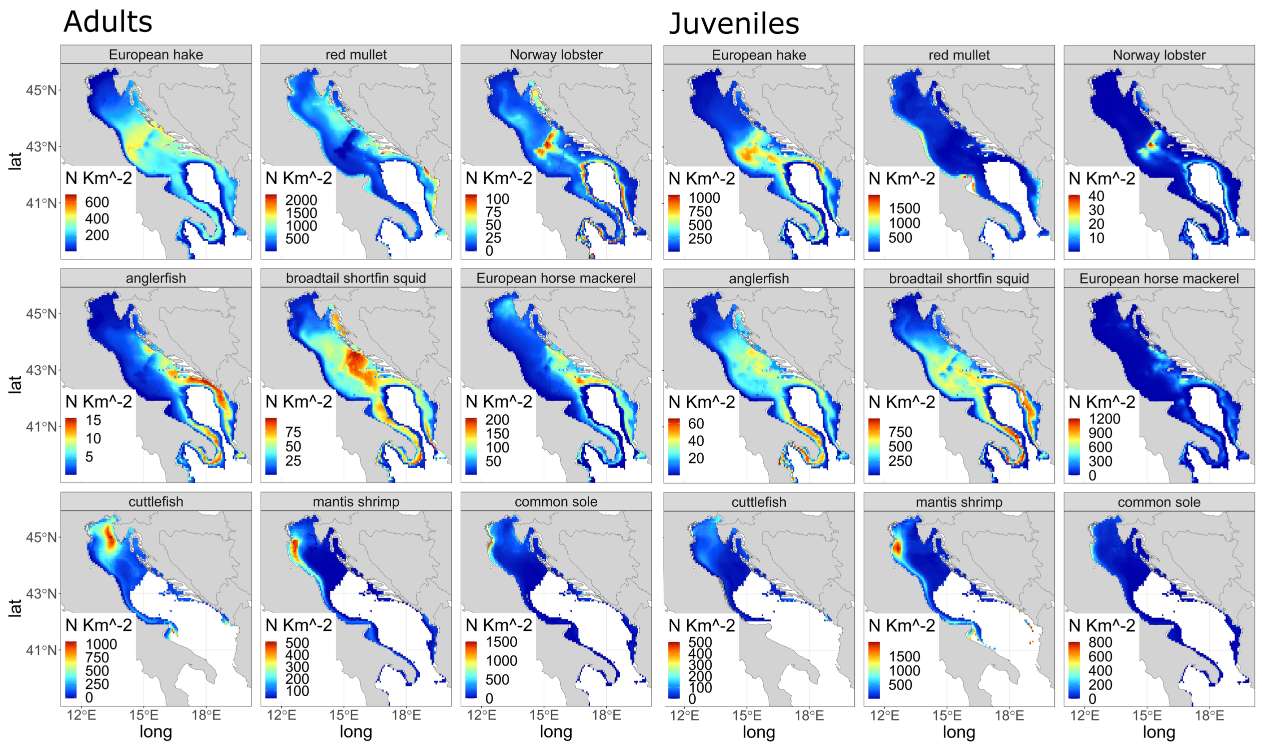

FIGURE 2
Distribution density for the “present” in N/km^2 for the species studied: adults (left panels) and juveniles (right panels).

$$d_{i,ens} = \frac{(d_{D-GAMi}* \ r^2_{D-GAM} + d_{TW-GAMi}* \ r^2_{TW-GAM} + d_{D-GLMMi}* \ r^2_{D-GLMM} + d_{GBMi}* \ r^2_{GBM})}{(r^2_{D-GAM} + +r^2_{TW-GAM} + r^2_{D-GLMM} + \ + \ r^2_{GBM})} \qquad (1)$$

In Equation 1, $d_{i,ens}$ are the density values of the e-SDM at each grid point i in the area computed as the weighted mean over the years for each time window, and r^2 is the value derived from Table 1 for each model (D-GAM, TW-GAM, D-GLMM, GBM).

We evaluated the bias (Supplementary Figure S2) between the predicted value for the period 2014-2018 and the observed survey data (2014-2018), using the following equation:

$$bias_i = \left(\frac{y_i - x_i}{x_i}\right) \qquad (2)$$

where x_i is the survey data for the period 2014-2018, and y_i is the model prediction derived from the ensemble model (Equation 1) for each haul and year *(i)* of the period 2014-2018.

2.5 Future projection

We calculated the relative anomaly density between the present period and each of the other periods (past, 2035 and 2050) as:

$$A_{w,i}(\%) = \left(\frac{d_{w\,i} - d_{present,i}}{d_{present,i}}\right) \ *100 \qquad (3)$$

Where d_i are the density values of the e-SDM at each grid point i in the area computed as the mean over the years for each window (*w= past, 2035 or 2050*), that is $d_i = \sum_{y=1}^{n} x_{i,y}\frac{1}{n}$, where n is the number of the years for each period (‘past’, ‘present’, ‘2035’ and ‘2050’) and x the density values for each year y and UTM location *(i)*.

The pairwise statistical comparison of the distribution (N/km^2) of the different scenarios (past/present, 2035/present, and 2050/present) was tested using the Mann-Whitney-Wilcoxon test ($p < 0.05$, see Table 2, Wilcoxon, 1945) to highlight the significant difference.

In addition, we applied the Getis-Ord-Gi* method (Getis and Ord, 1992, hereafter Gi*) to the density distribution to highlight the difference in hotspots between the chosen time windows (‘2035’ and ‘2050’). The Gi* statistic values are indicating where high or low density values cluster spatially. The larger the Gi*, the greater the clustering of high values (hot spot). The smaller the Gi*, the more intense the clustering of low values (cold spot).

Comparison of the areas with Gi* above the 75th percentile of the distribution (here used as a threshold for determining the hot spots areas) in the present and future (‘2050’) time window allowed to identify the potential ‘gained-lost-preserved’ areas in the basin.

3 Results

The AIC and the explained deviance of the four individual models are summarized in Supplementary Table S1 (Supplementary Material). Regarding r^2 (Table 1), on average, the delta approaches (D-GAM, D-GLMM) perform better than the others models with good explained deviation and r^2 usually higher.

Specifically, the best fits are observed for adults of European hake, mantis shrimp, cuttlefish, common sole and red mullet with

TABLE 2 Result of Mann-Whitney-Wilcoxon-test (with $p<0.05$) on density data between different scenarios: past-present, 2035 and present, and 2050 and present.

	past-present		2035-present		2050-present	
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
European hake	4.13E-07	0.16	<2.2e-16	<2.2e-16	<2.2e-16	<2.2e-16
red mullet	<2.2e-16	<2.2e-16	<2.2e-16	<2.2e-16	<2.2e-16	<2.2e-16
Norway lobster	<2.2e-16	<2.2e-16	<2.2e-16	4.70E-06	0.02	<2.2e-16
anglerfish	<2.2e-16	<2.2e-16	<2.2e-16	<2.2e-16	<2.2e-16	<2.2e-16
broadtail shortfin squid	4.00E-03	<2.2e-16	<2.2e-16	<2.2e-16	<2.2e-16	<2.2e-16
European horse mackerel	<2.2e-16	0.35	<2.2e-16	<2.2e-16	<2.2e-16	<2.2e-16
cuttlefish	0.45	0.26	<2.2e-16	<2.2e-16	<2.2e-16	<2.2e-16
mantis shrimp	<2.2e-16	<2.2e-16	<2.2e-16	<2.2e-16	<2.2e-16	<2.2e-16
common sole	<2.2e-16	1.025-05	<2.2e-16	9.07E-05	<2.2e-16	1.07E-09

The green cells indicate a significant difference; the blue cells indicate a non- significant difference.

D-GLMM (r^2 > = 0.65/0.75), followed by D- GAM ($r^2 > 0.70$) for adult European hake, and mantis shrimp. For juvenile the best fits are observed for European hake and mantis shrimp with D-GLMM ($r^2 = 0.76$ and 0.68 respectively) and for European hake, red mullet, cuttlefish with D-GAM ($r^2 > 0.70$) (Table 1).

The normal distribution of residuals derived from each fitted model and assessed with the Kolmogorov-Smirnov test shows results that are not significant for many species (green values in Supplementary Table S5), except for GBM for juveniles of cuttlefish (Supplementary Table S5), D-GAM (Gaussian fit) for mantis shrimp for both adults and juveniles (Supplementary Table S5), and D-GAM (Gaussian fit) and GBM for sole for both adults and juveniles (Supplementary Table S5).

Density values estimated with e-SDM in the 'present' period for all 9 demersal species (both adult and juvenile stage) are shown in Figure 2. The density of adult of European hake reaches 600 N/km^2 (Figure 2, adults), mainly in the eastern part of the Adriatic basin, while adult red mullet (Figure 2 adults) reaches more than 2000 N/km^2, in particular in the central and southern part of the Adriatic, near Croatia, Albania and Montenegro. Norway lobster (with an estimated maximum value of approximately 100 N/km^2, Figure 2 adults) is found mainly in the Jabuka/Pomo Pit area (central Adriatic Sea) and on the northeastern area near the Croatian coast as well as in the southern part of the Adriatic and in the Otranto Channel. The adult anglerfish (Figure 2 adults) shows only few individuals (~ 15 N/km^2) in the Otranto Channel, the southern Adriatic Sea (GSA 18) and the northern Ionian Sea (GSA 19). The adult broadtail shortfin squid (Figure 2 adults) distribution shows a maximum with values around 75 N/km^2 near the central Croatian coast and the southern Adriatic Sea, while the adult European horse mackerel (Figure 2 adults) reaches 200 N/km^2, mainly in the southeastern part of the Adriatic basin, along the coast of Albania and Montenegro and in the central part of Croatian coastlines. Regarding SOLEMON dataset, three adult species (Figure 2 adults) are: cuttlefish (Figure 2 adults) with a maximum of 1000 N/km^2 concentrated mainly along the northeastern and northwestern Adriatic coast, the Common sole (Figure 2 adults) with more than 1500 N/km^2 located mainly along the northwestern coast near the mouth of the Po river. This distribution is similar to the distribution of mantis shrimp (max. 500 N/km^2, Figure 2 adults).

Juveniles of European hake reaches a density of 1000 N/km^2 (Figure 2 Juveniles), similar to adults mainly in the central and southeastern part of the Adriatic basin, while juvenile mullet (Figure 2 Juveniles) reaches 1000-1500 individuals per km^2, mainly in the western part of the Adriatic, near Apulia region. Norway lobster (estimated maximum of 40 N/km^2, Figure 2 Juveniles) is found mainly in the Jabuka/Pomo Pit area, but it is also common in the southern part of the Adriatic and in the Otranto Channel. The juvenile anglerfish (Figure 2 Juveniles) shows individuals around ~ 60 N/km^2 in the Otranto Channel, in the central and southern Adriatic Sea (GSA 18) and in the northern Ionian Sea (GSA 19) around the Apulia region. The juvenile broadtail shortfin squid (Figure 2 Juveniles), with values around 750 N/km^2, is distributed near the central Croatian coast and the central and southern Adriatic Sea, while the juvenile European horse mackerel (Figure 2 Juveniles) is distributed mainly in the southeastern part of the Adriatic basin, along the Albanian and Montenegrin coasts, near the Italian coasts of Apulia region and in the central part of Croatia with values around 1200 N/km^2. The three SOLEMON species (Figure 2 Juveniles) are: cuttlefish with 500 N/km^2 mainly along north-northeastern Adriatic coast near the Venice lagoon, the mantis shrimp (max. 100 N/km2, Figure 2 Juveniles) is mainly distributed along the northwest coast near the Po' delta, similar to common sole (Figure 2 Juveniles) with more than 700 N/km^2.

In the future, with the exception of juveniles of red mullet and adults of European hake, all species show a similar pattern between adults and juveniles, with possible increases in density toward the north especially for species observed in the MEDITS survey.

In particular, the spatial distribution of differences derived from Equation 3 (Supplementary Figure S3) between the present time window and the other three time windows ('past', '2035', and '2050') shows significant negative changes in density between the 'past' and 'present' time periods for adult and juvenile fish, except for some species such as adults of Norway lobster (both adults and juveniles, Supplementary Figure S3) and adults of broadtail shortfin squid. Densities projections of several species in the '2035' and '2050' time periods show an increasing pattern: European hake, red mullet, anglerfish (especially in the central and western part of the basin), and European horse mackerel (adults and juveniles); a sharp decline was observed in SOLEMON species (cuttlefish, and sole, Supplementary Figure S3). In addition, the densities of anglerfish, broadtail shortfin squid of adults and anglerfish and European horse mackerel of juveniles (Supplementary Figure S3) are projected to decrease in the southeastern part of the basin, in GSA 18, near the coast of Montenegro and Albania (Supplementary Figure S3).

The comparison of median and interquartile range (Supplementary Figure S4) shows good improvement using the e-SDM for almost all species and age groups, especially in terms of uncertainty (i.e. interquartile range, particularly for adult species European hake, red mullet, broadtail shortfin squid, and cuttlefish, and juvenile species European hake, anglerfish and broadtail shortfin squid (Supplementary Figure S4). This suggests that, although not all models are good for the species studied (for example adults of Norway lobster, anglerfish and cuttlefish, and juveniles of Norway lobster, cuttlefish and mantis shrimp), the e-SDM is, on average, an excellent compromise that is a general improvement in most cases, especially for adult data that are better represented by surveys, because it captures the errors and patterns of all models by weighing the information on each model.

Nevertheless, it is clear that for some models and some species, such as TW-GAM for cuttlefish of adults and juveniles (Supplementary Figure S4) and D-GLMM for mantis shrimp of juveniles, does not represent a good model based on the whole (average) pattern. The use of the ensemble in this case 'dampens' the effect of the less informative models, also in terms of the statistical weight (r^2) of each model used to weight the e-SDM.

The values of Gi* (Figure 3) above the third quartile for 'present', '2035' and '2050', shows that the main aggregation zone for the MEDITS species (European hake, red mullet, Norway lobster, anglerfish, European horse mackerel, broadtail shortfin squid) is located in the central and eastern part of the basins (in summer), while additional important aggregation zones are represented by the Jabuka/Pomo Pit area (Norway lobster and European hake) (Froglia and Gramitto, 1988; Melaku Canu et al., 2021) and the Croatian coast, Montenegro and Albanian coast (for adults and juveniles of the all other species).

The hot spot area for adults (Figure 4, Adults) show that for European hake and red mullet adults are projected with important changes westward and northward respectively, while for Norway lobster is expected to loose areas in the central and southern part of the basin (between the Jabuka/Pomo Pit area and the southern part of the basin). For anglerfish the areas gained are in the central-eastern part of the basin, while for European horse mackerel no changes are projected. For SOLEMON species (mantis shrimp, cuttlefish, common sole), there is a lost area along the north coast of the Adriatic Sea, mainly for mantis shrimp and common sole, but an increase in gained areas for cuttlefish (green values) has been observed close to north-central part of the Adriatic Sea.

For juveniles (Figure 4) no changes are projected for European hake, while territorial gains are found for red mullet along the north-central part of the basin. Moreover, territorial losses are projected for Norway lobster in the central and southern part of the basin, while strong territorial gains are observed for anglerfish, European horse mackerel in the central part of the Adriatic Sea and west coast of the basin. For the SOLEMON juvenile's species, especially for cuttlefish, a lost area near the northeastern Adriatic Sea and few lost areas for mantis shrimps near the northwestern Adriatic Sea and the river Po can be recognized.

3.1 Assessment of the uncertainties in the predicted density estimation

The bias between predicted and observed values (Equation 2) (Supplementary Figure S2), illustrates the good performance of e-SDM with respect to the survey data. Table 3 summarizes the overestimation and underestimation of the bias equation averaged over grid resolutions, with colors highlighting the underestimation (light blue) or overestimation (red), as shown in Supplementary Figure S2, the latter for each survey point (i.e., averaged over years only for the 'present' scenario).

For adult species, values (Table 3, column Adults) are underestimated for, Norway lobster, and anglerfish. For juvenile species (Table 3, column Juveniles), values are underestimated for anglerfish, and cuttlefish. e-SDM shows the same over- and underestimates for the same species and life stages, with the exception of Norway lobster (Table 3) and cuttlefish (Table 3).

4 Discussion

The influence of the climate change on the Adriatic Sea has been extensively studied, considering food web structure (Albouy et al., 2014), local trophic status (Sfriso et al., 2019), the overall effect of climate on future biodiversity, comparison of SDMs and multispecies trophic models (OSMOSE; Moullec et al., 2022) or biotic response to long-term climatic changes (Scarponi et al., 2022). To date, and to the best of our knowledge, few studies in the Adriatic and Ionian Seas have examined projections of species distribution under climate change conditions (Sys et al., 2022; Poos et al., 2024) with such high spatial resolution and with such an ensemble of different models, including fishery-independent data as response variables from two types of surveys (MEDITS and SOLEMON). The survey data used in this study represent a very long time series of information related to commercial species in the Adriatic and Ionian Seas providing a good and satisfactory estimate of both biomass and abundance indices (kg/km^2 or N/km^2) of the studied populations and their life stages.

In our study we developed a quantitative (distribution in terms of N/km^2 and density differences, Figure 2 and Supplementary Figure S3, respectively) and qualitative (area gained/lost area Figure 4) representation of the projected future distribution of the main commercial species in both Adriatic and Ionian, one of the first attempt in using physical and biogeochemical projections

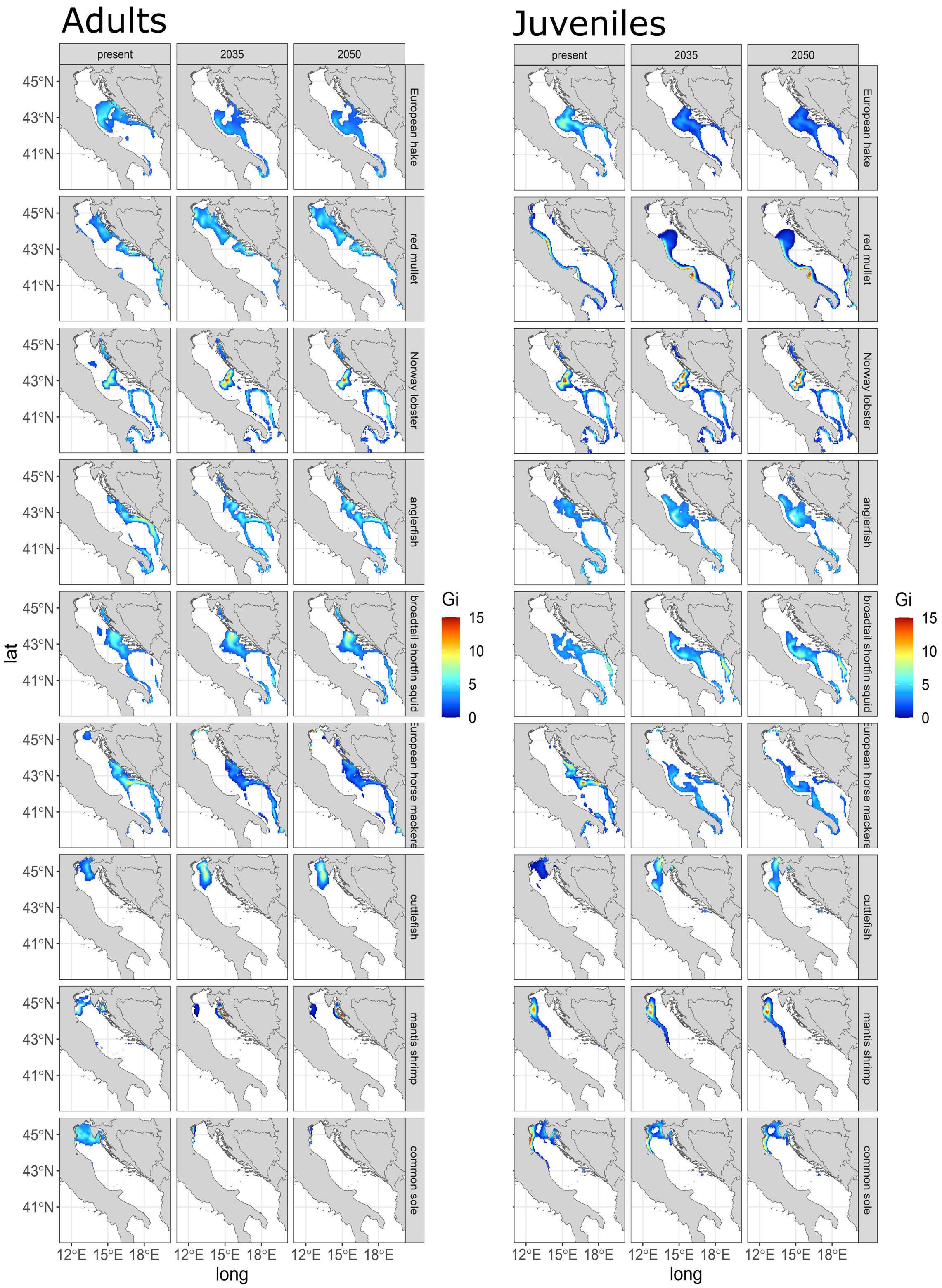

FIGURE 3
Hot-spot assessment with Getis ord Gi* above the third quartile (> = 75° percentile) for each species (left panel adults and right panel juveniles) for the main scenario, present (2014-2018) and future (2035, 2050).

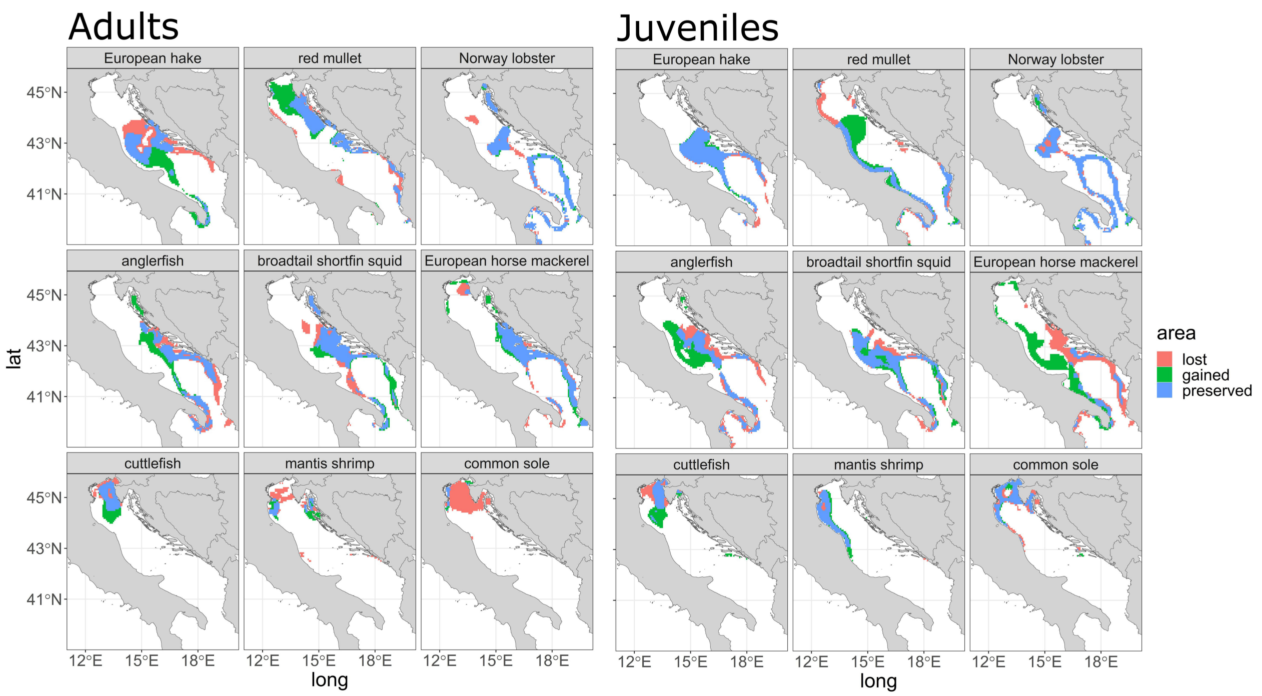

FIGURE 4
area gained, lost, and preserved (see legend) for each species for the year 2050 for adults (left panel) and juveniles (right panel). Each area is composed of grid cells that do not overlap (gained), overlap (preserved), and lack (lost) Getis ord-Gi* values > 75° percentile between the 'present' scenario and the '2050' scenario.

under RCP8.5 scenarios, as produced and analyzed in Reale et al., 2022. The species here modelled live in a temperate zone, in a dead-end basin where displacement and north migration is limited. Indeed, different spatial patterns between SOLEMON and MEDITS species were observed in our results. Species mostly distributed in the southern/central part of the study area such as red mullet, anglerfish, broadtail shortfin squid and European horse mackerel, exhibits a displacement towards the north (Figure 4), especially on the eastern and central coast of the Adriatic. Species derived from the SOLEMON survey, such as cuttlefish and mantis shrimp, show a shift from east to southwest (Figure 4), especially for adults, and a lost area for adults of common sole. This indicates that the northward shift in distribution density is more pronounced in the central and southern portions of the study area. Some species derived from the MEDITS survey are projected to increase in density (Supplementary Figure S3, 2035 and 2050 panel, for both adults and juveniles) toward the north, especially along the Croatian coast and in the central part of the basin (e.g. European hake for both life stages, and European horse mackerel).

TABLE 3 Result of relative overestimation and underestimation of species density calculated as average bias (from Equation 2) over the grid resolutions and years.

Bias	Adults	Juvenils
European hake	1.28	1.59
red mullet	1.81	2.09
Norway lobster	-0.42	0.78
anglerfish	-0.78	-0.41
broadtail shortfin squid	0.09	1.92
European horse mackerel	0.48	1.65
cuttlefish	0.79	-0.18
mantis shrimp	0.47	0.80
common sole	1.50	2.02

Average underestimated (light blue) and overestimated (red) densities are highlighted.

These changes are resulting from projected changes in the EOVs. The changes between 'present' (reanalysis) and '2050' (climate projections) in the physical and biogeochemical variables for climate scenarios of our data (see Reale et al., 2022) show for example an average increase of 1-1.5 C° in the bottom temperature of the Adriatic basin and changes of ~ -15% in phosphate concentration (200-600m, mmol m^{-3}), or -12% in nitrate concentration (200-600m, mmol m^{-3}). The projected changes in physical and biogeochemical variables could be responsible for the abundance and spatial distribution of some species seeking more suitable habitats (Figure 4). Due to the uncertainty of the analyzes (see *limitations*), it is important to consider that the adaptation of certain species to possible environmental changes may also vary (e.g. Poloczanska et al., 2016), but the environmental drivers have the largest impact on the spatiality of the resources considering that these models (Supplementary Table S4) also improve their performance (e.g. explained deviance and r^2) by using the biogeochemical variables employed (Panzeri et al., 2021a, b, 2023).

4.1 Implications for fisheries management

The temporal and spatial changes detected in the present study based on the data and variables used show shifts in the different species and their distribution. Furthermore, the predicted differences in density (Supplementary Figure S3) may indeed be significant (Table 2). In addition, growth, survival, and reproduction could be affected (Shoji et al., 2011), which in turn affects resources and fisheries (Bryndum-Buchholz et al., 2021). This study highlights that the main commercial species, which currently represent 60% of the total demersal landings in the area (FAO, 2022) could change their location and density in the near future, which will likely affect fishing activities and seasonal patterns. In particular, European hake, red mullet, anglerfish, and European horse mackerel (adult's stages) and red mullet, anglerfish, and European horse mackerel (juveniles) are the stocks that will be most affected by climate change in the future with unpredictable commercial and economic impacts.

Representation of the future distribution of the species could support management spatial planning in the area, by anticipating hot spots and thus optimizing planning of spatio-temporal closure, for example. Future developments might include long term simulations based on the Shared Socioeconomic Pathways (SSPs) emission scenarios and CMIP6 ensemble members (see Lovato et al., 2022) that include changes in atmospheric carbon concentration as well as socio-economic and policy changes.

The fisheries management in the studied area is based on different approaches, including the adoption of spatial measures such as FRA (Fisheries Restricted Area, GFCM-FAO, 2017). Plotting hotspots for juvenile and adult densities of species may help us understand future prospects for fisheries grounds and management measures, particularly in the FRA (e.g Jabuka/Pomo Pit). Possible future changes in suitable areas, as we have estimated in this work, could lead to a change for the species concerned and directly affect fisheries activities in the Adriatic and Ionian Seas.

Consequently, the potential changes in species distribution may require new adaptive fisheries management measures in the future, such as adaptive spatial planning with short- and long-term regulation or differentiated control of fishing pressure in relation to the species exploited, changing spatial and temporal protection areas at manageable time frequency but also accounting for foreseen changes (Hidalgo et al., 2022). This might induce the definition or re-definition of spatial fisheries area. We also consider that the most important changes are observed in the eastern part of the Adriatic and Ionian basins, with particular interest for the Croatian, Bosnia, Albanian and Montenegrin coasts, with lost or gained area depending on the species.

We recall that the trawl survey is mainly conducted in spring and summer (for MEDITS), and that the potential impacts and changes due to climate change are exacerbated by the warmer seasons (Kim et al., 2019) and are likely to affect the main area of hotspots (Figure 3) near the eastern part of the Adriatic. Therefore, management measures should also take into account the spatial and temporal heterogeneity of the area. This aspect explains the paramount importance recently assigned in the Mediterranean Sea scientific community to the development of eddy-permitting regional ocean models able to resolve even the sub-mesoscale dynamics (Lévy et al., 2018; see Reale et al., 2022 and the discussion herein).

We must also consider that the present and future distribution of species is influenced not only by the abiotic environment, but also by the biological interactions between species (e.g. predation, competition) and anthropogenic stressors (e.g. fisheries). These processes should also be fully assessed for fisheries management based on ecosystem approaches (e.g., Koen-Alonso et al., 2019). The development of multispecies models can be useful in management and in determining how particular species may be affected not only by climatic conditions but also by intra- and interspecific interactions. For example, the use of Joint species distribution models (e.g., Roberts et al., 2022) is now essential and could be considered in future analyses.

4.2 Limitations

Sources of uncertainty of this study are primarily related to the data used, which have been extracted from a spring-summer trawl survey for MEDITS and autumn-winter survey for SOLEMON. The spatial dynamics within years cannot be fully represented by annual trawl sampling because species have relevant seasonal movements, which is an inherent limitation of the data used that cannot be overcome by the different models used. Therefore, hotspots and distribution are more relevant for species whose important aggregation phases (reproduction for adults, nursery for juveniles) coincide with the sampling period (late-spring/early summer for MEDITS (Tsikliras et al., 2010) and autumn for SOLEMON species) (Scarcella et al., 2014). Ontogenetic changes and movements are fairly well represented for all species, although in some cases the sampling periods did not overlap with the life stages here investigated.

In multispecies trawl surveys, the availability to the gear of certain species or life stage can differ, as for benthopelagic species (e.g. European horse mackerel, Supplementary Figure S2), thus causing higher variability. In addition, the species considered here, such as European hake or anglerfish, could experience other effects of climate change, with possible positive (increase in prey) or negative (decrease in prey) effects given the mismatch between them, which in turn affects trophic dynamics and the temporal mismatch between prey and predator levels (e.g., Thackeray et al., 2010).

Given recent improvements in Copernicus Marine Service products, a second source of uncertainty regards the quality levels characterizing the physical and biogeochemical data used in the model. Results from model reanalysis and future scenario projections are affected by many uncertainties (see Richon et al., 2019; IPCC, 2022; Reale et al., 2022). Progresses in quality of the Mediterranean Sea CMS products are continuous (Salon et al., 2019) and a new reanalysis at higher resolution (increasing from 1/

16 to 1/24 of degree) has been recently made available (Cossarini et al., 2021). Higher quality and resolution can be included in our models providing a refinement of the results that will allow us to identify small scale patterns and the dependency of the species change patterns on mesoscale dynamics evolution (e.g. fronts and gyres). In addition, the use of discrete background variables such as seafloor eterogenity and properties could help improve the models used, especially for certain species such as Norway lobster.

5 Conclusions

Species adaptation to future climate change is difficult to account for because the successful establishment of a particular species in a new area depends not only on biotic and abiotic traits, but also on dispersal ability, demographic structure, and adaptability to new environmental conditions (Pinsky et al., 2020). In addition, we do not know whether species that arrive at a new site with similar conditions are likely to be more successful in their establishment than species that have not yet 'settled' due to expansion of suitable range in the future and reduction of current range (Chase and Leibold, 2009). We must also consider that a mismatch between survival processes and reproduction rates can occur if the rate of climate change is greater than a species' adaptation rate or exceeds the population's ability to cope with climate variability (Wang, 2022).

The e-SDM model-based approach has the aforementioned limitations and advantages associated with the inclusion of physical and biogeochemical variables derived from climate model projections (whose uncertainties are discussed in Reale et al., 2022), which are then used to evaluate the distribution of species under future climatic conditions.

With the model we developed, we aimed to determine the range of change in distribution under climate change of species that represent a large proportion of commercial landings, evaluating different aspects of their distribution and the shift of the current area of high aggregation (hot spot), since this area is strongly influenced by fisheries and will probably continue to be exploited in the future.

Data availability statement

Raw trawl survey data can be requested to the Ministry of Agriculture of Italy and Croatia. Oceanographic variables used in this work are available at Copernicus Marine Service. All treated data are available at the project FAIRSEA platform (https://fairsea.inkode.it/#/login) and access can be requested from the corresponding author.

Author contributions

DP: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. MR: Data curation, Writing – original draft, Writing – review & editing. GC: Data curation, Writing – review & editing. SS: Data curation, Writing – review & editing. RC: Writing – review & editing. MS: Writing – review & editing. WZ: Writing – review & editing. NV: Writing – review & editing. SL: Conceptualization, Data curation, Supervision, Writing – review & editing, Funding acquisition, Project administration, Writing – original draft.

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Conflict of interest

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

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1308325/full#supplementary-material

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