ICES Journal of Marine Science, 2025, Vol. 82, Issue 10, fsaf178
https://doi.org/10.1093/icesjms/fsaf178
Received: 25 November 2024; **revised:** 5 September 2025; **accepted:** 18 September 2025
Original Article

ICES CIEM International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

Spatial distribution and environmental preferences of the mesopelagic fish *Maurolicus muelleri* in the Eastern Mediterranean

Alexandros Alamanellis [1,2,*], Zacharias Kapelonis [1], Marianna Giannoulaki [1], Dionysios E. Raitsos [2], Vasilis D. Valavanis [1], Konstantinos Tsagarakis [1]

[1]Institute of Marine Biological Resources and Inland Waters, Hellenic Centre for Marine Research, Anavyssos 19013, Attica, Greece
[2]Department of Biology, National and Kapodistrian University of Athens, Athens 15772, Greece

*Corresponding author. Institute of Marine Biological Resources and Inland Waters, Hellenic Centre for Marine (HCMR), 46.7 km Athinon-Souniou Ave. P.O. BOX 712, Anavyssos 19013, Greece. E-mail: a.alamanellis@hcmr.gr

Abstract

Mesopelagic fish constitute the most abundant vertebrate group in the marine environment. Mueller's pearlside (*Maurolicus muelleri*) is present in the twilight zone across the Atlantic Ocean, including the Mediterranean; however, little is known about its distribution patterns and environmental preferences. Based on acoustic and biological sampling, we demonstrate that *M. muelleri* predominantly forms monospecific aggregations with characteristic echotraces. An ensemble of Species Distribution Models (SDMs) was applied, paired with satellite-derived environmental observations and model outputs to explore the potential habitat of the species in the Eastern Mediterranean Sea. Bottom depth showed the highest variable importance in all models, followed by surface chlorophyll-a concentrations (an index of phytoplankton biomass) and current geostrophic velocity. Extended areas of high probability of presence were identified near the shelf breaks throughout all sub-basins, in the zone of 150-250 m. *M. muelleri* is more likely to occur in productive regions than in oligotrophic ones, suggesting that ongoing Mediterranean ocean warming—which reduces primary productivity—may indirectly affect the species' abundance by limiting food availability. Inter-model variability indicated low uncertainty, which was attributed to the species' strong dependence on a narrow range of only a few environmental variables. The findings contribute to our understanding of the spatial distribution of a key mesopelagic fish in the Eastern Mediterranean Sea and its association with topographic and environmental drivers.

Keywords: silvery lightfish; hydroacoustics; biomod2; ensemble modeling

Introduction

The mesopelagic zone, also known as the twilight zone, is defined as the zone between the euphotic epipelagic and the bathypelagic zone. In terms of bathymetry, the mesopelagic zone is usually defined as the area between 200 m and 1000 m depth, covering 20% of the global ocean mass. Only a small fraction of sunlight reaches the mesopelagic zone (Behrenfeld 2010), thus rendering the conditions insufficient for photosynthesis and photosynthetic primary production.

Mesopelagic fish constitute the most abundant vertebrate group in the marine environment (Catul et al. 2011), being present in every ocean (Gjøsaeter and Kawaguchi et al. 1980) around the globe. They occupy the twilight zone during the day and many species perform a pattern of movements known as Diel Vertical Migration (DVM), reaching the epipelagic zone during the night to feed upon zooplankton. Subsequently, they play a key role in the energy influx within the mesopelagic ecosystem (Woodstock and Zhang 2022). The global biomass of mesopelagic species had been largely underestimated in the past, with older studies suggesting that it is ∼1 000 million tons (Gjøsaeter and Kawaguchi et al. 1980); in contrast, a more recent study has estimated the global biomass at one order of magnitude higher (between 11 000 and 15 000 million tons) (Irigoien et al. 2014), which calls for a reconsideration of their ecological importance. However, other recent studies of a more localized scale (Escobar-Flores et al. 2020, Dornan et al. 2022, Chacate et al. 2024) suggested lower mesopelagic fish density estimates than Irigoien et al. (2014). Their contribution in the food-web of the mesopelagic ecosystems emphasizes the need of understanding their assemblages and distribution.

Mesopelagic fish assemblages form distinct Deep Scattering Layers (DSL) and other characteristic echotraces that can be identified through acoustic means (e.g. Kapelonis et al. 2023). Underwater acoustics are commonly employed as a tool for assessing mesopelagic fish abundance and distribution (Olivar et al. 2012, Peña et al. 2014, Davison et al. 2015). Different mesopelagic fish species, due to their respective anatomy, size and behaviour inside the water column, may form echotraces of different density and other characteristics (Kaartvedt et al. 2009, Davison et al. 2015, Peña et al. 2023). By combining acoustic data alongside with the in-water verification via biological sampling, echotraces can be attributed to specific species or taxa. However, broad-scale sampling targeting the deep sea can be exceedingly time-consuming and expensive; therefore, tools to indirectly quantify the distribution of mesopelagic organisms can be valuable.

Species distribution models (SDMs) rely on the application of algorithms that combine available presence/absence or abundance data with environmental variables, in order

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to predict and visualize the spatial distribution of species over extended regions (Elith et al. 2006, Giannoulaki et al. 2013). SDMs are useful tools that contribute to understanding the dynamics between environmental parameters and habitat suitability, which is essential for ecosystem and fisheries management, including the prediction of distributional responses to climate change. SDMs are widely used in studies for marine species, however SDM approaches, based on a single model, are associated to a risk of uncertainty due to potential model bias. The application of ensemble SDM approaches helps accounting for model uncertainty and can produce improved predictions by considering the variability amongst results produced by different algorithms (Grenouillet et al. 2011, Ramirez-Reyes et al. 2021).

The Mediterranean Sea is a semi-enclosed basin that mostly exchanges water with the Atlantic Ocean through the Gibraltar's strait in the West, while its Eastern part is considered as one of the most oligotrophic areas in the world (Psarra et al. 2000). Nevertheless, it has been characterised as a marine biodiversity hot spot (Coll et al. 2010). The basin is defined by a predominately narrow continental shelf, yet shows considerable geographic heterogeneity. It is known to be greatly affected by major stressors like overfishing (Tsikliras et al. 2015, Vielmini et al. 2017) and climate change (Giorgi and Lionello 2008). The mesopelagic zone in the Mediterranean Sea is warmer and hosts a lower number of fishes compared to the adjacent Atlantic Ocean, with the most abundant families being Myctophidae, Sternoptychidae, Phosichthyidae, Gonostomatidae, Stomiidae and Paralepididae (Olivar et al. 2012, 2022).

The genus *Maurolicus*, belonging to the Sternoptychidae family, exhibits a worldwide distribution, while Mueller's pearlside, *Maurolicus muelleri* has a wide distribution in the Mediterranean Sea and North Atlantic Ocean (Rees et al. 2020) and is considered as one of the most abundant species in several seas (Alvheim et al. 2020, Alvarez et al. 2023). It is usually found in the shallower part of the mesopelagic zone, often considered to define its upper limit (Kaartvedt et al. 2019) and performs DVM for feeding purposes (Staby et al. 2011, Christiansen et al. 2019, 2021). Although not currently a target for commercial fishing, there have been attempts and an ongoing interest for its exploitation (Prellezo 2019, Vastenhoud et al. 2023). Studies have shown that it is part of the diet of various commercial and charismatic species, such as the tunas, *Thunnus thynnus* (Olafsdottir et al. 2016) and *Eythynnus alleteratus* (Falautano et al. 2007), gadoids (Giske et al. 1990), and marine mammals (Würtz and Marrale 1993, Dede et al. 2016, Giménez et al. 2018), suggesting that it is a species of great ecological interest. In the Eastern Mediterranean, *M. muelleri* is one of the most prevalent species, usually occupying areas in proximity to the seafloor, at the shelf break and upper slope (Kapelonis et al. 2023). Despite its ecological significance and widespread occurrence in the Mediterranean Sea and Atlantic Ocean, little is known about the specific habitat preferences of *M. muelleri*. Understanding its environmental preferences is an important step towards advancing knowledge on the dynamics of the mesopelagic ecosystem. Thus, linking distribution data from acoustic surveys with environmental parameters could provide crucial insights into its ecological role, potential climate change impacts, and the consequences of its exploitation.

The objectives of the current study were to (i) model the distribution of *M. muelleri* using field data and ensemble species distribution modelling, (ii) investigate the importance of topographic and environmental (remotely-sensed) parameters in predicting the species' suitable habitat; and (iii) use remote sensing data to map the species' suitable habitat and identify areas with high probability of presence. To achieve these objectives, species presence and absence data derived from acoustic expeditions in the Ionian and Aegean Seas (Eastern Mediterranean) were combined with a set of environmental parameters through 10 different SDM algorithms. An ensemble algorithm was created and the probability of the species' presence was projected in maps of the study area, providing knowledge for understanding the ecology and distribution of the *M. muelleri* in the Eastern Mediterranean mesopelagic zone.

Materials and methods

Study areas

The study area covered several parts of the Eastern Mediterranean, including open seas and islands as well as enclosed gulfs around the Greek mainland. The Aegean Sea is located in the eastern part of the Mediterranean (Fig. 1) and is the area where the majority of the Greek fisheries operate. It is characterized by high environmental variability, for instance the Northern part of the Aegean Sea is considered one of the most productive areas of the Eastern Mediterranean due to nutrient rich water inflows from rivers and the Black Sea (Lykousis et al. 2002, Karageorgis et al. 2003, Tsiaras et al. 2012, 2014), while the central and southern parts are quite oligotrophic. The Cretan Sea is located at the southernmost part of the Aegean, north of the island of Crete (Fig. 1), and is the deepest basin of the Aegean, reaching ∼2500 m depth (Georgopoulos et al. 2000). It is considered one of the most oligotrophic areas in the Eastern Mediterranean and the majority of its primary productivity is attributed to upwelling from gyres and vertical mixing of the water column (Psarra et al. 2000). On the west Aegean Sea, between Evia Island and the mainland, is located the Euboan Gulf (Fig. 1), a generally shallow gulf with a deep (∼440 m) basin in its Northern part, that is considered oxygen deficient from ∼350 m and below (authors' unpublished data). The Saronic Gulf, with a maximum depth of ∼450 m, is also part of the west Aegean Sea, located south of the Attica peninsula.

The Ionian Sea, located between the Greek and Italian mainland (Fig. 1), is the deepest sub-basin in the Mediterranean Sea with a maximum depth of 5121 m (Emig and Geistdoerfer 2004). The Eastern Ionian, is considered oligotrophic compared to the Aegean Sea, with no influence from big river inflows (Pitta et al. 1998) and a relatively narrow continental shelf. Located at the east end of the Ionian Sea, the Gulf of Corinth (Fig. 1) is a deep gulf with a maximum depth of 935 m and a steep slope, that is connected to the Ionian through the much shallower Patraikos Gulf (Kapelonis et al. 2023). It is considered of great ecological importance as it is hosts large and permanent populations of marine mammals, especially stripped dolphins (Bearzi et al. 2011) and is Identified as an Important Marine Mammal Area (Bonizzoni et al. 2019).

Biological sampling and *Maurolicus muelleri* echotraces

The presence of *M. muelleri* was explored with data from acoustic surveys conducted in the Aegean and Ionian seas

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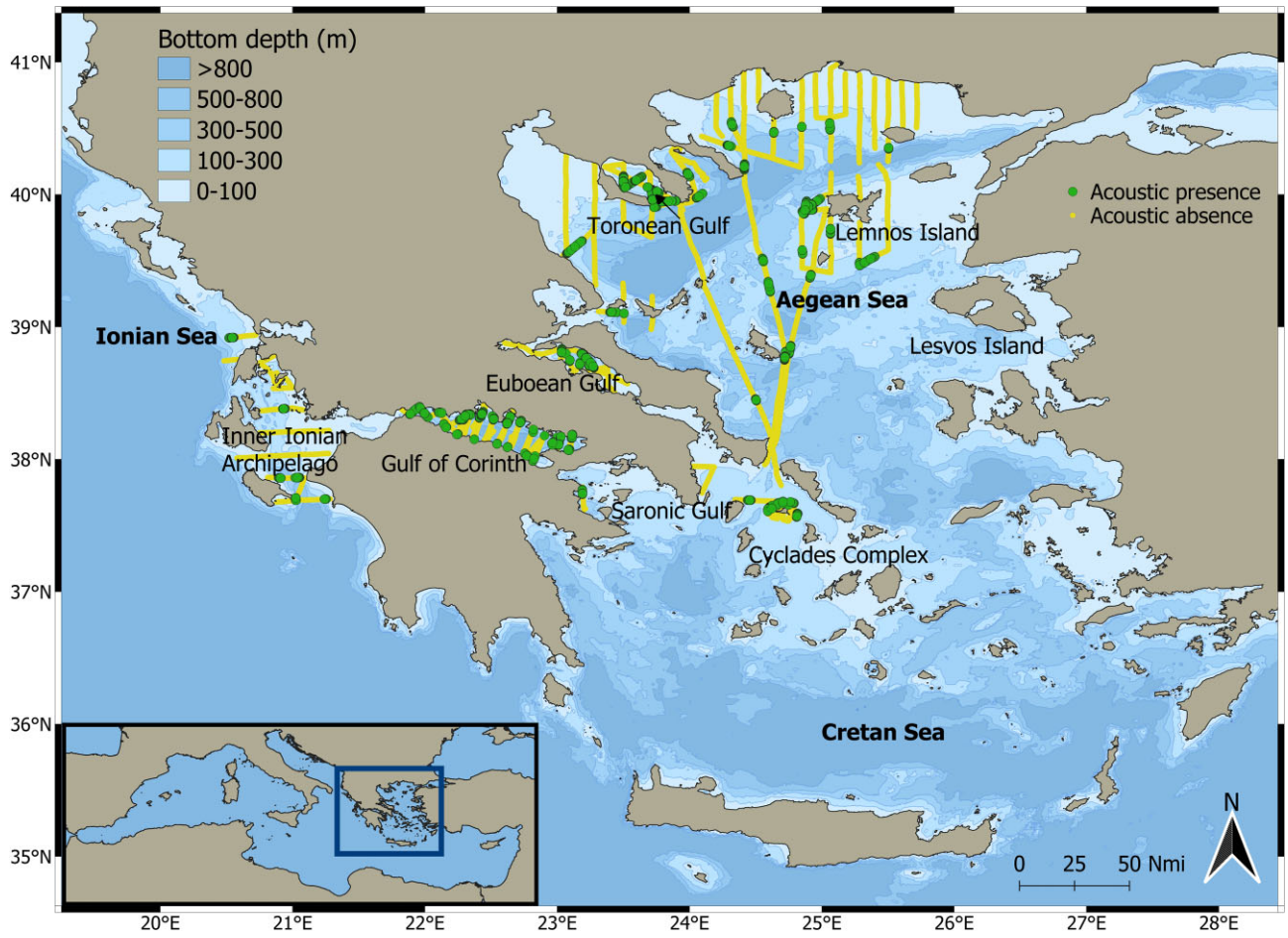

Figure 1. Bathymetric map of the Ionian and Aegean Seas (Eastern Mediterranean), featuring acoustic sampling presence (green) and absence (yellow) of *M.muelleri* characteristic echotypes in 2018–2020.

(Fig. 1, Table S1) on board the R/V *PHILIA*, in the framework of monitoring and research projects targeting small pelagic and/or mesopelagic fish (Leonori et al. 2021, Kapelonis et al. 2023), as well as opportunistically-collected acoustic data during the time period 2018–2020. Acoustic data were collected using a hull-mounted Simrad EK80 split beam echosounder, operating in continuous-wave (CW) mode with fast ramping, using a pulse duration of 1024 ms and traveling at a speed of ~8 kn. The ping rate was manually adjusted throughout the surveys, depending on the local bottom depth on each survey location. Out of the four split-beam transducers available in the RV's EK80 system (38, 120, 200 and 333 kHz), the 38 kHz frequency was the most appropriate in operating throughout the depth range of detected *M. muelleri* echotraces and was used for the analysis. The echosounder system was calibrated before each survey with the standard target method (Table S2) (Demer et al. 2015). Echo sounding took place during daytime in predefined transects and during the whole day on opportunistic transits. Only the daytime values from the echograms were used for the analysis due to changes in the position and shape of the *M. muelleri* aggregations, attributed to the DVM they perform during nighttime. The total length of the analysed dataset was approximately 2500 nmi (Fig. 1).

Biological sampling for echotrace identification was conducted using a custom pelagic trawl of 27 m total length and 24.5 m total width, 7 m vertical opening, 12 m horizontal opening and a 16 mm (stretched) mesh cod-end. The trawl was typically towed at 3–4 knots by the same vessel that performed the acoustic sampling. A SCANMAR trawl monitoring system was used to achieve the appropriate trawling depth and monitor the net operation. Thirty-four hauls took place in parallel with the acoustic surveys (i.e. in the period 2018–2020), while 10 additional hauls (three in 2017 and seven in 2022) (Fig. 2, Table S3) were considered for the identification of characteristic echotraces (from hereon referred to as echotypes) formed by *M. muelleri*.

The percentage contribution (in weight) of *M. muelleri* in hauls targeting mesopelagic assemblages is listed in Table S3, while the location of the hauls and corresponding echograms of selected hauls are shown in Fig. 2. Biological sampling confirmed that the echotype associated with *M. muelleri* presence was largely monospecific. Out of the 44 hauls, *M. muelleri* was completely absent in 25 and had only a minor (<2%) contribution in four additional hauls (Table S3, Fig. 2a, f). Its contribution was high in 15 hauls, in 10 of which it contributed 98%-100% by weight and only a few or no individuals of other species were concurrently caught (Table S3, Fig. 2a, b, d). The shoals of *M. muelleri* as appeared in the echograms corresponding to these monospecific hauls, displayed a distinct behaviour compared to other mesopelagic fish: their echotraces appeared as sparse, extended clusters of smaller densely populated schools (Fig. 2b, d) that occupied areas often larger than 1 nmi in length and usually occurring in areas with bottom depths of less than 100 m to 250 m. Thus, the pres-

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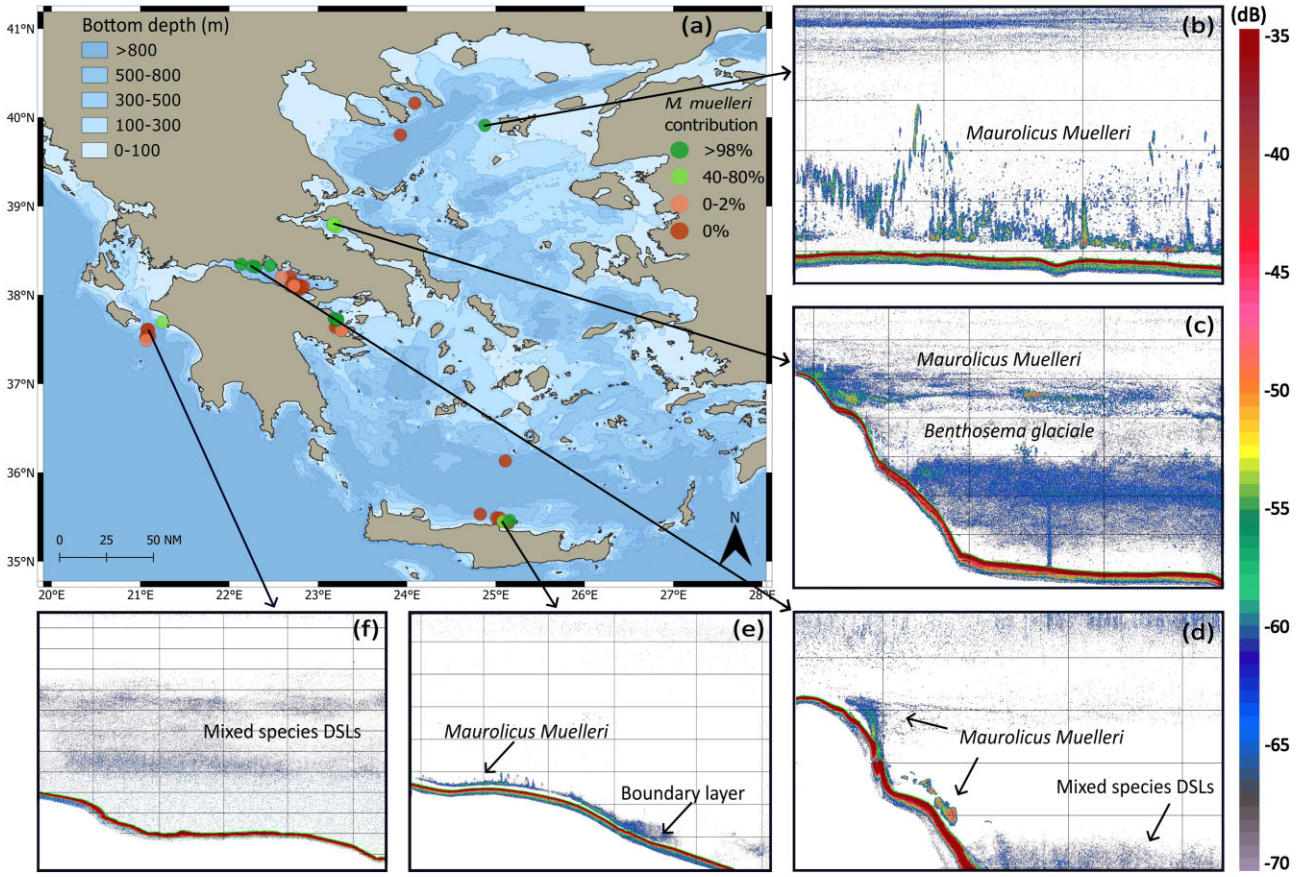

Figure 2. (a) Map of the study area, indicating the position (dots) of the pelagic hauls held for biological sampling; the colours of the dots indicate the percentage contribution of *M. muelleri* in the total catch (by weight). The arrows link the hauls with the corresponding Sv [dB re 1 m^{-1}] echograms that were recorded (b–f). (b), (d) Echograms showing characteristic *M. muelleri* aggregations, as verified with daytime biological samplings (>98% contribution of the species) West of Lemnos Island and in the Gulf of Corinth respectively. (c) Echograms from the N. Euboean Gulf. Oblique hauls were performed containing 40%–80% *M. muelleri* individuals. The upper scattering layer is likely formed by *M. muelleri*, and the deeper layer by *Benthosema glaciale*. (e) Echotype containing *M. muelleri* individuals (40%–80%) in the Cretan Sea. Characteristic *M. muelleri* aggregations are progressively succeeded by dense layer formations (f) Typical mesopelagic DSLs with absence (0%) of *M. muelleri* individuals, as verified during daytime biological sampling in the South Ionian Sea. The distance between vertical grid-lines on the echograms is 1nmi and between horizontal grid-lines is 50 m. The minimum backscatter strength threshold used in the echograms is −70 dB re 1 m^{-1}. See Figure 1 for location names.

ence of *M. muelleri* aggregations was distinguishable from the typical mesopelagic DSLs (Fig. 2f) that were found deeper in the water column during daytime. When targeting those deeper mesopelagic DSLs, no *M. muelleri* individuals were collected in any of the hauls performed (Fig. 2a, Table S3). Echotraces of juvenile *M. muelleri* aggregations appeared in shallower zones than larger individuals, as e.g. indicated by biological sampling data gathered inside the gulf of Corinth (Fig. 2d). The remaining five hauls with 40%-80% *M. muelleri* contribution fall under two categories. First, three oblique hauls in the North Euboean Gulf (Fig. 2c, Table S3: hauls No 20, 36, 37) had a mixed catch of *M. muelleri* and *Benthosema glaciale*. Acoustic and biological samplings inside the North Euboean Gulf revealed that the echotype of *M. muelleri* slightly differed from its typical echogram-appearance in the rest of the study area. The *M. muelleri* echotype appeared as a mix of shoals with typical DSLs at depths of around 100–150 m, without strong dependence to the shelf brake (Fig. 2c). Directly below the *M. muelleri* aggregations, resided a deeper mesopelagic DSL (Fig. 2c), most probably consisting of *B. glaciale* as evidenced by biological sampling. The mesopelagic echotypes of the N. Euboean Gulf presented a closer resemblance to the echotypes found in the Norwegian Fjords, where a shallower scattering layer consisted mostly of *M. muelleri* is followed by a deeper scattering layer consisted mostly of *Benthosema glaciale* (Kaartvedt et al. 2009). Secondly, there was a limited number of hauls (Table S3: hauls No 33, 41) that *M. muelleri* was present along with other mesopelagic species; in such cases the *M. muelleri* echotype was in close proximity to dense layers at short distance from the seabed (Fig. 2e). Since such layer-type formations usually didn't contain *M. muelleri* when sampled, it was assumed that in these two hauls, the species was caught at the boundary of its distribution, when the two echotypes overlapped. Therefore, such acoustic layers were not taken into account for modelling, likely ignoring a small portion of the species' distribution.

Acoustic data analysis

Acoustic data was analysed using Echoview software (Echoview Software Pty Ltd 2021) and a calibration file was uploaded within the software. The sound velocity and absorption were tuned for each transect, based on the environmental conditions of the area (temperature and salin-

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Table 1. List of environmental variables considered, data sources, available resolutions and applied transformations.

Variable		Transformations	Source	Sensor/product	Resolution
DEPTH	Sea Bottom Depth (m)	cubic root, z-transform	simrad ek80, gebco.net	GEBCO_2023	450 m
CHL	Sea Surface Chlorophyll-a Concentration (mg/m^3)	reversed, z-transform	oceancolor.gsfc.nasa.gov	MODIS-A SMI	4 km
SLOPE	Sea Bottom Slope (degrees from North)	log, z-transform	gebco.net	GEBCO_2023	450 m
UADT	zonal component of the absolute geostrophic velocity (m/s)	z-transform	www.aviso.altimetry.fr	SSALTO/DUACS (merged product)	0.125°
VADT	meridional component of the absolute geostrophic velocity current (m/s)	z-transform	www.aviso.altimetry.fr	SSALTO/DUACS (merged product)	0.125°
PAR	Photosynthetic Active Radiation ($mol{\cdot}m^{-2}{\cdot}s^{-1}$)	z-transform	oceancolor.gsfc.nasa.gov	MODIS-A SMI	4 km
SLA	Sea Level Anomaly (m)	z-transform	www.aviso.altimetry.fr	SSALTO/DUACS (merged product)	0.125°
SST	Sea Surface Temperature (°C)	z-transform	oceancolor.gsfc.nasa.gov	MODIS-A SMI	4 km
SBT	Sea Bottom Temperature (°C)	z-transform	marine.copernicus.eu	MEDSEA_MULTIYEAR_PHY_006_004_E3R1	4 km
ZEU	Euphotic Depth (m)	z-transform	oceancolor.gsfc.nasa.gov	MODIS-A SMI	4 km
POC	Particulate Organic Carbon (mg/m^3)	reversed, z-transform	oceancolor.gsfc.nasa.gov	MODIS-A SMI	4 km
EKE	Eddy Kinetic Energy (cm^2/s^2)	reversed, z-transform	www.aviso.altimetry.fr	SSALTO/DUACS (merged product)	10 km
SAL	Salinity (psu)	square root, z-transform	marine.copernicus.eu	MEDSEA_MULTIYEAR_PHY_006_004_E3R1	0.333°
DTC	Distance to Coast (m)	cubic root, z-transform	Euclidian distance	GIS calculated	400m

ity) recorded by CTD casts. The bottom was classified using Echoview's post-processing bottom detection algorithm and manually corrected where necessary. Various aggregations within echograms were identified and manually classified into small pelagic, shallow-mesopelagic (potentially *M. muelleri*) and deep-mesopelagic echotypes. Classification was guided by biological ground-truthing of acoustic marks as well as expert judgement and prior knowledge and data gathered on similar aggregations in the area (Kapelonis et al. 2023), to assist the expert-based procedure of recognizing the echotypes of *M. muelleri* by their distinct shape and location inside the water column. The aggregations that resembled the characteristics attributed to *M. muelleri* were manually labelled. Acoustic data were divided into a number of intervals based on an elementary distance sampling unit (EDSU) with a length of 200 m to conserve the local character of individual echotypes of *M. muelleri* with respect to the bottom topography. Using a minimum S_V (dB) threshold of -70 dB re 1 m^{-1}, the Nautical Area Scattering Coefficient (NASC, s_A) [m^2 nmi $^{-2}$] for the defined *M. muelleri* aggregations was calculated and echo integrator values were exported. The -70 dB re 1 m^{-1} S_V threshold was selected after an initial review of the data; this threshold was deemed sufficient to resolve the presence/absence of the *M. muelleri* echotypes, while effectively removing all noise from the echogram alongside with some amount of backscatter from other targets (particles and other organisms). Species presence was assigned to each interval with a non-zero *M. muelleri* NASC, and absence was assigned otherwise. Exploring the presence/absence (rather than acoustic density/abundance) of *M. muelleri* was deemed more suitable for the acoustic dataset, given the limitations that were introduced due to the limited temporal distribution of the acoustic observations and the greater amount of uncertainty that abundance modelling introduces. Out of 24 045 EDSUs analysed, *M. muelleri* was identified in 1 922, with approximately 90% of the estimated presence occurring in the depth zone of 100-300 m (Supplementary Material Fig. S2).

Environmental data

In order to associate *M. muelleri* presence with environmental parameters, a list of variables was explored and their values were retrieved for each interval sampled. The variables considered (based on relevance to mesopelagic fish presence) were mainly related to the pelagic environment, including surface variables that have been shown to affect vertically migratory species (Peña 2024) such as *M. muelleri*. Bathymetry data were directly obtained from the acoustic integration data by means of the average bottom depth per interval, while a set of 13 environmental variables was acquired from respective databases (Table 1). Satellite and hydrodynamic model data were used as inputs for the modelling exercise because they are available for the entirety of the study area (even in locations that acoustic data exist but no *in situ* (CTD) data were collected, such as during opportunistic acoustic data recordings) and to be used for mapping projections (see below). For satellite and model-derived parameters, annual mean values (instead of monthly or daily ones) were deemed more appropriate and were used, because (i) the acoustic (presence) data available, were not evenly distributed seasonally and spatially (Table S1) and (ii) the species is not thought to perform extensive seasonal horizontal migrations. The latter is supported by the inspection of seasonal presence/absence data from the Gulf of Corinth, a subregion that has been extensively monitored with seasonal surveys (Kapelonis et al. 2023). Specifically, the examination of those presence-absence data shows extensive overlap in different seasons, both in the horizontal distribution (Fig. S6) and in the bathymetric preferences (Fig. S7) of *M. muelleri*, leading to the conclusion that seasonal horizontal migrations are limited. Variables related to temperature,

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light, chlorophyll and organic matter and variables related to hydrology and topography were acquired for the needs of SDM projection (see below). The exact list of environmental variables and more information on each variable, i.e. transformations, spatial resolution and data source(s), is listed in Table 1.

Data preprocessing

All variables were tested for collinearity in order to omit those that were highly correlated, to improve the interpretability of the models (including diagnostic/evaluation metrics), to reduce the model error for the SDM algorithms, and to avoid model overfitting (Breiner et al. 2015). Four of the variables (CHL, EKE, POC, ZEU) presented high Pearson's Correlation Coefficient values (PCC > 0.7; Supplementary Material Fig. S1), thus only CHL was kept and the rest were not used for the SDM training. Model fitting is more successful when the data follow Gaussian distributions; thus, transformations were applied to environmental data where necessary, to approximate the Gaussian distribution (Table 1, Supplementary Material Fig. S3). All the environmental variables data were standardized by subtracting the mean and scaling to unit variance (i.e. z-transform), to provide similar value ranges for all variables.

The presence percentage of *M. muelleri* in the acoustic data used was approximately 9% (Table S1), which denotes a zero inflated distribution. It has been shown that the number of absences used in SDMs has great influence on their performance (Barbet-Massin et al. 2012). The preferred presence/absence ratio appears to be different for each type of SDM, with machine learning techniques such as gradient boosting machine (GBM), random forest (RF) and multiple adaptive regression splines (MARS), having higher accuracy when the presence/absence ratio is closer to 1, while regression techniques such as generalized additive (GAM) and generalized linear models (GLM) can cope with higher percentage of absence data (Barbet-Massin et al. 2012). The magnitude of the influence that presence/absence ratio has on SDM accuracy also varies amongst different techniques, with little influence on regression techniques and high influence on machine learning techniques (Barbet-Massin et al. 2012). In addition, the 1:1 presence/absence ratio, is shown to provide better SDM predictions, when absence data are derived from a large area (Hong et al. 2019). Thus, the presence/absence data used in the present study were balanced using an algorithm, to randomly remove absence values from the dataset until the number of presence and absence datapoints was equal.

Modelling

The Biomod2 R software package (Thuiller 2003, Thuiller et al. 2023), was used to fit multiple SDMs and produce an ensemble model. Biomod2 combines any number of the following 10 SDM algorithms: classification tree analysis (CTA), GAM, GBM, GLM, surface range envelop (SRE), artificial neural network (ANN), RF, MARS, flexible discriminant analysis (FDA) and maximum entropy (Maxent), to form an ensemble SDM model, which predicts statistics for the probability of the targeted species' presence in the study area.

All 10 available SDM algorithms were included in the modelling procedure. The cross-validation strategy used for individual SDM performance evaluation, was the "random" Biomod2 strategy. When using this strategy, the dataset is split in two groups (80% and 20% of data), all the models use a randomly selected 80% of the data for training, then the remaining 20% of the data are used for calculating two different evaluation metrics: the true skill statistic (TSS) and the receiver operating characteristic (ROC) area under the curve (AUC). Both of them are calculated from specificity and sensitivity values for each individual SDM, using the true presence ratio and false presence ratio deriving from the two groups of the test dataset. TSS values > 0.6 and AUC ≥ 0.8 are considered good to excellent (Komac et al. 2016).

Different combinations of custom tuning settings (e.g. type of formula: quadratic or binomial in GLM and number of trees in Random Forest and GBM) were tested for each individual SDM algorithm by running it three times for each set of settings, using a different part of the dataset for training (80%) and validation (20%) each time and then comparing their mean evaluation metrics, TSS and AUC. The default Biomod2 settings showed the highest performance in every individual model, thus they were used for the final model runs.

Variable importance indexes were calculated for each individual SDM by Biomod2; environmental variables that showed really low importance indexes (<0.1) in all SDMs were removed one at a time and the SDMs were ran again, until all variables with low importance indexes were removed. The retained set of variables included Sea Bottom Depth (DEPTH), Sea Surface Chlorophyll-a Concentration (CHL), Sea Bottom Slope (SLOPE), Photosynthetic Active Radiation (PAR), meridional component of the absolute geostrophic velocity current (VADT) and zonal component of the absolute geostrophic velocity UADT (degrees from North), which were used for model training. All variables that were removed, were individually placed back in with the final set for an extra test run but none showed higher variable importance on those test runs, thus the final variable set remained the same.

The SDMs that met the evaluation metric thresholds, in particular TSS > 0.7 and AUC > 0.8, were combined to create an ensemble model algorithm using a weighted mean based on their TSS scores. Response curve diagrams were created for each environmental variable, to identify how the range of the variable values influenced the probability of *M. muelleri* presence.

Projections

The final ensemble algorithm was used to predict the probability of *M. muelleri* presence in the eastern Ionian and Aegean Seas. Using Biomod2 projection function and three different environmental parameter datasets for the years 2018, 2019 and 2020, three maps were created that presented the probability of presence (0–1) of the species for each year. An additional set of three maps presenting the coefficient of variation between the SDMs for each year was created. The maps were rendered using the QGIS software version 3.4.11 (QGIS Development Team 2019) and were processed to provide a clear image of the probability of presence gradients. The presence-probability maps for the time period 2018–2020 were combined through Qgis and two final maps were created showing the average probability of presence and the standard deviation for the time period 2018–2020.

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Table 2. Evaluation metric scores and Variable importance in each of the Species Distribution Models that were tested.

		Evaluation metric score		Variable importance					
SDMs		TSS	AUC	DEPTH	CHL	SLOPE	UADT	VADT	PAR
RF	Random forest	0.952	0.997	0.546	0.206	0.093	0.206	0.065	0.061
CTA	Classification tree analysis	0.863	0.950	0.799	0.213	0.122	0.270	0.091	0.157
GBM	Gradient boosting machine	0.856	0.971	0.904	0.093	0.025	0.027	0.001	0.035
MAXENT	Maximum entropy	0.814	0.958	0.904	0.048	0.061	0.062	0.010	0.057
MARS	Multiple adaptive regression splines	0.809	0.948	0.864	0.160	0.014	0.078	0.000	0.060
FDA	Flexible discriminant analysis	0.777	0.943	0.947	0.130	0.008	0.025	0.000	0.050
ANN	Artificial neural network	0.777	0.927	0.977	0.083	0.024	0.068	0.030	0.059
GLM	Generalized linear model	0.773	0.927	0.959	0.066	0.011	0.030	0.029	0.021
GAM	Generalized additive model	0.646	0.879	0.718	0.110	0.013	0.278	0.111	0.030
SRE	Surface range envelop	0.473	0.737	0.628	0.067	0.197	0.106	0.110	0.054

Models are listed in order of decreasing TSS. TSS: True skill statistic; AUC: Receiver operating characteristic area under the curve; DEPTH: Sea Bottom Depth; CHL: Surface Chlorophyll-a Concentration; SLOPE: Sea Bottom Slope; VADT: meridional component of the absolute geostrophic velocity current; UADT: zonal component of the absolute geostrophic velocity; PAR: Photosynthetic Active Radiation.

Results

Modelling

Biomod2 individual model runs were 80% successful, with eight out of ten algorithms that the software package supports, showing higher evaluation metric scores than the acceptable predetermined threshold (TSS > 0.7, AUC > 0.8) (Table 2). DEPTH was the highest contributing variable in all modelling methods with mean variable importance index of 0.82 across all models. CHL concentration was second with a mean variable importance index of 0.12 across all models, followed by UADT (0.11), SLOPE (0.06), PAR (0.06) and VADT (0.05). CHL and UADT demonstrated their highest variable importance values in the two top-performing algorithms (RF and CTA) that were used in the ensemble (Table 2). The last three environmental parameters (SLOPE, PAR, VADT) had substantially lower impact in model training.

The ensemble modelling merged algorithm presented great fit to the data with evaluation metric scores well above thresholds (TSS = 0.88, AUC = 0.99). According to the response curve diagrams the highest probability of presence was associated with depths ranging from 200 m to 240 m, CHL concentration ranging from 0.4 mg/m^3 to 1.5 mg/m^3 and UADT (west-east direction, sea current speed) ranging from -0.04 m/s to -0.02 m/s (Supplementary Material Fig. S4).

Projections

Three different maps were projected using the Biomod2 ensemble model, one for each year, presenting the probability of *M. muelleri* presence in the study area from 2018 to 2020. The three maps presented almost identical patterns (Fig. 3b, Supplementary Material Fig. S5) due to bathymetry being the key variable in model training, which remains unchanged through the years. Variability between the three different years was low and small differences were identified in areas that presented high probability of presence in the entirety of the time period (2018–2020) (Fig. 3b, Supplementary Material Fig. S5). The probability of presence was generally higher in the North and North-East Aegean Sea (Fig. 3a, Supplementary Material Fig. S5), with key areas of abundance being between 150 m and 250 m depth, with aggregations following bathymetric contours at the boundaries of deep basins (e.g. the North Aegean Trough as well as south of Lemnos and west of Lesvos islands; see Fig. 1 for region names). In addition, a second extended area with somewhat lower probability of presence was identified in the Aegean Sea, covering similar depth ranges around the Cyclades Island complex and the Argo-Saronic Gulf (Fig. 3, Supplementary Material Fig. S5). The probability of presence was also higher in the northern subbasins, decreasing progressively in the southern areas, following the downwards trend of Surface Chlorophyll-a Concentration from the more productive North to the South Aegean Sea. *Maurolicus muelleri* suitable habitats were further identified by the model inside enclosed Gulfs presenting smoother bottom slopes, such as the Toronean Gulf and the northern part of the Euboean Gulf, which provide extended areas with suitable depth ranges and Surface Chlorophyll-a Concentrations. In the Ionian Sea, the areas with high probability of presence were generally narrow and in close distance to the shore (Fig. 3, Supplementary Material Fig. S5). This is probably due to local topographic characteristics like the occurrence of steeper slopes and narrow continental shelf. Higher probabilities were identified inside the Gulf of Corinth and in the Inner Ionian Sea archipelago (Fig. 3, Supplementary Material Fig. S5). Variability between individual model projections (Fig. 4) was minimal (standard deviation < 0.2) in areas with high probability of presence (>0.8) in the ensemble SDM projections (Fig. 3a), and presented higher values (standard deviation > 0.2) in the areas with lower probability of presence (Fig. 3a).

Discussion

Maurolicus muelleri forms monospecific aggregations in the Mediterranean Sea, as evidenced in the current study by utilizing underwater acoustics paired with targeted biological samplings. This renders *M. muelleri* a great candidate for SDM application and can subsequently contribute to the knowledge of the distribution and population dynamics of the species, which, in the study area (Kapelonis et al. 2023) and the Mediterranean Sea in general (Olivar et al. 2012), is one of the most abundant mesopelagic fish. Herein, the Biomod2 ensemble SDM framework was applied (TSS = 0.88, AUC = 0.99) to model the distribution of *M. muelleri* in the Eastern Mediterranean around Greece. Studies that are based on single-algorithm projections, may suffer from unquantifiable uncertainty (Harris et al. 2024); however, the current approach minimizes the risk of model-related bias and the high variability of results through the procedure of weighing each

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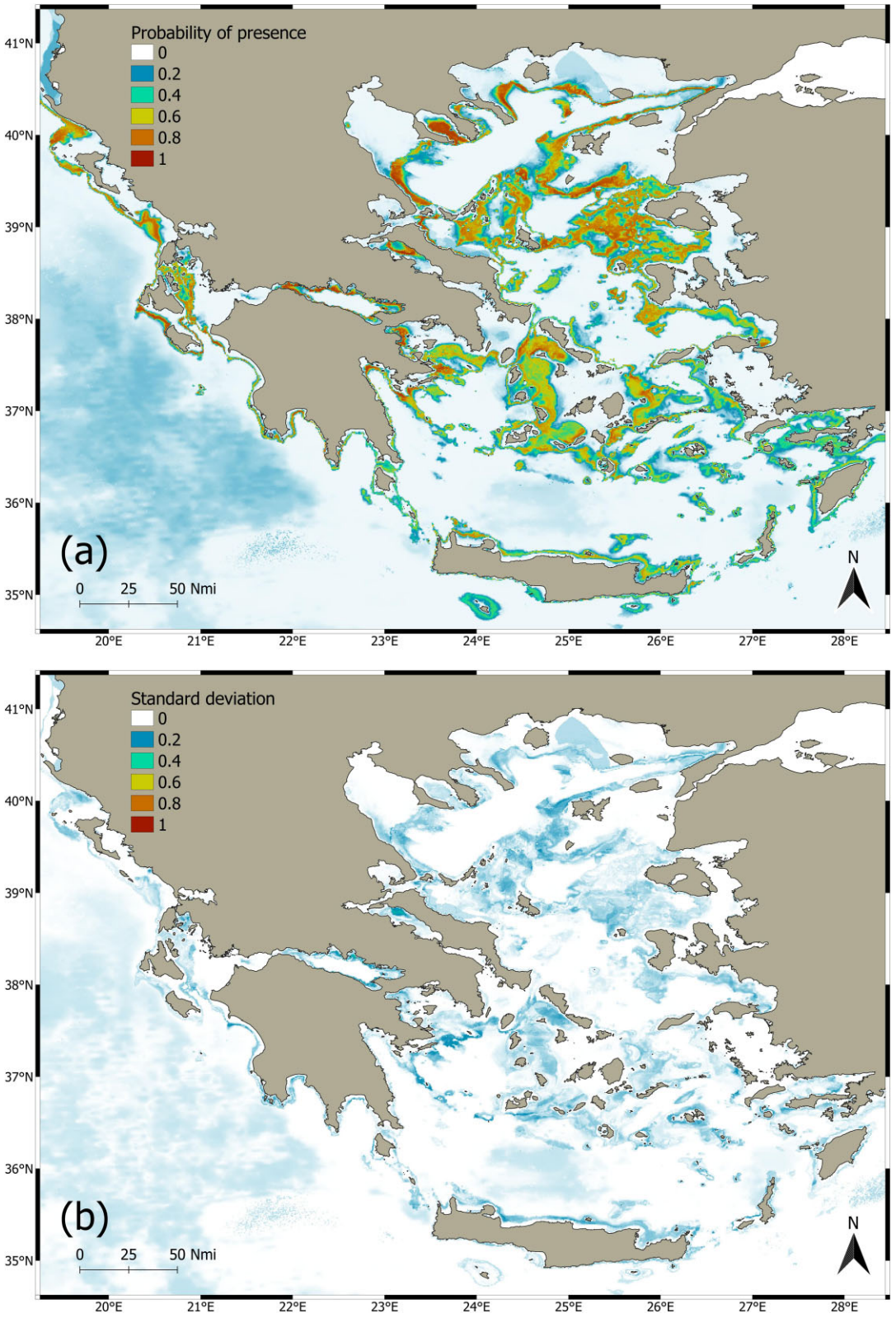

Figure 3. *Maurolicus muelleri* (a) average probability of presence and (b) standard deviation maps for the time period 2018–2020 in the Ionian and Aegean Seas.

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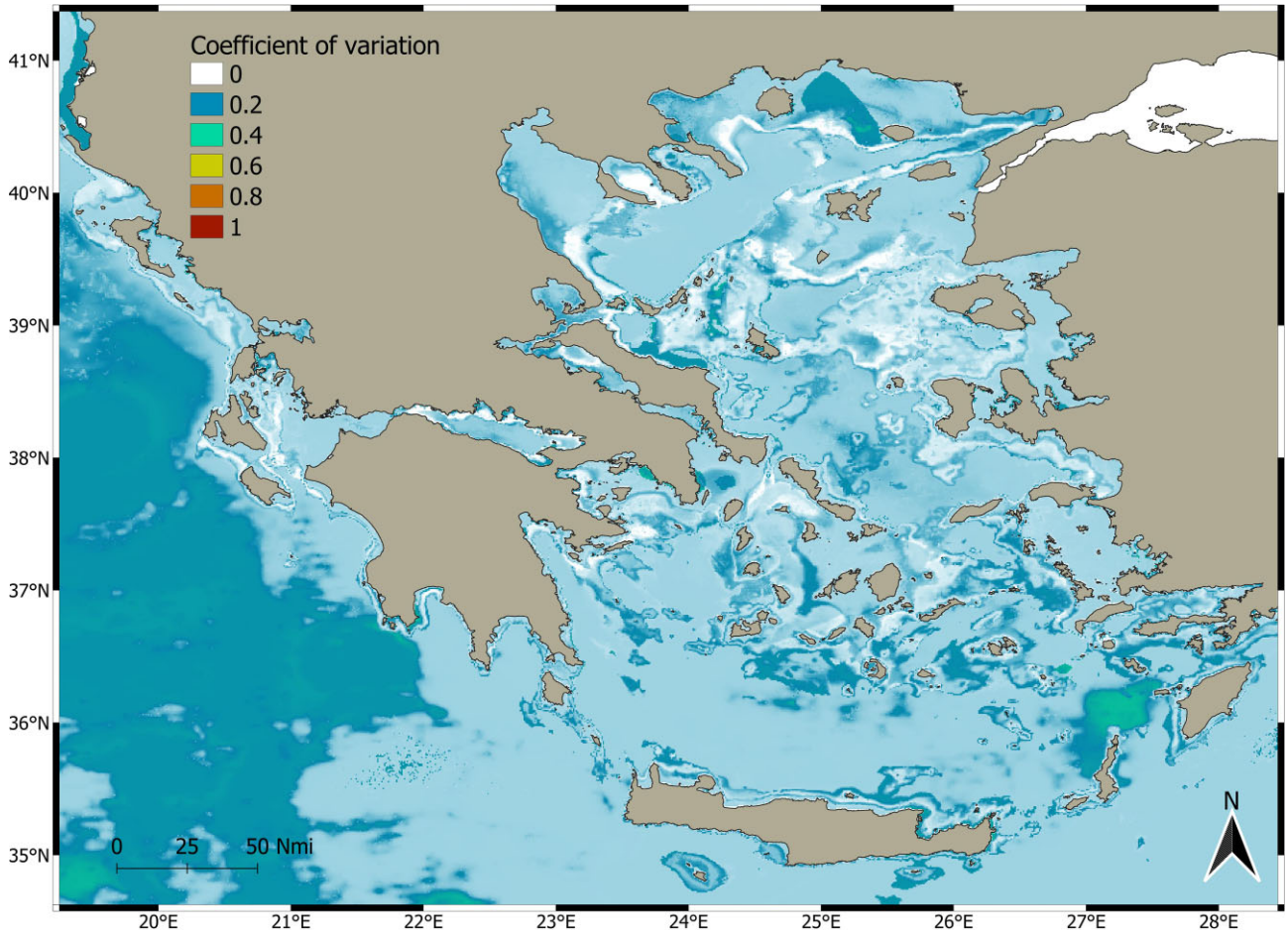

Figure 4. Coefficient of variation of the probability of presence predicted by the eight individual SDMs that were used, for the year 2018 in the study area.

individual SDM based on its performance and then combining all to produce an ensemble model.

Input data were collected by utilizing acoustic surveys targeting *M. muelleri* and other mesopelagic fish, opportunistic acoustic recordings (e.g. recordings during long transits between surveys), as well as acoustic surveys targeting different fish groups (e.g. small pelagic fish) in an effort to increase spatial coverage. The distinct acoustic typology of the aggregations of this species (Fig. 2, Table S3), allows applying species distribution models with a high degree of certainty. The sub-basins in the Eastern Mediterranean Sea considered here, serve as a great study area for SDM applications, as they are characterized by high variability in topography and environmental parameters; examples include the deep Ionian Sea and the topographically complex Aegean Sea archipelago, the highly productive Northern Aegean and the oligotrophic South Aegean, as well as the existence of deep Gulfs with varying characteristics (e.g. with steeper or smoother slopes).

Overall, SDM performance in the current study was high, with eight out of ten SDMs being above the evaluation metric thresholds (TSS > 0.7, AUC > 0.8), even with the relatively strict thresholds that were set (Allouche et al. 2006, Beaumont et al. 2016). The large number of SDMs with high performance used to compose the final ensemble algorithm, likely contributes to the performance of the latter (TSS = 0.88, AUC = 0.99). Low variability was observed between the individual SDM projections -especially in the areas with high probability of presence. This is in part attributed to bottom depth being the dominant driver in all algorithms of the ensemble model.

Mesopelagic fish distributions are known to be associated to bottom depth (Sutton et al. 2017), especially in smaller-scale studies or basins where bottom-depth is a limiting factor (Ross et al. 2010). Similarly, bottom depth was the key predictor for habitat suitability with the highest mean variable importance (0.83) in the current study. The former is not the case in larger open-ocean ecosystems, where bottom depth ranges do not act as a limiting factor, and dynamic environmental parameters (e.g. SST) appear to be the leading driver in similar SDM approaches (Escobar-Flores et al. 2018, Liu et al. 2024). In the current study, the importance of bottom depth as a predictor can be explained by visualizing the monospecific aggregations of the species. They occupy a bathymetrically niche area (~150-250 m), that is located shallower than the typical DSLs and often in stronger association with the seabed. The distribution of *M. muelleri* in the Eastern Mediterranean doesn't seem to overlap extensively with other mesopelagic fish aggregations. In addition, juvenile fish seem to occupy shallow areas and are often observed closer to the surface compared to larger individuals, a behaviour that is likely related to differences in feeding strategy and avoidance of intraspecific competition. *Maurolicus muelleri* shoaling behaviour appears to be similar in different parts of the world; shoals are found in similar depth ranges

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(~150-200 m) during daytime in the North Atlantic Ocean (Staby et al. 2011, Thorvaldsen et al. 2023), with juveniles occurring higher in the water column than larger individuals (Staby et al. 2011, Thorvaldsen et al. 2023). They have been reported to occupy areas near the continental shelf, in the North (Gjøsaeter et al. 1980) and South Atlantic Ocean (Armstrong and and Prosch 1991). Furthermore, *M. muelleri* is the most abundant fish species of the upper mesopelagic zone in the Norwegian Fjords (Gjøsaeter et al. 1980), similar to the Eastern Mediterranean Sea (Kapelonis et al. 2023). As a species that occupies the shallower part of the mesopelagic zone, it's position within the water column seems to be directly associated with light intensity (Staby et al. 2011, Kaartvedt et al. 2019, Christiansen et al. 2021). Moreover, the proximity of the shoals to the bottom and the continental shelf break (Kapelonis et al. 2023) could be related to upwelling features and increased turbulence often occurring near the shelf break, which subsequently increase food availability. The combination of these two features could explain the bathymetrically niche area that *M. muelleri* occupies. As a zooplanktivorous species that performs DVM to feed near the surface during nighttime, while being in close proximity to the bottom during daytime and subsequently is part of demersal fishes' diet (Giske et al. 1990); *M. muelleri* substantially contributes to benthic-pelagic coupling. This, clearly highlights its important role in the Eastern Mediterranean pelagic and benthic ecosystems.

The mean variable importance of CHL and UADT (0.12 and 0.11 respectively) is low compared to DEPTH, however they presented substantially higher variable importance (>0.2) in the two top-performing individual SDMs (CTA: TSS = 0.86, RF: TSS = 0.95) and in the ensemble algorithm (weighed by TSS score), which render them important predictors of *M. muelleri* distribution. CHL concentration, has been shown to be one of the most important variables for species habitat suitability and biomass prediction of small pelagic (e.g. Giannoulaki et al. 2013) and mesopelagic fish (Irigoien et al. 2014). UADT, a variable associated with sea current movement on the North-South axis, was also highlighted as an important predictor for Atlantic mackerel habitat suitability in the Mediterranean Sea (Giannoulaki et al. 2017). Both UADT and CHL are associated with productivity and food availability. Their relatively low variable importance though, could be attributed to the usage of presence/absence data in the SDM runs instead of abundance data. A modelling approach based on abundance information could probably further highlight the effect of variables related to circulation, productivity and/or food availability, because their absolute values and gradient are expected to also affect population density in addition to the species presence.

The annual projected maps (2018–2020) suggested low variance in the probability of the species' presence as the dynamic environmental parameters presented a smaller effect, compared to the non-dynamic DEPTH. Some variability was identified only in areas with high probability of presence, i.e. values varying from 0.8 to 1 between years 2018 and 2020 (Fig. 3b, Supplementary Material Fig. S5). SST and SBT, were amongst the variables that had minimal impact in all individual models and were excluded from the final ensemble algorithm. Nevertheless, CHL, which was the second most impactful environmental parameter, is known to be influenced by changes in sea temperature (Raitsos et al. 2013, Dunstan et al. 2018), mostly due to vertical mixing within the water column. The Mediterranean Sea, as a semi-enclosed basin, is considered an area prone to climate change and has been previously described as a climate change "hot spot" (Giorgi 2006). Warming in the Mediterranean Sea has been associated with stronger stratification of the water column and with a decrease of primary productivity and higher zooplankton mortality rates (Kalloniati et al. 2023, Darmaraki et al. 2024). Juvenile *M. muelleri* individuals are known to exhibit a "bolder behaviour" for feeding purposes, by occupying spaces significantly closer to the surface during daytime (Christiansen et al. 2021, Kapelonis et al. 2023, Thorvaldsen et al. 2023). Thus, they strongly rely on the productivity of the epipelagic ecosystem. In the current study, the different effects of oligotrophic and more productive regions on *M. muelleri distribution* can be observed through the final projection (Fig. 3a). *M. muelleri* probability of presence is substantially higher in the more productive regions such as the North Aegean Sea (Fig. 1), compared to the oligotrophic Cretan Sea (Fig. 1) in the same bottom depth range; this provides additional insight on the effect of primary production on *M. muelleri* presence. Based on this, *M. muelleri* presence in the Eastern Mediterranean is expected to be negatively affected by climate change through lower primary productivity and reduced food availability, should the oceanic warming continue.

Recent studies have shown that *M. muelleri* is major zooplankton consumer (Bernal et al. 2023, Badouvas et al. 2024) serving at the same time as prey for commercial fish such as tunas and charismatic megafauna including dolphins (Giske et al. 1990, Falautano et al. 2007, Olafsdottir et al. 2016, Giménez et al. 2018). Areas where the projected probability of *M. muelleri* presence is high, overlap to a great extent with main fishing grounds for commercial species in the Greek Seas (Maina et al. 2016). Specifically, *M. muelleri* projected distribution presents high resemblance with the fishing grounds for Blackmouth catshark (*Galeus melastomus*) in the North and Central Aegean Sea and overlaps significantly with fishing grounds for commercial species such as Atlantic horse mackerel (*Trachurus trachurus*), European hake (*Merluccius merluccius*) and Shortfin squid (*Illex coindenti*), mostly in the North and Central Aegean Sea, the Saronic Gulf and the Inner Ionian Archipelago (Maina et al. 2016). The habitats of the Common dolphin (*Delphinus delphis*) and Bottlenose dolphin (*Tursiops truncatus*) during the early summer period (Giannoulaki et al. 2017), also cover a great part of *M. muelleri* spatial distribution in the North-East Aegean, the Inner Ionian Archipelago and the Cyclades Island Complex. Several of those commercial and PET species feed on *M. muelleri* individuals, setting *M. muelleri* an important part of the marine food webs in the Eastern Mediterranean Sea ecosystems (e.g. Giske et al. 1990, Würtz and Marrale 1993, Falautano et al. 2007, Dede et al. 2016, Giménez et al. 2018). Climate-induced changes in the projected habitat of *M. muelleri*, are further highlighted when considering the overlapping distribution of *M. muelleri* and other commercial and/or Protected Endangered and Threatened (PET) species in the study area.

Although mesopelagic fish have become of recent research interest (Caiger et al. 2021), knowledge on their abundance, distribution and species-specific patterns in behaviour and environmental preference are poorly understood. This is partly attributed to the fact that, thus far, they have not been

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commercially exploited and monitored, and to the many challenges faced when collecting data on-and samples of mesopelagic fishes, including accessibility of the deep-sea and costs associated with surveying these environments. The current study provides insights on *M. muelleri* spatial distribution and geographic features that can determine *M. muelleri* potential habitat. It can also help identify areas important for mesopelagic fish and other species that rely on them, for future research and for monitoring the species' population dynamics. Moreover, it has significantly contributed to the general knowledge concerning the ecology of the mesopelagic zone in the Eastern Mediterranean Sea. Nevertheless, further aspects of *M. muelleri* and the mesopelagic zone dynamics remain to be explored. Abundance data could be utilized to explore the potential impacts of abundance-related parameters that can be overlooked when investigating presence/absence data. This type of abundance modelling could be beneficial for biomass estimations, since dedicated surveys over extended areas are not likely to be implemented for non-commercial fish species. Composition of the mesopelagic-boundary community DSLs (Reid et al. 1991), that are likely to occasionally contain *M. muelleri* mixed with other mesopelagic species, should be further explored and included in SDMs alongside with monospecific aggregation data, for additional insight on the species' distribution. Future projections of environmental data can be used in SDM to provide information on the magnitude of climate change impacts on *M. muelleri* habitat extent. Finally, the current approach could be applied to additional echotraces from the twilight zone (e.g. DSLs at different depth zones) to increase our knowledge on other mesopelagic fishes and the ecology of the mesopelagic zone in general.

Acknowledgements

We thank the two anonymous reviewers and the editor for their constructive comments that significantly improved the quality of this manuscript. Also, we thank the captain and the crew of the Research Vessel PHILIA and the onboard scientists who participated in the cruises.

Author contributions

Alexandros Alamanellis: Investigation, Data Curation, Software, Formal analysis, Visualization, Writing—Original Draft; **Zacharias Kapelonis**: Supervision, Methodology, Investigation, Data Curation, Visualization, Conceptualization, Software, Formal analysis, Writing—Review & Editing; **Marianna Giannoulaki**: Methodology, Writing—Review & Editing; **Dionysios E. Raitsos**: Methodology, Supervision, Writing—Review & Editing; **Vasilis D. Valavanis**: Data Curation, Writing—Review & Editing; **Konstantinos Tsagarakis**: Conceptualization, Supervision, Methodology, Investigation, Funding acquisition, Writing—Review & Editing.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Conflict of interest: The Authors declare that there is no conflict of interest.

Funding

Data collection and analysis were performed in the framework of projects (i) MesoBED "Mesopelagic fish: biology, ecological role and distribution of a disregarded trophic link," funded by the Hellenic Foundation for Research and Innovation and the General Secretariat of Research and Innovation (Greece) (Project no 449), (ii) Greek National Fisheries Data Collection Programme, implemented to support the Common Fisheries Policy co-financed by the European Maritime and Fisheries Fund (EMFF) and the Ministry of Rural Development and Food, Directorate General of Fisheries (Greece), (iii) RePHIL "Hellenic Research Fleet—Reconstruction of the Research Vessel PHILIA," funded by the Operational Program (OP) "Competitiveness Entrepreneurship and Innovation" (NSRF) for the period 2014-2020 and co-financed by the European Regional Development Fund (ERDF) (MIS 5002682) and iv) TWINKLE "Life in the twilight: new knowledge on the biology and ecology of the mesopelagic zone in the context of global change," carried out within the framework of the National Recovery and Resilience Plan Greece 2.0, funded by the European Union—NextGenerationEU (Implementation body: HFRI, Project no 15565). Raitsos D.E. was supported from the Hellenic Foundation for Research and Innovation (H.F.R.I.) under the 2nd Call of "Research Projects to Support Faculty Members & Researchers" scheme (Programme OPTIMISE, Grant Number: 04808).

Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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Handling editor: Alina Wieczorek

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