Habitat preferences of *Phycis blennoides* (Pisces: Gadiformes): environmental factors and fishing-related ontogenic deepening

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ABSTRACT: *Phycis blennoides* is a component of the ecosystem of the Atlantic waters of northern Spain and a species of commercial interest for fisheries in this region. However, little is known about the distribution of this species. The present study analyses the relationships between different environmental and spatial variables and distribution of *P. blennoides*. Biological (presence—absence, abundance, biomass and total length) and environmental data were collected from a bottom trawl survey carried out off the northern coast of Spain. These data were used in 2-step generalised additive models to examine both the relative significance of physical factors in influencing *P. blennoides* distribution and to generate density distribution maps. Additionally, the role of fishing effort on *P. blennoides* body size distribution with depth was analysed. Geospatial analyses showed that changes in annual abundance did not influence physical habitat preference. Most of the variation in spatial distribution was explained by the sampling position and depth. The analyses showed that *P. blennoides* exhibited habitat preferences in the waters of Galicia and the Cantabrian Sea, with higher values of presence, abundance and biomass on the upper slope and on fine-grained sediment bottoms. *P. blennoides* biomass increased with depth, probably due to the increased mean size of individuals with depth. Modelling results suggest that the observed ontogenetic deepening appears to be mainly driven by the life history strategy of the species, but is also reinforced by fishing effort.

KEY WORDS: *Phycis blennoides* · Spatial distribution · Generalized additive models · GAMs · Environmental drivers · North-eastern Atlantic

1. INTRODUCTION

Today, many fish stocks are either over-exploited, depleted, fully exploited or recovering from exploitation (FAO 2022) due to decades of poor or non-existent management. This issue is especially severe in deep-sea species. There is a need for effective fisheries management, not only to recover those stocks that are outside safe biological limits, but also to ensure food security by providing a sustainable and stable supply of fish. However, fisheries management is strongly influenced by fluctuations in the distribution and abundance of fish species, which, in turn, are influenced by fluctuations in the environment

(Boehlert & Schumacher 1997). This has led to considerable efforts to predict the spatial distribution of fish species.

A distribution model (DM) is a useful numerical tool for relating species distribution data (occurrence and/or abundance at known locations) to environmental variables. The model can be used to understand the auto-ecology of the species and/or to predict the species' distribution across the study area. Among the different DM methods, generalized additive models (GAMs) (Hastie & Tibshirani 1990) have been commonly applied to model the spatial distribution and environmental preferences of commercial (e.g. Maravelias et al. 2007, Katsanevakis et al. 2009,

González-Irusta & Wright 2016, 2017) and non-commercial (e.g. Damalas et al. 2010, Arronte et al. 2022) fish species. These studies illustrate not only the role that environmental factors play in species abundance and distribution, but also the importance of these types of studies in understanding the effects of environmental variables on the distribution, abundance and dynamics of fish species for an effective and sustainable fisheries management.

In the present study, we sought to identify these potential interactions in the greater forkbeard *Phycis blennoides* (Brünnich, 1768), a commercially important fish species. This deep-sea benthopelagic fish is widely distributed in the north-eastern Atlantic, from Norway and Iceland to Cape Blanc in West Africa, and in the Mediterranean (Cohen et al. 1990). In the north-eastern Atlantic, *P. blennoides* inhabits the continental shelf and slope at depths between 125 and 1260 m (Merrett et al. 1991, Sánchez 1993).

On the northern continental shelf of Spain, *P. blennoides* is a fish species commonly found in deep-sea sedimentary habitats (Sánchez 1993). It plays a significant role in benthic—pelagic coupling by feeding on benthic crustaceans during the early years of its life cycle (Sorbe 1977) and serving as a prey source for pelagic top-predators (Lassalle et al. 2011, Corrales et al. 2022). The species is commercially exploited by both bottom trawl and deep-water longline fisheries (Punzón et al. 2011). It is also a relatively valuable by-catch for the mixed demersal trawl fishery targeting species such as hake *Merluccius merluccius*, megrim *Lepidorhombus* spp. and monkfish *Lophius* spp. For the deep-water longline artisanal fishery, it is not only a seasonal target species, but also a by-catch for the fleet targeting conger *Conger conger* and common mora *Mora moro*. In addition, it can be a sporadic and alternative target species for the *M. merluccius* longline artisanal fishery when this species is scarce or when the economical revenues from its exploitation are low.

Whilst in the Mediterranean Sea the biology of *P. blennoides* (e.g. MacPherson 1978, Gallardo-Cabello 1980, Massutí et al. 1996, Ragonese et al. 2002) and the effect of environmental variables on its abundance, distribution and size (e.g. Katsanevakis & Maravelias 2009, Katsanevakis et al. 2009, D'Onghia et al. 2010) has been studied, in the north-eastern Atlantic there are no studies on the factors influencing its spatial distribution, and information on the population structure and dynamics of the species is scarce, with most data coming from grey literature (e.g. ICES technical reports) and from works on the bathymetric distribution and/or feeding habits of demersal species (e.g. Sorbe 1977, Mauchline & Gordon 1984, Merrett et al. 1991,

Sánchez 1993). In this area, only data on its age and growth in the Cantabrian Sea and north-west of the Iberian Peninsula (Casas & Piñeiro 2000) has been collected, and its behavioural ecology and feeding habits in the southern Atlantic French coast (Sorbe 1977, Uiblein et al. 2003) and landings, discards and length composition in some regions (ICES 2022) have been studied.

In the present paper, long-term data from a scientific bottom trawl survey have been used to predict the preferential habitat (the proportion of potential habitat used on average over time) of *P. blennoides* in the trawlable grounds off the north-eastern Spanish coast. The main objective of the present study was to model, for the first time in this area, the effects of spatial, temporal and oceanographic variables on its relative abundance and biomass using GAMs. In addition, and based on previous works on its size—depth distribution in the Mediterranean (MacPherson & Duarte 1991, Massutí et al. 1996), the relationship between its body length and depth was also examined.

2. MATERIALS AND METHODS

2.1. Study area

The study area comprised the northern Spanish shelf (southern Bay of Biscay, north-eastern Atlantic), where 2 distinct areas with different sedimentological and hydrographic characteristics can be identified: the Galician waters (ICES Division IXa) and the Cantabrian Sea (ICES Division VIIIc) (Fig. 1) (Fernández-Salas et al. 2015).

The Galician shelf comprises a narrow strip (30 km wide from the coast) where frequent, strong and seasonal upwelling of cold and dense North Atlantic Central Water (NACW) results in nutrient enrichment of the area, ensuring high productivity (Figueiras et al. 2002). The Cape of Finisterre acts as a natural boundary of the Galician waters, and the shelf north and west of the Cape is characterised by sandy bottoms, while south of the Cape, the inner shelf is covered by muddy bottoms and the middle and the outer shelf by sandy bottoms, due to the presence of many sea-drowned valleys ('rías') and the large Miño River (López-Jamar et al. 1992, Fernández-Salas et al. 2015).

The Cantabrian Sea shelf is very narrow (4–25 km wide), with a steep slope, cut by several submarine canyons and with many rocky outcrops distributed irregularly (Fernández-Salas et al. 2015). Cape Peñas is a natural boundary of the Cantabrian shelf, with the area to the west wider and sandy and the eastern area
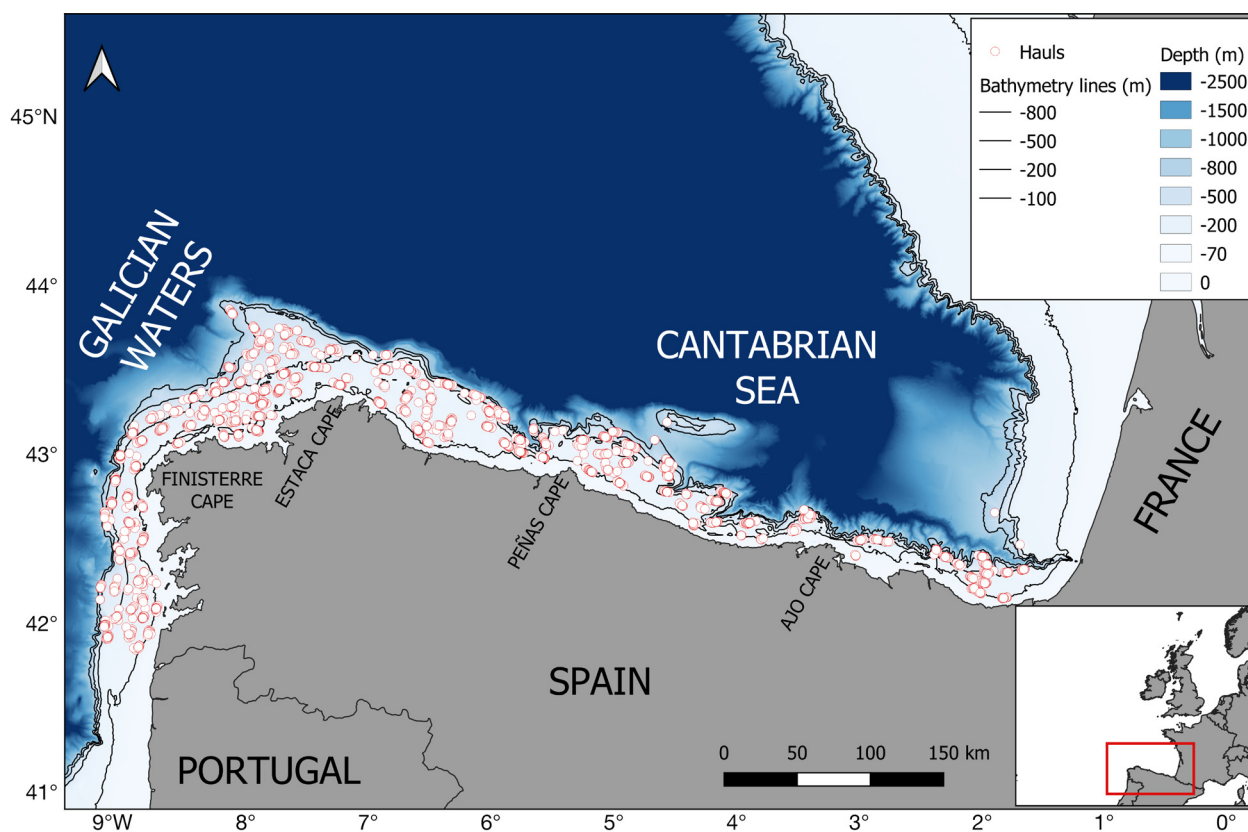
Fig. 1. Study area showing the distribution of hauls carried out during the study period (1998—2019)

narrower and muddier. In general, muddy sediments are located at the edge of the shelf and slope and are associated with the discharge of French rivers on the shelf of the easternmost part of the Cantabrian Sea (Rey & Medialdea 1989). Oceanographically, the area is under the influence of the extension of the Iberian Poleward Current (IPC) and maintains a regular pattern of hydrographic conditions throughout the year, with vertical mixing in winter and stratification in summer (Sánchez & Gil 2000).

2.2. Biological data

Data was obtained from the DEMERSALES bottom trawl surveys (ICES code: SPGFS WIBTS-Q4), carried out by the Spanish Institute of Oceanography (IEO) (ICES 2023), which are carried out annually every autumn (September and October) on the soft bottoms of the northern continental shelf of Spain for demersal fisheries and ecosystem assessment (Step 1 in Fig. 2). The methodology of these surveys has remained unchanged throughout this historical series. Trawling operations were carried out during daylight hours at a speed of 3.0 knots using a baca 44/60 otter trawl gear (ICES 1991) with a haul duration of 30 min from ground contact monitored by a Scanmar net control system. The survey area was stratified in 3 depth strata (70—120, 121—200 and 201—500 m) and a stratified random sampling scheme was applied. The number of hauls per stratum was proportional to its trawlable area. Moreover, additional hauls shallower than 70 m and deeper than 500 m were conducted every year whenever possible. During the study period (1998—2019), a total of 2814 valid hauls were carried out, covering a depth range from 36 to 846 m (Fig. 1). For each haul, total weight, total length (TL) and number of *Phycis blennoides* specimens were recorded.

2.3. Environmental layers

The temporally invariant environmental data layers (bathymetry, slope, sediment type and percentage of organic matter) and the annual layers for near-bottom temperature and near-bottom salinity were those used in Arronte et al. (2022) (Step 2 in Fig. 2). The values of the environmental variables included in the
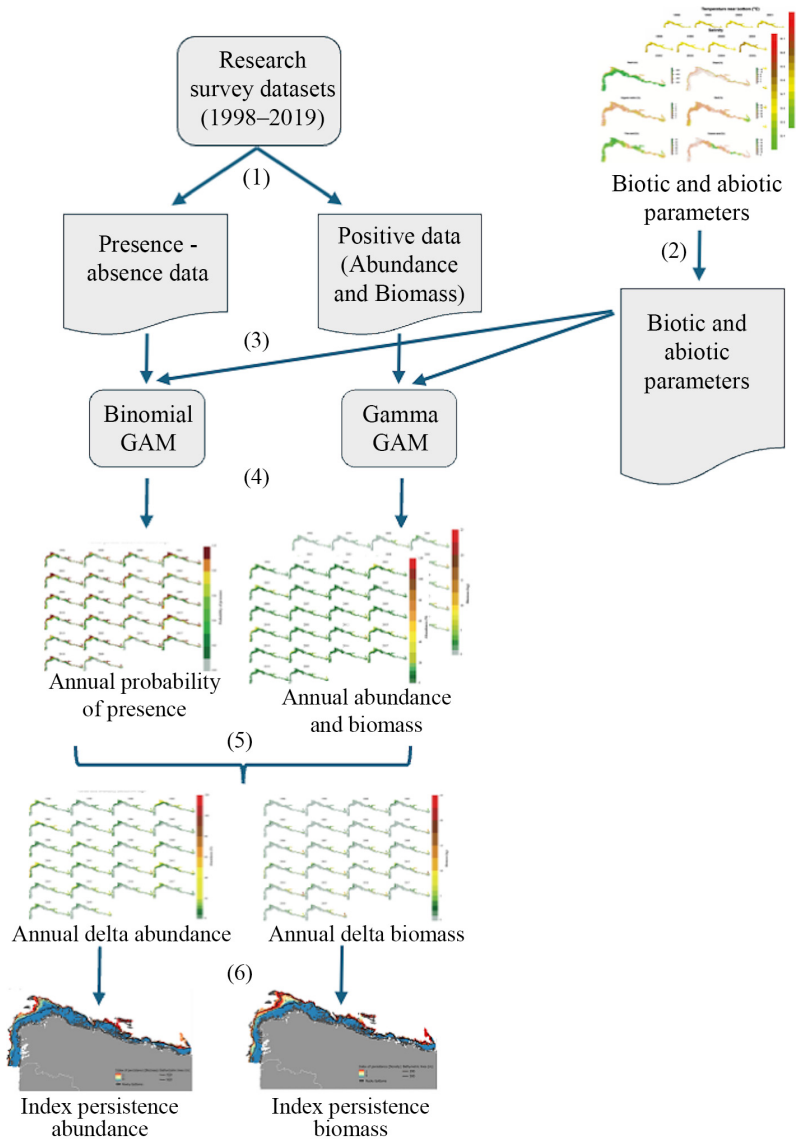
Fig. 2. Schematic of the different steps followed to predict the spatial distributions of *P. blennoides* across the northern Spanish continental shelf using a delta generalized additive modeling approach. (1) Extraction of presence–absence data and positive abundance and biomass data from the DEMERSALES surveys datasets. (2) Relevant environmental and habitat parameters to to be incorporated into generalized additive models (GAMs). (3) Fitting of binomial GAMs and gamma GAMs, using presence–absence data and positive abundance and biomass data, respectively, in conjunction with the environmental and habitat parameters. (4) Predictions of annual probabilities of presence, and abundance and biomasses given a non-zero event using binomial and gamma GAMs, respectively. (5) Predictions of annual spatial distributions through the combination of binomial and gamma GAMs according to the delta method. (6) Conversion of the annual delta maps of abundance and biomass into 2 unique maps using the index of persistence. Schematic modified from Grüss et al. (2014)

culated to a final resolution of 3 × 3 km. The DEMERSALES survey only samples soft bottoms. Thus, and due to the presence of rocky outcrops patchily distributed in the study area (Fernández-Salas et al. 2015), rock data were downloaded from the EMODnet Geology portal (https://www.emodnet-geology.eu/) and areas with rocky substrates were removed from the environmental layers before their inclusion in the analyses. Therefore, the model predictions only covered soft bottom areas, and the distribution of *P. blennoides* on rocky bottoms was not analysed in the present work.

2.4. Data analysis

Prior to modelling, all explanatory covariates were checked for collinearity. Thus, collinear variables, as defined by variance inflation factors (VIFs) > 3.0 and Pearson's R correlation coefficients > 0.7, were not allowed in the same model (Zuur et al. 2009). No variable pairs were found with VIF values > 3 (Table S1 in the Supplement at www.int-res.com/articles/suppl/m745p147_supp.pdf), but strong correlations were found in sediment type (Table S2). Based on previous works on the biology of the species, mud was omitted from the models prior to fitting.

2.4.1. Abundance and biomass data

Abundance and biomass were modelled separately using GAMs (Hastie & Tibshirani 1990, Wood 2017). This regression technique is particularly suitable for analysing spatial distribution, as the responses are not normally distributed and there are not necessarily linear or monotonic relationships between the response and the explanatory variables. As the data came from a scientific survey, a large number of zero-value observations were obtained. The analysis of such zero-inflated data is somewhat problematic, as zero-value observations could mask the underlying spatial dependence of

analysis were obtained by estimating the haul position as the mean point between the shoot and haul positions and extracting the value at that point from the environmental layers. Considering the inherent location errors in the data matrix, all layers were cal-

species on environmental variables (Maravelias et al. 2012). A 2-step approach (delta model) was implemented to account for the overdispersion and zero-inflation (Barry & Welsh 2002, Potts & Elith 2006) encountered in the data matrix of *P. blennoides*. Delta GAMs have proven effective in ecological studies to analyse the spatial distribution and abundance of marine species (e.g. Maravelias et al. 2012, Asjes et al. 2016, Rubec et al. 2016, González-Irusta & Wright 2016, 2017, Langton et al. 2021, Arronte et al. 2022).

First, the probability of presence of *P. blennoides* was analysed using a binomial error distribution and a logit link function. Then, the abundance (number of individuals) and biomass (kg), calculated for 30 min of trawling and removing the zeros, was modelled using a gamma GAM and a log link function (Steps 3 & 4 in Fig. 2). In addition, the model equations included a 'gamma = 1.4' to help against overfitting by the smoothers; it puts a heavier penalty on each degree of freedom in the generalised cross validation (GCV) score without compromising model fit (Wood 2017). Finally, the presence—absence model was multiplied by the abundance or biomass model to produce 2 delta models (one for the abundance and one for the biomass) (Step 5 in Fig. 2). Thus, the 2-step model approach produced 5 models (one probability of presence model, one abundance model, one biomass model and 2 delta models). All GAMs were built in R (R Core Team 2022) with the package 'mgcv' (Wood 2017), with smoothers constrained to 4 knots (the exception was the haul position [interaction longitude: latitude], which was restricted to 16 knots) and selecting cubic regression spline smoothing as it produces the most robust GAM with the lowest residual deviance and GCV values (Wood 2017). To account for potential spatial effects from unmeasured drivers (or endogenous spatial autocorrelation) that could result in otherwise unexplained patterns, the coordinates (longitude and latitude) of each trawl were included in the model year by year. Finally, it was decided a priori that year should be included as a categorical variable, whether a year effect was found to be present or not, with the attempt to remove any temporal effects through multi-collinearity with the other covariates. The full binomial model for presence—absence was:

$$
\begin{aligned}
Pr_p = \beta_1 &+ s(depth) + s(temperature) \\
&+ s(salinity) + s(organic\ matter) + s(slope) \\
&+ s(coarse\ sand) + s(fine\ sand) \\
&+ s(haul\ position\ by = f(year)) + f(year) + \varepsilon
\end{aligned}
\tag{1}
$$

where Pr_p is the probability of presence of *P. blennoides*, β_1 is the intercept, s is the anisotropic smoothing

function, f indicates the parametric coefficients included as factors, and ε is the error term. The full models for the predicted abundance (Pr_a) and predicted biomass (Pr_b) of *P. blennoides* were modelled using the same variables as the binomial model.

2.4.2. Body size data

Prior to any modelling of the relationship between body size and depth, an exploratory analysis was conducted to determine if the increase in the mean size with depth observed in the Mediterranean (MacPherson & Duarte 1991, Massutí et al. 1996) was also present in the study area.

As the number of hauls in which the species was present (1151) would make it difficult to interpretate the depth-body size trend, hauls were grouped into a 10 m depth bin. For each interval, the geometric mean (in cm) of TL was calculated to minimise the negative effect that the extreme values and asymmetric distributions could cause. The change in size with depth was then tested by regression analysis. The species showed a significant positive correlation (Fig. S1) and, therefore, its mean size was modelled.

Fishing effort has been identified as one of the possible factors responsible for the change in depth distribution with age (Audzijonyte & Pecl 2018, Frank et al. 2018). Therefore, we decided to include the trawling fishing effort (otter and pair trawl) in the mean size model to analyse the possible effect of fishing on the presence of large individuals in deeper waters. It should be noted that trawling effort was only used as an explanatory variable for mean size, but not for abundance and/or biomass spatial distribution, due to the commercial value of *P. blennoides*, which could lead to an increase in effort in areas with high biomass values, creating potential spurious relationships between the species and environmental variables. The spatial distribution of the swept area was obtained using vessel GPS positions from the vessel monitoring systems (VMS) and logbook data (gear information). Both were provided by the Spanish Ministry of Agriculture, Food and Environment (pers. comm.). VMS pings not related to fishing activity were removed using speed and other criteria (see Punzón et al. 2016 for further information on the analysis of VMS data). The mean annual swept area for each cell (km^2) was converted to the number of trawls per cell by dividing the mean annual swept area by the cell area (3×3 km cell) (Fig. S2). Fishing effort was calculated as the mean trawling effort for the period 2009—2019 and biological data were con-

strained to the same period to ensure consistency of results.

The full model for the mean length was:

$$Pr_{ml} = \beta_1 + s(depth) + s(fishing\ effort) + f(year) + \varepsilon \tag{2}$$

where Pr_{ml} is the predicted mean length (in cm) of *P. blennoides* in a given haul (*h*), β_1 is the intercept, s is an anisotropic smoothing function (cubic regression spline), and ε is the error term. The model was constructed using a gamma GAM, a log link function, 4 knots, and a 'gamma = 1.4' as in the abundance and biomass models.

All model selection was carried out using the R package 'MuMIn' (Bartoń 2019) and the optimal (best-fitting) model was selected based on the lowest Akaike's information criteria (AIC) (Wood 2017). The relative importance of each variable was tested by removing the targeted variable from the final model and calculating the deviance variation. Finally, with the R package 'spdep' (Bivand et al. 2013), the spatial autocorrelation in the residuals of the presence–absence, abundance, and biomass final models was tested using Monte Carlo simulation (1000 permutations) of Moran's *I*.

2.5. Spatial dynamics of *Phycis blennoides* distribution

The relationship between the abundance and biomass of *P. blennoides* and its spatial distribution in the study area for each year of the period 1998–2019 was determined using geostatistical aggregation curves (Petitgas 1998) and the space selectivity index (Ssp) (Tamdrari et al. 2010). The combination of both tools provides a comprehensive understanding of the spatio-temporal dynamics of the species distribution. The curves represent the proportion of total abundance (number; N) and total biomass (kg; W) of *P. blennoides* observed per surface unit, as a function of the proportion of space (hauls) occupied by the species. The Ssp is a dispersion parameter, analogous to variance, that provides information on the level of aggregation and it was used to discriminate between different spatial dynamics. The statistical significance of variations in Ssp between years was tested using bootstrapping. Following Petitgas (1998), the data set for all the years combined was randomly resampled 1000 times with replacement. The N- and W-curves were recalculated using this dataset and the mean Ssp and 95% confidence intervals were calculated using the boot and boot.ci functions from the 'boot' pack-

age in R (Canty & Ripley 2019). If the annual Ssp value for a given year fell outside the confidence interval, the null hypothesis (no significant variation in Ssp between years) was rejected. Further information on the calculation of geostatistical aggregation curves and Ssp can be found in Petitgas (1998) and Tamdrari et al. (2010), respectively.

2.6. Evaluation of the models

The accuracy of each of the 6 models (one probability of presence model, one abundance model, one biomass model, 2 combined delta models [one for abundance and one for biomass] and one mean size model) was tested using cross-validation. According to Meyer et al. (2018), there is a risk of over-fitting (autocorrelation) in spatial data and its impact between training and test data must be reduced to make the estimated performance of the model suitable not only for a specific local region but also for the entire dataset. Therefore, we followed a spatial cross-validation strategy (Roberts et al. 2017) to evenly distribute the partitioned spatial data across the entire study area. In the present study, spatial cross-validation was performed using a checkerboard strategy by applying the function 'spatialBlock' from the R package 'blockCV' (Valavi et al. 2019) to divide the data into training and test sets using spatial blocks. The size of the spatial blocks (24.7 km) was set using the function 'spatialAutorange' from the same package, which allowed us to use the range of the spatial autocorrelation in the explanatory variables. The data present in each group of blocks (see Valavi et al. 2019 for a further description of the checkerboard strategy) were then randomly assigned as test or training data. Finally, each training and data set was randomly subsampled, selecting 80% of the data from each set in each iteration to prevent duplicate data. The process was repeated 10 times and, in each iteration, the area under the curve (AUC) (Fielding & Bell 1997), the kappa value (Cohen 1960), and the true skill statistics (TSS) (Allouche et al. 2006) were calculated to evaluate the ability of the training subsample to predict the probability of presence. The AUC is a threshold-independent model evaluation indicator that measures the ability of the model to correctly predict where a species is present or absent. AUC values vary from 0 to 1, with a value ≤0.5 indicating that the model has no predictive ability and a value ≥0.7 indicating that the model is acceptable (Peterson et al. 2011). Both kappa and TSS are threshold-dependent measures of model accuracy for presence–absence

predictions. Kappa corrects the overall accuracy of model predictions by the accuracy expected to occur by chance, and TSS measures specificity (proportion of correctly predicted absences) and sensitivity (proportion of correctly predicted presences) in the form TSS = (specificity + sensitivity) -1. Both range from -1 to $+1$, where $+1$ indicates perfect agreement, a value $\leqslant 0$ indicates performance no better than random and a value >0.4 is considered an acceptably accurate model (Landis & Koch 1977, Zhang et al. 2015).

Abundance, biomass and mean size models were evaluated using the Spearman correlation coefficient between observed and predicted abundance, biomass and mean size values respectively. This was also done for the delta and mean size models. Spearman's rank values range from -1 to $+1$, where 0 represents a complete lack of correlation and an absolute value $\geqslant 0.4$ is considered as the threshold for an acceptable correlation (Fowler et al. 1998). Evaluation metrics were calculated using the 'evaluate' implementation in the R package 'dismo' (Hijmans et al. 2022) and 'cor' in the package 'stats' (R Core Team 2022).

2.7. Combining the delta maps

To combine the prediction of the aggregation of the 22 yr into a single final map for abundance and for biomass, we followed the methodology of Colloca et al. (2009) and González-Irusta & Wright (2017). Applying their methodology, the delta maps were converted into binary maps using a threshold for abundance and biomass for each year. The threshold was computed using geostatistical aggregation curves calculated from the abundance and biomass predictions (using the cells as surface unit) and the point where the tangent to the curve had a slope of 45°. This point was used as a threshold for identifying aggregation grounds for each year, as it corresponds to a change in the spatial distribution of fish from a dispersed to an aggregated pattern. This threshold was calculated separately for abundance and biomass and for each year of the study period. The threshold was then applied to the delta models to delineate the aggregation areas for abundance and biomass in each year. A more detailed explanation of the methodology can be found in Colloca et al. (2009). Once the 44 maps were converted into binary maps, the index of persistence (I_i) was calculated as:

$$I_i = \frac{1}{n} \sum_{k=1}^{n} F_v \qquad (3)$$

where n is the number of years considered and F_v is the value of each cell in each binary map. F_v was considered 1 (the cell is considered suitable for aggregation) if the predicted abundance (P_a) or biomass (P_b) in the cell was higher than its corresponding threshold, and 0 otherwise (the cell is not considered suitable for aggregation). I_i ranges between 0 (cell i never had a value above the threshold) and 1 (cell i always had a value above the threshold) for each cell in the study area. The I_i allows us to display 2 unique maps: one for abundance and one for biomass (Step 6 in Fig. 2).

3. RESULTS

3.1. Model performance

Model evaluation outcomes are presented in Table 1. The final model for presence probability showed AUC, kappa and TSS values above the threshold criteria for a good performance, indicating accurate model performance. The Spearman coefficients for presence—absence, abundance, biomass, the 2 delta and the mean size models ranged from 0.49 to 0.62, surpassing the threshold for these statistics and signifying an adequate correlation between observed and predicted values in the 6 models. Additionally, results of the Monte Carlo simulation of Moran's I indicated no significant spatial autocorrelation (p > 0.05) in the residuals of any of the 3 final models (Table S3).

3.2. Aggregation curves

Geostatistical aggregation curves, associated annual Ssp values, mean values and the 95% confidence intervals for abundance and biomass are shown in

Table 1. Evaluation outcomes (mean ± SD) for the probability of presence, abundance, biomass, and the combined delta models. The probability of presence model was evaluated using area under the curve (AUC), kappa and true skill statistics (TSS). Abundance, biomass, mean size and delta models were evaluated by calculating the Spearman coefficient

Model	AUC	Kappa	TSS	Spearman
Binomial (presence)	0.82 ± 0.02	0.53 ± 0.03	0.52 ± 0.04	—
Gamma (abundance)	—	—	—	0.52 ± 0.04
Gamma (biomass)	—	—	—	0.54 ± 0.03
Gamma (mean size)	—	—	—	0.49 ± 0.05
Delta model (abundance)	—	—	—	0.62 ± 0.04
Delta model (biomass)	—	—	—	0.59 ± 0.03

Fig. 3. The Ssp values for all the years were within the confidence intervals, indicating no significant differences among years. The 95% confidence intervals of the Ssp values for abundance (range 0.88–0.94) and for biomass (range 0.89–0.94) indicated a high concentration of *Phycis blennoides*, with fluctuations between years but without any trend. The analysis of both the aggregation curves and the Ssp values indicated that, for the study area and for the period 1998–2019, the local fish density changed at the same rate as total biomass. This indicates that the density at each point remained a constant proportion of the population abundance, suggesting that the species can consistently utilise available habitat and maintain a similar spatial distribution despite fluctuations in abundance and/or biomass.

3.3. Presence–absence, abundance, and biomass

P. blennoides was caught in 40.9% (1151 out of 2814) of the valid hauls carried out across bathymetric depth range of DEMERSALES surveys (36–846 m). The best binomial model explained 46.2% of the presence–absence deviance and of the initial 9 variables included in the full binomial model, only percentage of organic matter and temperature were not included in the final model (Table 2). The haul position (Δdeviance = 291.52) was the most important factor controlling the presence of *P. blennoides*, followed by depth (237.87) and year (182.67) (Table 2). The effect of depth on the probability of presence was positive with increasing probability with increasing depth (Fig. 4a). Substrate type had a significant effect on the probability of presence of the species. Thus, coarse sand showed a decreasing trend, with the highest probability of occurrence in areas without coarse sand and the Pr_p showing a peak for values of fine sand contents around 70% (decreasing with higher and lower
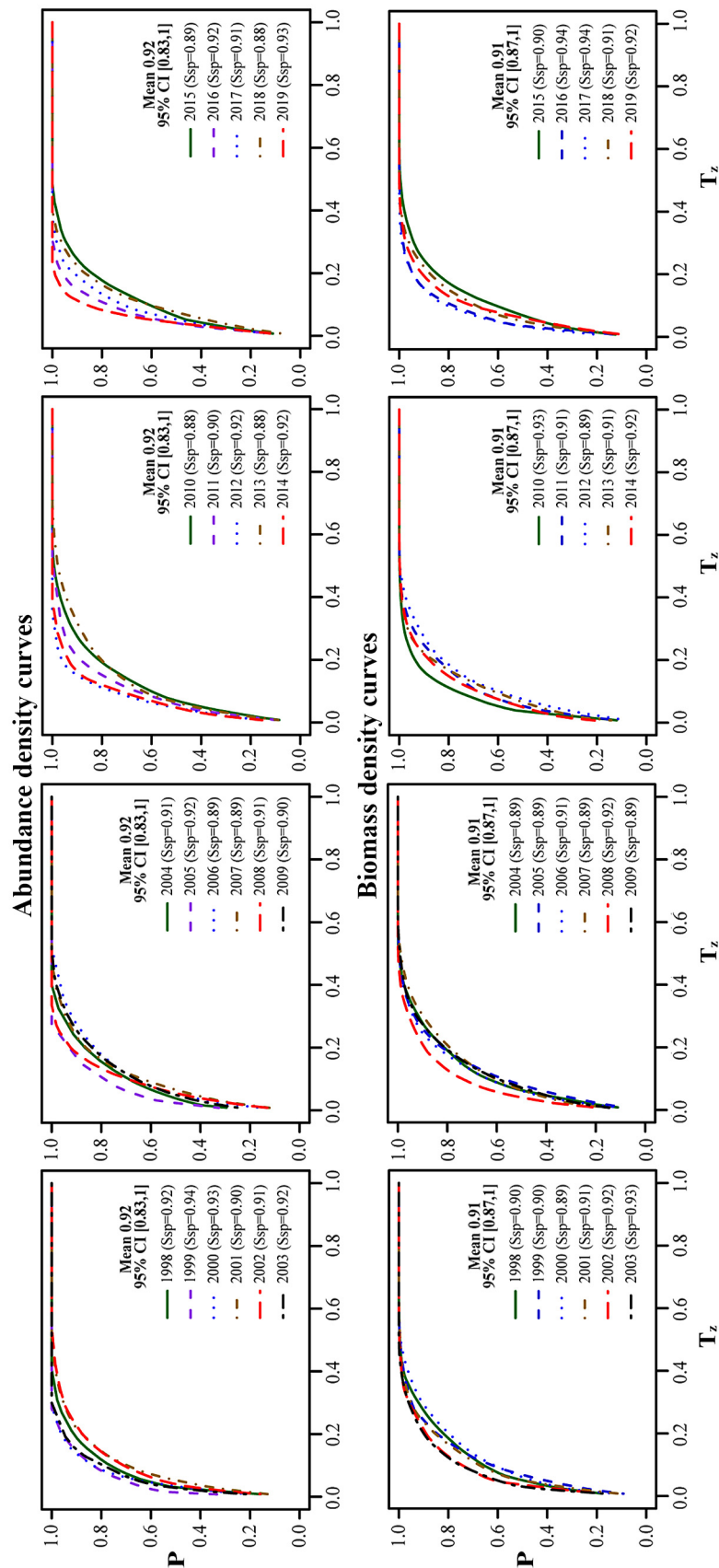

Fig. 3. Annual geostatistical aggregation curves and space selectivity index (Ssp) values for *Phycis blennoides* abundance and biomass for the study period (1998–2015). The curves relate the proportion of total biomass (P) per surface unit (T_z). Mean value and 95% confidence interval of Ssp are shown for each variable and for the entire study period. To facilitate visual analysis, the data is presented in 4 panels for each variable

Table 2. Relative importance (Δdeviance), degrees of freedom (df) or estimated degrees of freedom (edf) and statistical significance (p-value) of the explanatory variables for the presence—absence (binomial) model (N = 2814, deviance explained = 46.2%). Deviance variation in the final model after elimination of the variable

Variable	Δ deviance	df/edf	Chi	p
Spatial effect	291.52	9.11	244.14	<0.001
Depth	237.87	2.88	224.37	<0.001
Year	182.67	21	197.8	<0.001
Fine sand	61.91	2.89	56.25	<0.001
Coarse sand	45.65	2.35	57.27	<0.001
Slope	12.91	2.68	9.29	<0.05
Salinity	3.68	1.00	6.07	0.084

Table 3. Relative importance (Δ deviance), degrees of freedom (df) or estimated degrees of freedom (edf) and statistical significance (p-value) of the explanatory variables for the abundance (gamma) model (N = 1151, deviance explained = 53.2%). Deviance variation in the final model after elimination of the variable

Variable	Δ deviance	df/edf	*F*	p
Spatial effect	267.52	9.93	3.54	<0.001
Depth	216.75	2.95	56.14	<0.001
Year	163.43	21	9.81	<0.001
Fine sand	63.19	2.73	27.63	<0.001
Organic matter (%)	33.58	2.83	8.67	<0.001
Slope	14.41	2.16	5.46	<0.01

percentages) (Fig. 4b,c). Salinity values higher than 35.7 and slope values around 6° increased the probability of encountering the species (Fig. 4d,e). The year significantly affected the probability of presence, with the highest probability of occurrence in 2013, the lowest in 2016 and no clear trend observed (Fig. 4f). Although salinity did not have a statistically significant effect on Pr_p (Table 2), it was retained in the final model because removing this variable worsened both the AIC score and the explained deviance. During the study period, the highest presence probabilities were observed in the deepest parts of the study area, except the western part of the Cantabrian Sea, where low probabilities of presence were observed in most years (Fig. S3).

The best model for abundance (ind. haul^{-1}) explained 53.2% of the deviance (Table 3). Depth, fine

sand, organic matter, slope, haul position by year and year were the variables included in the final model. As observed in the presence—absence model, haul position (Δdeviance = 267.52), depth (216.75) and year (163.43) were the most important factors controlling species abundance (Table 3). Abundance increased with increasing depth up to around 450 m and then progressively decreased to the deepest limit of the studied depth range (Fig. 5a). Sediment characteristics influenced P_a, with abundance increasing with the percentage of fine sand up to around 75% (Fig. 5b), and with a positive trend for values of organic matter content > 4% (Fig. 5c). Slope values between 4.0° and 6.0° appeared to be associated with higher abundance values (Fig. 5d). The effect of year showed a significant effect on the species abundance with a maximum in 1998, a minimum in 2005 and no clear trend (Fig. 5e). A high inter-annual variability in species abundance was
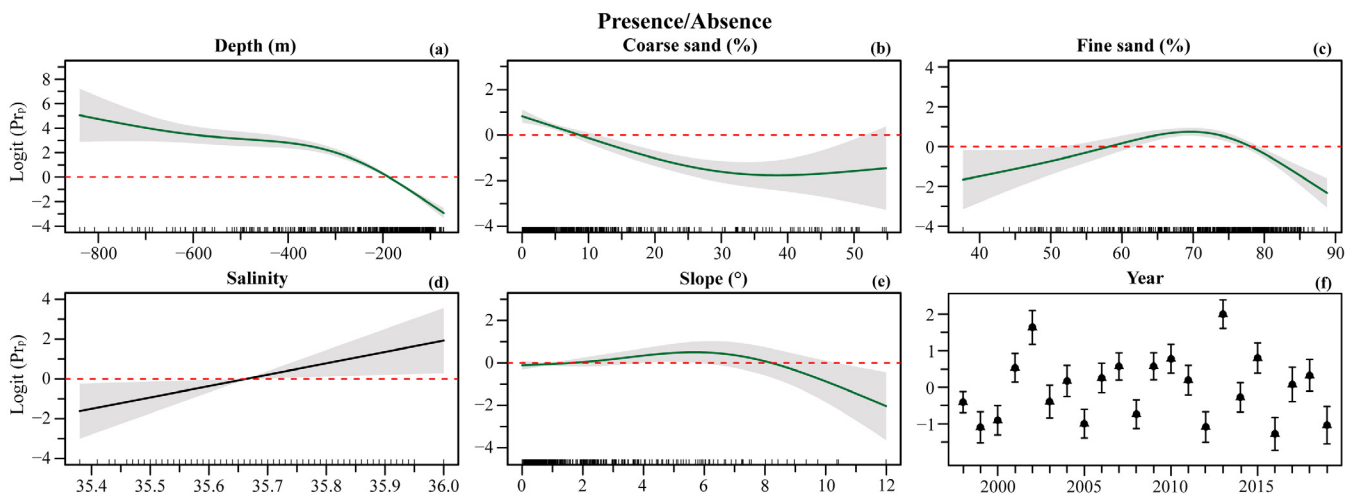

Presence/Absence

Fig. 4. (a—e) Effect of the continuous explanatory variables on the predicted probability of presence (Pr_p) of *Phycis blennoides* and (f) the coefficient value for the different levels of the explanatory variable year which was included as factor. Shaded areas indicate 95% confidence intervals around response curves. Error bars in (f) are ±SD. Rug plots indicate the distribution of the observed values. Significant relationships are shown in green

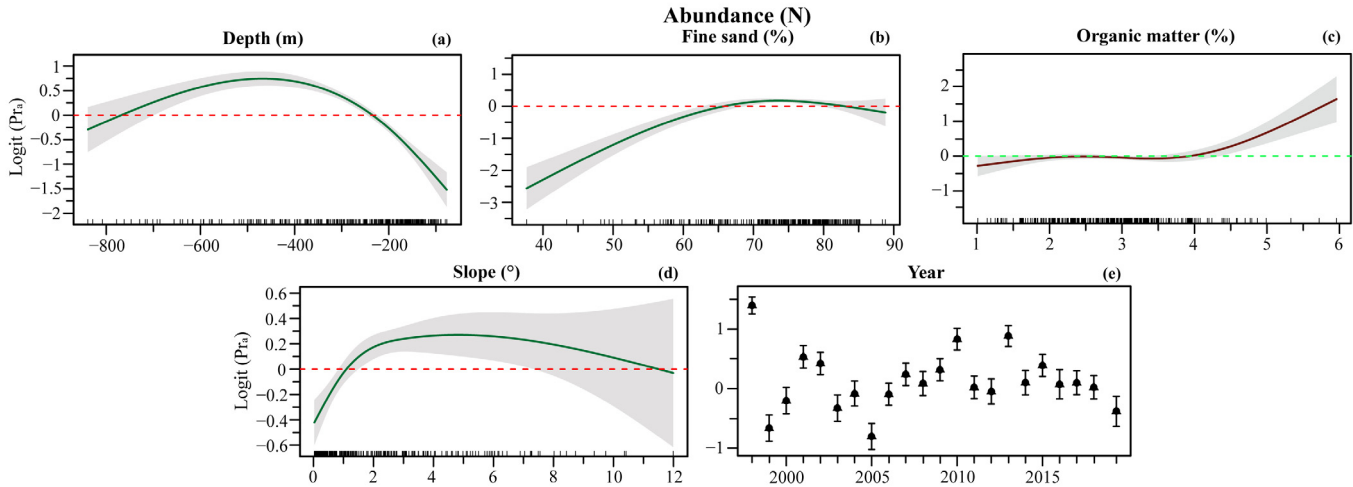Fig. 5. (a−d) Effect of the continuous explanatory variables on the predicted abundance (Pr$_a$) of *Phycis blennoides* and (e) the coefficient value for the different levels of the explanatory variable year which was included as factor. Shaded areas indicate 95% confidence intervals around response curves. Error bars in (e) are ±SD. Rug plots indicate the distribution of the observed values. Significant relationships are shown in green

Table 4. Relative importance (Δ deviance), degrees of freedom (df) or estimated degrees of freedom (edf) and statistical significance (p-value) of the explanatory variables for the biomass (Gamma) model (N = 1151, deviance explained = 60.0%). Deviance variation in the final model after elimination of the variable

Variable	Δ deviance	df/edf	F	p
Spatial effect	466.48	6.65	1.94	<0.05
Year	155.41	21	7.07	<0.001
Depth	108.36	2.64	31.67	<0.001
Organic matter (%)	96.59	2.82	18.56	<0.001
Fine sand	92.67	2.72	30.92	<0.001
Coarse sand	13.64	2.02	4.68	<0.001
Slope	7.64	1.22	2.38	<0.01

observed, with the upper slope of the Galician waters and the eastern half of the Cantabrian Sea exhibiting the highest abundance in nearly all years of the study period (Fig. S4).

For the biomass of *P. blennoides*, the best gamma model explained 60.0% of the data deviance and, of the 9 initial variables, only temperature and salinity were not included in the final model (Table 4). Haul position (Δdeviance = 466.48), followed by year (155.41) and depth (108.34) were the 3 most important variables in the final model. Biomass increased with increasing depth up to around 600 m and remained stable up to the maximum depth surveyed (Fig. 6a). Substrate characteristics had a significant effect on
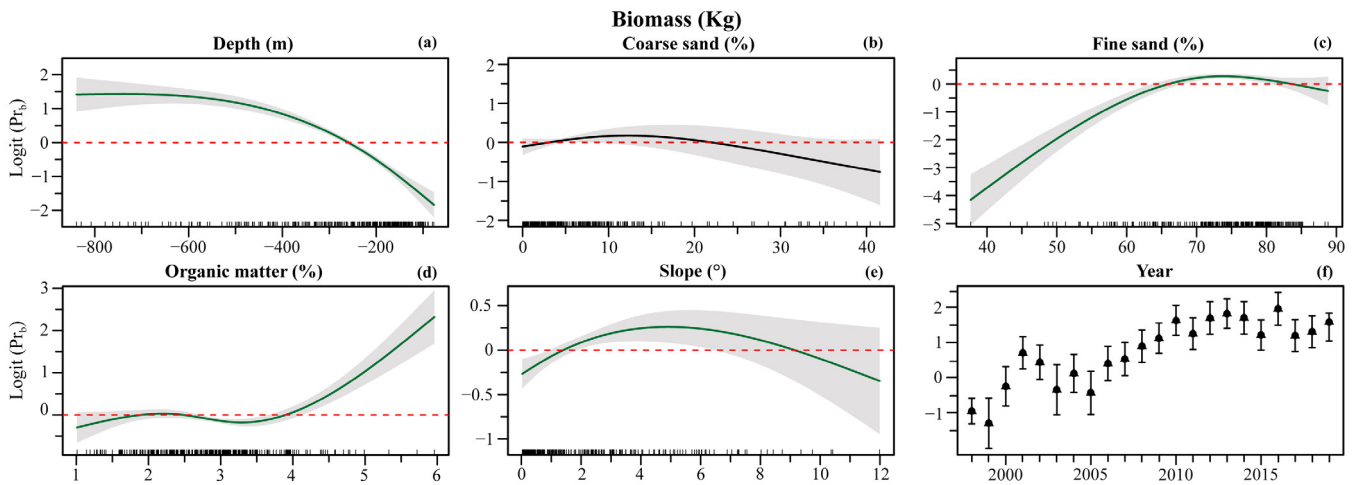

Fig. 6. (a−e) Effect of the continuous explanatory variables on the predicted biomass of *Phycis blennoides* (Pr$_b$) and (f) the coefficient value for the different levels of the explanatory variable year which was included as factor. Shaded areas indicate the 95% confidence intervals around response curves. Error bars in (f) are ±SD. Rug plots indicate the distribution of the observed values. Significant relationships are shown in green

species biomass. Thus, coarse sand contents up to 15% (Fig. 6b), fine sand content up to around 75% (Fig. 6c) and organic matter contents above 3.5% (Fig. 6d) were related to high biomass values. Slope values between 5.0° and 6.0° were associated with the highest biomass values (Fig. 6e). The inter-annual variation of the coefficient values showed a significant effect and a positive trend, with the lowest coefficient occurring in 1999 and a general increase in the following years (Fig. 6f). In general, Galician waters showed low values with almost zero-values in 1999, 2003 and 2005, while the eastern half of the Cantabrian Sea showed the highest values of biomass in most of the years (Fig. S5).

3.4. Delta maps

The annual delta maps for abundance and biomass (Figs. S6 & S7), obtained by multiplying the presence—absence maps with the abundance and biomass maps, show that, in Galician waters, the areas of high abundance of the species for both variables are usually located on the upper slope of the area between Cape Finisterre and Cape Estaca de Bares, with a deeper distribution for the biomass values. In the Cantabrian Sea, the areas with higher values for both abundance and biomass are found in its eastern half, mainly on the

upper slope. Finally, the distribution of I_i values for abundance and biomass, which range from 0 (the area was never predicted to be suitable for aggregation in any of the years from 1998 to 2019) to 1 (the area was predicted to be suitable for aggregation in all the years), are shown in Figs. 7 & 8, respectively. *P. blennoides* is persistent in deeper Galician waters (shelf and upper slope) and the upper slope in the Cantabrian Sea between Cape Peñas and the easternmost part of the study area.

3.5. Mean length model

TL of the captured specimens varied from 8 to 72 cm, with a mean (±SD) length during the study period of $23.8 ± 9.6$ cm (Fig. S8). The gamma model for the mean length explained 53.8% of the deviance and all variables were included in the final model (Table 5). Fishing effort (Δdeviance = 11.07) and depth (Δdeviance = 9.16) were the 2 most important variables. Mean length increased with increasing depth (Fig. 9a,c) and with decreasing trawling effort (Fig. 9b,d). No discernible trend was identified over the 10 yr period analysed (Fig. 9e). However, within this timeframe, it appears that there has been a gradual increase in mean size, particularly from a depth of 200 m onwards (Fig. S9).
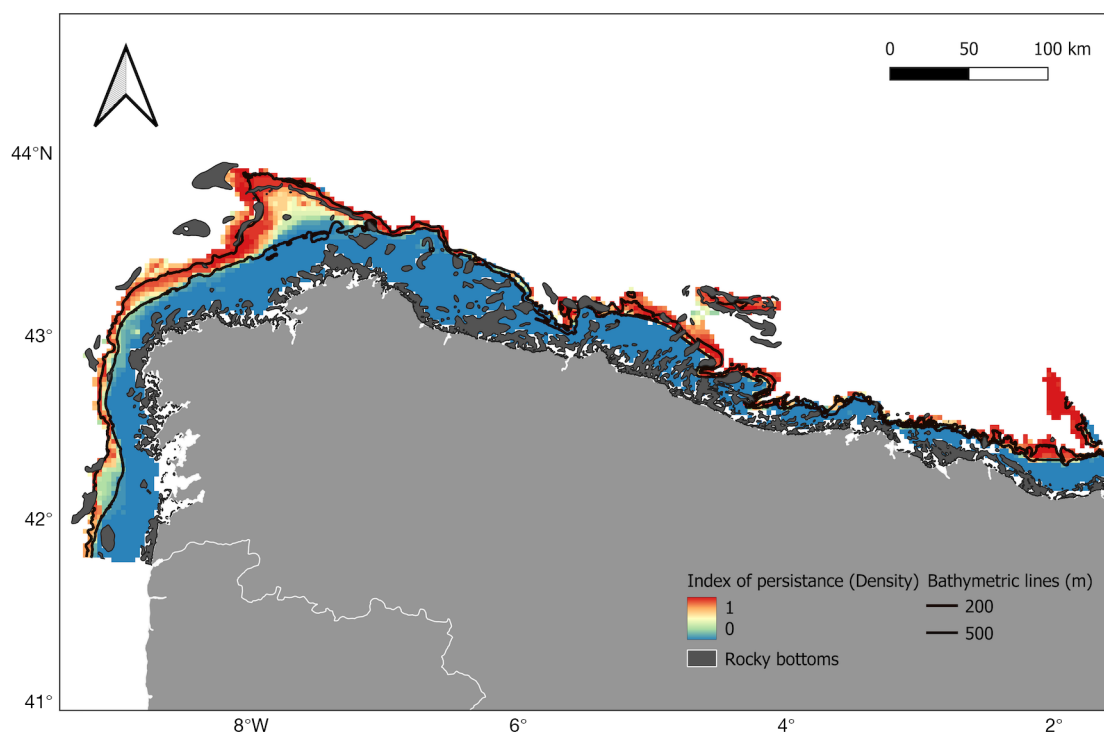

Fig. 7. Distribution of the index of persistence for *Phycis blennoides* abundance in the study area. The index ranges from 0 (no aggregations were found in any of the studied years) to 1 (aggregations were found in all the study years)
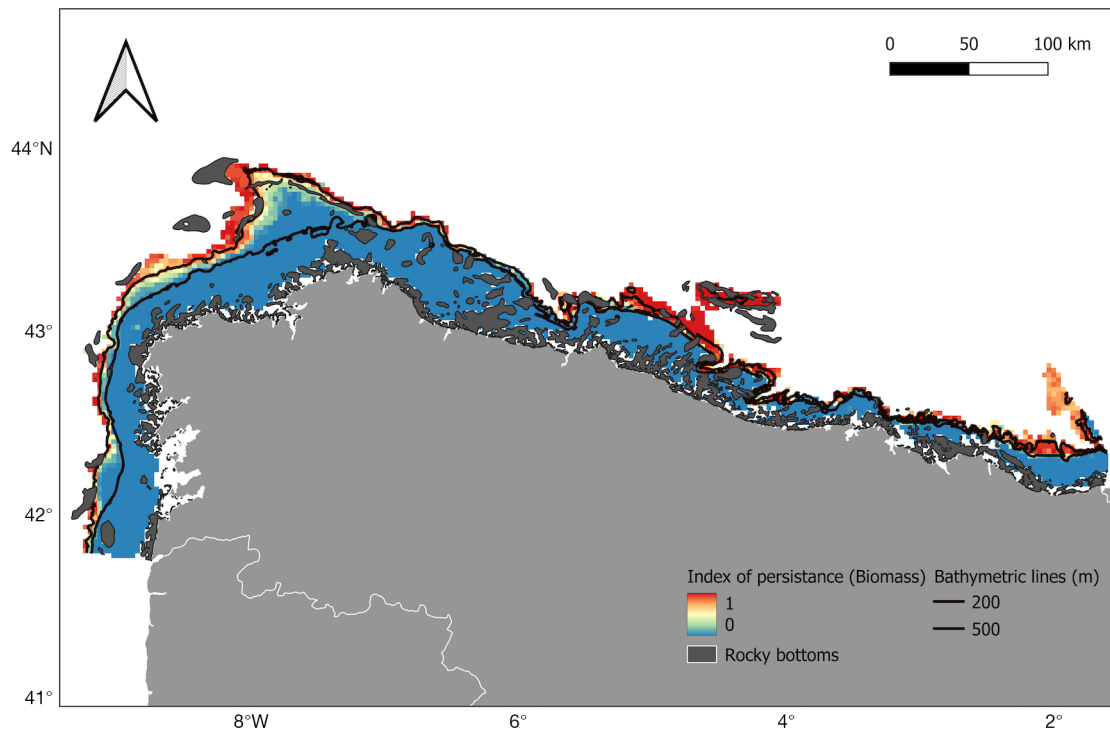
Fig. 8. Distribution of the index of persistence for *Phycis blennoides* biomass in the study area. The index ranges from 0 (no aggregations were found in any of the studied years) to 1 (aggregations were found in all the study years)

Table 5. Relative importance (Δ deviance), degrees of freedom (df) or estimated degrees of freedom (edf) and statistical significance (p-value) of the explanatory variables for the mean total length (gamma) model (N = 689, deviance explained. = 53.8%). Deviance variation in the final model after elimination of the variable

Variable	Δ deviance	df/edf	*F*	p
VMS	11.07	2.81	73.68	<0.001
Depth	9.16	1.00	126.70	<0.001
Year	7.34	10	9.74.1	<0.001

4. DISCUSSION

Long-term datasets are an effective tool for describing the relationship between fish and their habitat (Feyrer et al. 2007). The present study utilised fishery-independent survey data collected over a 22 yr period and delta GAMs to identify some of the potential drivers influencing the habitat use and spatial distribution of *Phycis blennoides*, a commercially exploited but understudied gadiform species, along the continental shelf and upper slope of Galicia waters and the Cantabrian Sea (north of Spain).

All models explained relatively high values of deviance (from 46.2 to 60%) and showed acceptable values in the evaluation metrics, within the range or better than previous delta GAMs studies on fish distribution (e.g. Asjes et al. 2016, González-Irusta & Wright 2017, Langton et al. 2021, Arronte et al. 2022). During the period of study (1998–2019) the 'consistent spatial pattern' (Petitgas 1998) was best at describing the spatial distribution pattern of the species in the study area, indicating that the prediction of the physical habitat preference of the species should not have been confounded by changes in its annual abundance. In the north-eastern Atlantic, this pattern has been previously reported for other gadiform species including *Merluccius merluccius*, haddock *Melanogrammus aeglefinus*, whiting *Merlangius merlangus*, and silvery pout *Gadiculus argenteus* (Petitgas 1998, Asjes et al. 2016, González-Irusta & Wright 2016, 2017, Arronte et al. 2022).

The present study has demonstrated the significant influence of environmental factors such as sediment characteristics, water depth, and slope on the distribution, abundance, and biomass of *P. blennoides* off the north-eastern Spanish coast. Bottom sediment characteristics play an important role in the spatial distribution of several demersal fishes (e.g. Mahon & Smith 1989, Demestre et al. 2000, Katsanevakis et al. 2009), and *P. blennoides* is no exception. Modelling results suggested a preference for fine sand and a tendency to
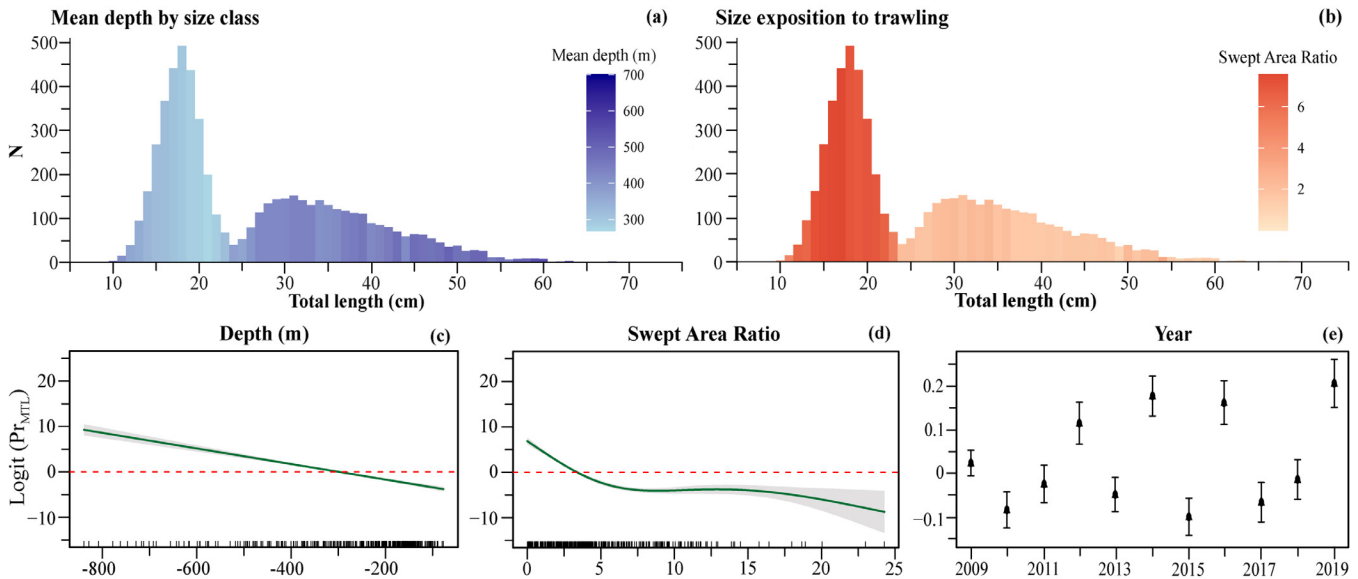
Fig. 9. Length—frequency distribution by (a) depth and (b) trawling effort. (c,d) Effect of the continuous explanatory variables on the predicted mean length (Pr_{ml}) of *Phycis blennoides* and (e) the coefficient value for the different levels of the explanatory variable year which was included as factor. Shaded areas indicate the 95% confidence intervals around response curves. Error bars in (e) are ±SD. Rug plots indicate the distribution of the observed values. Significant relationships are shown in green

avoid coarser sediments, consistent with previous studies in the Mediterranean (Demestre et al. 2000, Pallaoro & Jardas 2002). The importance of sediment characteristics in the spatial distribution of demersal fishes is known to be due to the trophic interactions between fishes and the epi- and endobenthic fauna (Hinz et al. 2003). In the north-eastern Atlantic, the diet of *P. blennoides* is mainly based on crustaceans, with teleosts as secondary prey (Sorbe 1977, Mauchline & Gordon 1984, I. Preciado pers. comm.), and its preferred type of soft bottoms are characterized by the presence of important prey species such as *Alpheus glaber*, *Solenocera membranacea*, *Processa* spp. or *Munida* spp. (Serrano et al. 2006, 2008). Mud, silt, and fine sand are associated with depositional zones and, therefore, have a higher percentage of organic matter (Serrano et al. 2006). These sediment types favour the abundance of endo- and epibenthic species, providing a greater availability of food resources for the species. This may partly explain the significant and positive effect of these bottom types on *P. blennoides*, as prey distribution can shape the spatial pattern of a species by concentrating predators in prey-dense areas (Perry & Smith 1994). In line with this, the significant positive effect of sediments rich in organic matter content is associated with higher abundances and larger sizes of benthic prey species (Serrano et al. 2006, 2008), thereby increasing food availability for *P. blennoides*. Depth was the most important environmental driver in all models (presence—absence, abundance, biomass,

and mean length). This was an anticipated outcome, as many essential drivers of fish distribution, whether abiotic, such as temperature, salinity, or light, or biotic, such as food availability or predation, change in association with depth (Carney et al. 1983, Cartes & Sardá 1993). As it is often difficult to disentangle the direct effect of these variables, depth has been identified as the main gradient along which population changes occur when analysing continental shelf and upper slope assemblages, not only in the study area (Sánchez & Serrano 2003), but also elsewhere (Fujita et al. 1995, Kallianiotis et al. 2000). The higher values of relative abundance and biomass of *P. blennoides* on the upper slope and its scarcity on the continental shelf are consistent with previous findings for this species in the study area (Sánchez 1993) and in the Mediterranean Sea (Massutí et al. 1996, Pallaoro & Jardas 2002, Katsanevakis & Maravelias 2009).

The shapes of the relative abundance and biomass curves were different, with abundance decreasing after the peak and biomass remaining stable after the maximum value was reached. This is a consequence of the observed increase in body size with depth. This pattern, known as 'bigger-deeper', is a well-known general trend in many demersal fishes (e.g. MacPherson & Duarte 1991, Collins et al. 2005, Frank et al. 2018 and references therein) and has previously been reported for *P. blennoides* in the north-eastern Atlantic (Mauchline & Gordon 1984) and the north-western Mediterranean (e.g. MacPherson & Duarte 1991, Massutí et al.

1996, Pallaoro & Jardas 2002), although no significant size−depth variation was observed in the north-eastern Mediterranean (Labropoulou et al. 2008).

Traditionally, this phenomenon, first described more than a century ago and named Heincke's law (Frank et al. 2018), has been related to fundamental aspects of the ecology and behaviour of the species involved (MacPherson & Duarte 1991, Collins et al. 2005). In *P. blennoides*, as proposed by Sedberry & Musick (1978) for its congener longfin hake *Phycis chesteri*, the occurrence of smaller, younger individuals in shallow waters and the movement to deeper waters with age could serve as a mechanism to reduce intraspecific competition and predation by larger individuals on smaller specimens. However, cannibalism in *P. blennoides* appears to be minimal (Sorbe 1977, Morte et al. 2002, I. Preciado pers. comm.), and fish are secondary prey in the diet of larger individuals in deeper waters. Perhaps the movement of larger *P. blennoides* individuals to deeper areas is the species' response to the progressive development of pelvic fins and tactile and taste functions with age, resulting in a change from a more visual predation and supra-benthic prey species in younger individuals to epi- and endobenthic feeding habits in older specimens (Gallardo-Cabello 1980). Gradual changes in its diet with age have been observed not only in the Atlantic (Sorbe 1977, I. Preciado pers. comm.), but also in the Mediterranean (MacPherson 1978, Gallardo-Cabello 1980).

Another proposed explanation for the observed size distribution is the impact of fisheries on fish stocks through 2 different effects of fishing. Fishing gears are typically designed to selectively remove larger individuals, which can result in a higher proportion of smaller individuals in areas where fishing effort is most intense. In line with this, Frank et al. (2018) analysed the depth distribution at age of Atlantic cod *Gadus morhua* off the eastern Scotian Shelf (north-western Atlantic), a gadiform whose stock has experienced drastic reductions in fishing mortality since the early 90s. Their findings indicated that 72% of the observed deepening was due to fishing, while ontogeny contributed to the remaining variance. In contrast, Audzijonyte & Pecl (2018) and Baudron et al. (2019) found no evidence of higher abundance of medium and large specimens in several north-eastern Atlantic stocks that have experienced significant reductions in fishing pressure. Mortality caused by intensive fishing can also result in genetic changes, including alterations in growth rate, length and age at maturity, behavioural modification in response to fishing, and a lack of recovery in over-fished stocks even after substantial reductions in fishing mortality (Law 2000, Walsh et al. 2006, Allendorf et al. 2008).

In the study area, trawling has been banned at shallower than 100 m depth since 2000, trawling effort is significantly higher in the 200−500 m depth stratum than in deeper waters or on the continental shelf (<200 m) (González-Irusta et al. 2018), and its intensity has decreased over the last 2 decades due to a reduction in the number of trawling vessels by more than 55% (MAPA 2020). In addition, *P. blennoides* stock is managed under the Spanish Fisheries Management Plans which include, among other measures, total allowable catches (TACs) and quotas for fish stocks (EU 2004). Likely due to these factors, the study area has not only experienced a decrease in fishing mortality since the early 2000s, but also an increase in the relative biomass of numerous demersal species (Arroyo et al. 2017).

In the case of *P. blennoides*, its abundance has shown high annual variability with no clear trend, but its biomass has increased since the mid-2000s. This increase could be attributed to the reduction in fishing effort in the upper slope over the last 2 decades, which appears to have allowed individuals to attain larger sizes in these areas, rather than a higher abundance of medium and smaller individuals in shallower waters. In other words, the 'bigger-deeper' size distribution of *P. blennoides* seems to be mainly driven by the life-history strategy of the species and enhanced by fisheries, since the reduction in fishing mortality in recent years has resulted in a gradual increase in the mean length of the species, particularly below 200 m depth. However, this decrease has not led to an increase in the species' abundance or in its probability of occurrence. Perhaps this a reflection of evolutionary changes in response to fisheries mortalities. After decades of fishing pressure, fishing may have induced a reduction in genetic diversity in *P. blennoides*, with a consequent reduction in adaptive ability and/or changes in growth and maturation, as has been observed in other gadiform species (Law 2000, Hutchinson et al. 2003). This hypothesis requires further investigation and is beyond the scope of this article.

Understanding the spatial and temporal distribution of commercially valuable marine fish species and their relationship to the environment (encompassing both habitat and environmental preferences) is a fundamental requirement for the effective management and conservation of marine resources. Here, we have provided essential information that enhances our knowledge of the habitat preferences of *P. blennoides* which can be incorporated into management initia-

tives and used to understand the population dynamics of this species. This study demonstrates that GAM-based habitat modelling is a valuable tool for standardising survey indices and creating plausible distribution maps while considering environmental factors and their impact on species distribution.

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