Developing species distribution models for critically endangered species using participatory data: The European sturgeon marine habitat suitability

Anaïs Charbonnel [a,*], Patrick Lambert [a], Géraldine Lassalle [a], Eric Quinton [a], Antoine Guisan [b], Lise Mas [c], Guillaume Paquignon [d], Marie Lecomte [e], Marie-Laure Acolas [a]

[a] INRAE, UR EABX, 50 Avenue de Verdun, Gazinet-Cestas Cedex, 33612, France
[b] Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland
[c] CAPENA, 33470, Gujan-Mestras, France
[d] OFB, Délégation de Façade Atlantique, 1 rue Eugène Varlin, 44100, Nantes, France
[e] CNPMEM, 134, Avenue de Malakoff, 75116, Paris, France

ARTICLE INFO

ABSTRACT

Increasing knowledge on distribution and habitat selection of coastal fish species is essential for the management of marine environments, and can be provided through the use of Species Distribution Models (SDM). Opportunistic and participatory data, such as recreational or commercial bycatch data, can provide precious information at large scale and low cost to estimate fish spatial distributions, but are subject to biases (e.g. lack of absence data, non-random sampling scheme). The European sturgeon (*Acipenser sturio*) is a critically endangered diadromous fish and its marine habitat preferences are unknown. The goal of this study was to investigate key variables driving *A. sturio* distribution and predict its current distribution in inshore waters along the European Atlantic coast. We developed two correlative SDM in *A. sturio* marine habitats based on incidental observations (2012–2021) and two different sets of environmental predictors. In both attempts, six methods which differ according to the biases they aim to reduce (i.e. oversampled areas or environmental conditions, dependence between calibration and validation datasets) and the input dataset used (i.e. random pseudo-absences or target-group pseudo-absences) were applied at various stages of the model building and evaluation process. By comparing potentially biased and bias-corrected predictions, we found similar satisfactory level of evaluation and spatial patterns of habitat suitability. Marine areas predicted as the most suitable were distributed along the French Atlantic coast, the Seine and Somme bays, and at a lesser extent around the Rhine delta and in some coastal areas of the Cantabrian Sea (Northern Spain). We found a strong influence of the bathymetry, temperature, and salinity as well as an influence of the bottom current velocity and of the distance to the source population in explaining *A. sturio* marine distribution, while the nature of the substrate was not retained by the models. Results of this study could pave the way toward more integrated conservation measures for this critically endangered fish.

1. Introduction

Coastal ecosystems are key areas to sustain marine fish and invertebrate populations (Bradley et al., 2020) in addition to provide goods and services for humans (e.g. food production, tourism) (Rönnbäck et al., 2007). However, coastal marine habitats and their associated species are under increasing pressure and impacted by a variety of human activities such as habitat degradation, overfishing, pollution and climate change (Crain et al., 2009; Halpern et al., 2008). As a result,

increasing our scientific knowledge on the ecology, distribution and habitat selection of species is essential to support the management of marine environments (Crain et al., 2009).

Species Distribution Models (SDM) (Guisan et al., 2017) are useful tools for linking species presences/absences or abundances with a set of environmental variables to examine their relative influence on the species habitat selection. SDM also produce habitat suitability maps which are increasingly considered to support spatial and conservation planning (Guisan et al., 2013; McShea, 2014). However, their

application is more recent in marine than in terrestrial environments (Melo-Merino et al., 2020).

Species occurrence data are available from traditional survey techniques for many species but they are more limited for larger, less abundant species (Eble et al., 2020). In this context, participatory science offers an alternative by providing large amount of data collected over large areas (McKinley et al., 2017) while increasing citizen and stakeholders' awareness and thus, their contribution in biodiversity conservation (Peter et al., 2019).

Recreational or commercial bycatch (i.e. fishery-dependent) data can provide valuable information to estimate fish spatial distributions (Pennino et al., 2016). While collected at lowest cost, some biases are inherent to these opportunistic observations, including the non-random sampling design (Murphy and Jenkins, 2010). For example, the intensity of fishing tends to decrease further from the port of origin or from the coast. Fishing boats tend also to fish preferentially in areas where high abundances of the target species are expected (Pennino et al., 2019). Hence, building SDM from bycatch data is challenging and requires that these limitations be correctly integrated in the modelling framework (Noviello et al., 2021).

When the survey effort is unknown, thinning the observation data is a method commonly used to correct sample biases (Inman et al., 2021; Steen et al., 2021). This technic aims at reducing the prevalence of oversampled environmental conditions (i.e. environmental filter) (Varela et al., 2014) or oversampled areas (i.e. spatial filter) (Aiello-Lammens et al., 2015). Opportunistic observations usually do not have information regarding the locations where the species are absent (monitoring taken place but only the species presences declared) (Bradter et al., 2018). To overcome this problem, a widely-used method is to generate virtual absences, called *pseudo-absences,* which are used instead of monitored absences in the input dataset (Barbet-Massin et al., 2012). Pseudo-absences can be selected in different ways, in varying numbers, and with various weights (Barbet-Massin et al., 2012; Phillips et al., 2009). The most common way is to randomly generate a large number of virtual absences within the study area (i.e. random pseudo-absences) (Barbet-Massin et al., 2012). Another way, called *target-group pseudo-absences*, consists of using sites where species of the same taxonomic group have been surveyed and where the targeted species was not detected (Phillips et al., 2009). Whereas random pseudo-absences is the strategy with the least assumptions (Guisan et al., 2017), the sampling of target-group pseudo-absences is usually based on ecological reasoning (Phillips et al., 2009). Finally, to overcome the lack of an independent dataset to evaluate the model predictive ability, internal cross-validation is recommended (Hijmans, 2012). Random partitioning was demonstrated to generate dependences between calibration and evaluation datasets, which then affect the model coefficients and statistical inference (de Oliveira et al., 2014). Hence, a recent method, called *block cross-validation,* generates spatially separated datasets to address this issue (Valavi et al., 2019).

In the case of rare species, not targeted at sea but considered as bycatch such as diadromous fish, participatory data can be the best way to provide data on many individuals at a low cost, to assess their ecology in the marine environment. The European sturgeon (*Acipenser sturio*) is a large-bodied fish (McDowall, 1997) that undertakes anadromous migrations through riverine, estuarine and marine habitats (Bemis and Kynard, 1997). The species has conservative life-history strategies, such as slow growth, late sexual maturation and long life span (Williot et al., 2011a) which takes place more than 90% at sea. While *A. sturio* had an almost pan-European distribution a century ago (Lassalle et al., 2011), its distribution at sea is now reduced to the European side of the Atlantic Ocean, from Norway to Spain (Rochard et al., 1997). Since the beginning of the 19th century, the species has been facing several threats resulting from human activities, such as habitat degradation (Rochard et al., 1990; Williot and Castelnaud, 2011), overfishing (Fernández-Pasquier, 1999) or river engineering and damming (e.g. barriers to migration) (van Puijenbroek et al., 2019). *A. sturio* has been listed as

critically endangered on the IUCN Red List (Gessner et al., 2010b). There is a fishing ban in France since 1982 and the species is listed since 1992 in Annexes II and IV of the European Habitat directive. A European restoration action plan was presented in 2007 (Rosenthal et al., 2007) and implemented in national action plans in France and Germany (Gessner et al., 2010a; MEDDTL, 2011; MTES, 2020). The last remaining population, in a critical state, is found in the Gironde-Garonne-Dordogne (GGD) system. This population was saved from global extinction by the building of an *ex-situ* brood stock during the 1990's for restocking purposes (Williot et al., 2011b) that occurred between 2007 and 2015 (Roques et al., 2018). Some researches have been conducted to assess the species riverine and estuarine habitat use (Acolas et al., 2017; Carrera-García et al., 2017; Taverny et al., 2002). However, there is a lack of studies characterizing its marine habitat and these are mainly focusing on describing the fish characteristics in the marine environment (Letaconnoux, 1961; Rochard et al., 1997). This knowledge gap hampers a proper conservation and management of the species.

The goal of this study was thus to (i) investigate key variables steering *A. sturio* marine distribution and (ii) generate predictions of its current distribution in inshore waters along the European Atlantic coast. We combined incidental observations (2012–2021) and selected explanatory variables to create two ensemble models with different sets of variables, given the relationships that exist between some of the descriptors. While one ensemble model only contains environmental variables, the other one includes a geographic constraint (i.e. the distance to the GGD system) and therefore takes into account the natal river of the individuals. Six SDM methods, which differ according to the biases they aim to reduce (i.e. oversampled areas, oversampled environmental conditions or dependence between calibration and validation datasets) or the input distribution dataset used (i.e. random pseudo-absences, target-group pseudo-absences), were implemented in both ensemble models, at various steps of the model building and evaluation process. We aimed at producing a final consensus map of suitable habitats for this species at sea, i.e. representing an agreement between all models and methods.

2. Materials and methods

2.1. Study area

The present study was carried out in the temperate marine waters over the large continental shelf of the northeastern Atlantic Ocean (Fig. 1). The Bay of Biscay is composed of complex hydrological and climatic regimes with strong spatial and temporal dynamics (Koutsikopoulos and Le Cann, 1996). The circulation of water masses in the English Channel and the North Sea is conditioned by the tides, winds and water density (Hardisty, 1990). Benthic habitats across the study area consist of coarse-grained and mixed sediments (53.14%), sands (30.51%), mud to muddy sands (11.64%), and rock and boulders (4.72%) (EMODnet Geology). This area is subject to high pressures from human activities such as marine traffic, pelagic and demersal fishing, tourism activities, coastal discharges, sand extraction and dredged sediment disposal (Borja et al., 2019; Lorance et al., 2009). In the present work, the bathymetric limit was set at 150 m depth beyond which environmental conditions were considered as unsuitable for *A. sturio*, as the species was never observed in deeper waters (Letaconnoux, 1961; Rochard et al., 1997). Lagoons and estuaries were also not considered.

2.2. Observations of A. sturio at sea

Observations of *A. sturio* mainly came from the French database STURWILD (2012–2021; data extraction on the July 02, 2021; Center for Aquaculture, Fisheries and the Environment in New Aquitaine - CAPENA, National Committee of Maritime Fisheries and Marine Fish Farming - CNPMEM, French National Research Institute for Agriculture,
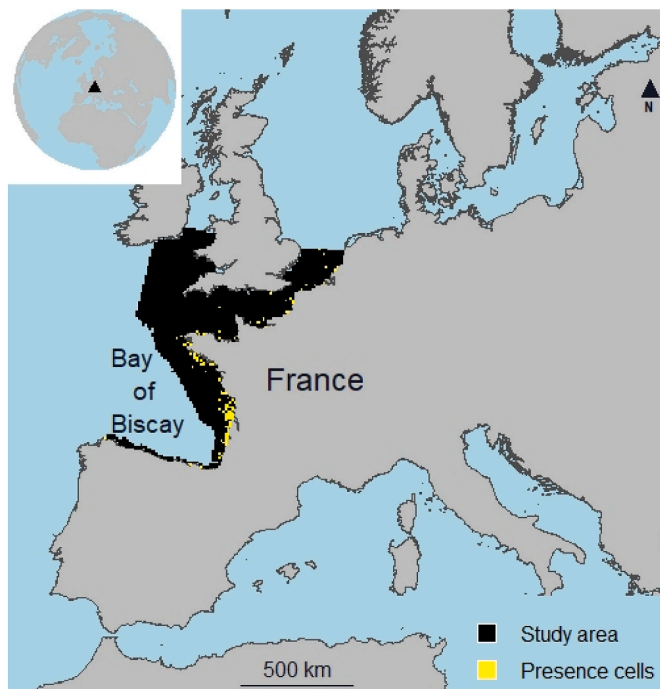
Fig. 1. Location of the study area and presence cells of *A. sturio* (n = 110; 2012–2021).

Food and Environment - INRAE). A total of 311 observations at sea were collected from incidental observations by professional and amateur fishermen or citizens. These data were complemented with 5 observations from the Obsmer database (i.e. commercial fisheries operating on all French maritime facades) (Cornou et al., 2021) and 1 incidental observation declared in Germany (Gessner, *comm. pers.*). The study area was then converted into a grid of 10 × 10 km cells to deal with the uncertainty of the observation locations, leading to a total of 3095 cells. A cell with at least one observation was considered as a presence, resulting in 110 presence cells over the period (Fig. 1).

2.3. Environmental variables

Given the limited knowledge on the marine ecology of *A. sturio*, we calculated a wide variety of variables (i.e. physico-chemical, geographic, topographic, hydrodynamic, substrate types) based on what was commonly used for bentho-demersal or diadromous species in previous SDM studies (e.g. Breece et al., 2018; Huff et al., 2012; Trancart et al., 2014). Twelve variables were selected since they (i) were related to the species presences according to point biserial correlations (Elith et al., 2006; Sillero et al., 2021); (ii) had absolute values of Pearson correlation coefficients <0.58; (iii) showed variance inflation factor <10, as recommended by Sillero et al. (2021) and (iv) presented the most variation spatially across the study area (Table 1, Supplementary Table S1). For 3D variables (i.e. available at multiple depths), we used the environmental information on the seabed to be consistent with the ecology of Acipenseridae species (Bemis et al., 1997). The parameters (i. e. mean, range) were calculated for each year at a monthly resolution, and then averaged over the entire 2012–2020 period. For substrate variables, the simplified Folk classification system (Folk, 1954) was used to make four categories: "mud to muddy sands", "sands", "coarse-grained and mixed sediments" and "rock and boulders". Then, we calculated the shortest distance from each cell center to the nearest patch boundary of each substrate category with the *geosphere* R package (Hijmans, 2019), creating the four substrate variables. The distMOUTH variable (all abbreviations and definitions of variables are given in Table 1) was calculated for each cell as the shortest distance to the

Table 1
Variables selected for species distribution modelling. The models in which the variables were included as well as the sources were also specified. The salinity was measured using the Practical Salinity Scale.

Categories	Variables (abbreviations)	Units	Models	Sources
Physico-chemical	Mean annual temperature on the seabed (2012–2020; TEMP_MEAN_10km)	°C	I & II	MARS 3D (https://marc.ifremer.fr)
	Mean annual salinity on the seabed (2012–2020; SAL_MEAN_10km)	/	II	
	Inter-monthly mean range of dissolved oxygen on the seabed (2012–2020; OXY_RANGE_10km)	mg/L^{-1}	I & II	ECOMARS 3D (https://marc.ifremer.fr)
	Mean light attenuation coefficient on the seabed (2012–2020; LIGHT_MEAN_10km)	m^{-1}	II	
Hydrodynamic	Mean amplitude of sediment displacement on the seabed (2012–2020; DISP_MEAN_10km)	m	I & II	WW3-NORGAS-2MIN (https://marc.ifremer.fr/)
	Mean current speed on the seabed (2012–2020; VEL_MEAN_10km)	m/s^{-1}		MARS 3D (https://marc.ifremer.fr)
Substrate	Distance to mud or muddy sand substrate (distMUD_SAND_10km)	km	I & II	EUSeaMap 2021 (Vasquez et al., 2021)
	Distance to sandy substrate (distSAND_10km)	km		
	Distance to coarse or mixed substrate (distMIX_COARSE_10km)	km		
	Distance to rock substrate (distROCK_10km)	km		
Topographic	Bathymetry (BATHY_10km)	m	I	EMODnet Bathymetry (www.emodnet-bathymetry.eu)
Geographic	Distance to the river origin (i.e. Gironde estuary; distMOUTH)	km	I	Calculated with the *raster* package in R (Hijmans, 2020)

Gironde estuary, excluding terrestrial environments and marine environments deeper than 150 m (*raster R* package) (Hijmans, 2020). The distribution and spatial variation of the twelve environmental variables selected were displayed in Supplementary Figs. S1 and S2. Due to strong nonlinear relationships, two pairs of variables (i.e. distMOUTH and BATHY_10km *vs* SAL_MEAN_10km and LIGHT_MEAN_10km) were not included together in the same model. As both pairs could be relevant in the marine species ecology, the choice was made to carry out two separate models: the first containing the 12 variables except the pair of variables SAL_MEAN_10km and LIGHT_MEAN_10km (model I), the second also containing the 12 variables except the pair of variables distMOUTH and BATHY_10km (model II; Table 1). As the distMOUTH variable reflected a dispersal constraint from a single source (i.e. the GGD system), the model I was only focused on the population from the GGD system. Hence, the observations for which the origin of individuals was known, and not from the GGD system, were deleted for the model I input dataset. Thus, 107 presence cells were used for model I against 110 for model II.

2.4. Species distribution models: basic method

To model the *A. sturio* marine distribution, an ensemble modelling

approach was used from seven algorithms (generalised linear model - GLM, generalised additive model - GAM, multivariate adaptive regression splines - MARS, flexible discriminant analysis - FDA, Maxent, random forest - RF and gradient boosting machine - GBM) with the *Biomod2* package in R (Thuiller et al., 2009; Araújo and New, 2007). The settings used for each algorithm were listed in Supplementary Table S2.

As there was no absence data available from our participatory dataset, we generated 2 sets of 2000 random pseudo-absences on the whole study area. This high number of pseudo-absences aims to optimize model performance and ensure the selection of enough informative pseudo-absences. They encompassed the environmental conditions where the species can potentially occur in the study area (Barbet-Massin et al., 2012). The much larger number of pseudo-absences compared to presences generates a very low prevalence. In order to avoid negative prevalence effects, the prevalence was then set to 0.5 to give equal weights to presence and pseudo-absence cells (Jiménez-Valverde and Lobo, 2006). We implemented 10 random replications and used 80% of the datasets for model calibration and the remaining 20% for evaluation. We evaluated single and ensemble models with the Area Under the ROC Curve (AUC), the threshold maximizing True Skill Statistic (MaxTSS), the threshold maximizing Kappa (MaxKappa) and the Boyce Index (Allouche et al., 2006; Hirzel et al., 2006; Lobo et al., 2008). Ensemble predictions over the study area were computed using the mean of single-model outputs with Boyce index superior to 0.5. The continuous predictive maps produced displayed a habitat suitability index (HSI) ranging from 0 to 1000.

The relative contribution of each variable included in the ensemble model was calculated using the ranking measure proposed by the *get_variables_importance* function in *Biomod2* (Thuiller et al., 2009). A top-down approach was then used to keep a reasonably small number of variables in models I and II. The overall model approach described above was applied to both models, each containing 10 variables at the start. The variable with the lowest mean relative contribution was removed and the ensemble modelling approach was rerun, and so on until each final ensemble model contained the five most important variables.

2.5. Alternative methods to reduce potential biases

The quality of the presence/pseudo-absence datasets (i.e. participatory data with an unknown but certainly uneven sampling effort, random pseudo-absences) and the cross-validation approach used with the basic method (i.e. repeated random splits) can be source of several biases (Peterson and Soberón, 2012; Phillips et al., 2009) (Supplementary Table S3). To evaluate these possible biases, some alternative methods were conducted, in addition to the basic one, on both final ensemble models with their respective five most important variables (Table 2).

To reduce the problem linked with oversampled areas, we used spatial and environmental filters (Castellanos et al., 2019). The spatial filtering of aggregated presence cells was performed (*Spat_filter* method) by using the R package *spThin* (Aiello-Lammens et al., 2015) with a neighbour distance threshold of 15 km. The clustering level before and after the spatial thinned procedure was measured with the nearest neighbourhood index (NNI) (Clark and Evans, 1954). The NNI ranges from 0 (i.e. clustered pattern) to 2.15 (i.e. regular pattern) while 1 means a random pattern. We also used two environmental filters to remove redundant information (i.e. presence cells with similar environmental conditions) by using the *envSample* R function (Varela et al., 2014) (https://github.com/SaraVarela/envSample). For the first environmental filter (*Env_filter_VAR* method), we used the distMOUTH variable and the distance to the coast to represent the environmental space. The aim was to limit the likely oversampling near the coast and the Gironde estuary (i.e. coastal zones more intensely prospected and observers close to the Gironde estuary, where stocking occurred, probably more aware of this practice). For the second environmental filter

Table 2

Detailed description of selected presence and pseudo-absence cells and cross-validation approach for each method. Abbreviations: *Basic*, basic method; *Spat_filter*, spatial filtering of presence cells; *Env_filter_PCA*, environmental filtering of presence cells using the first two axes of a PCA including the 5 final variables at presence cells; *Env_filter_VAR*, environmental filtering of presence cells using the distMOUTH variable and the distance to the coast; *PA_target_group*, inventoried pseudo-absences from target-group species; *Block_CV*, block cross-validation approach.

Presence cells	Pseudo-absence cells	Cross-validation
Basic All: 107 (model I)/110 (model II)	Random: 2000	Random with 20 iterations (i.e. 2 sets of pseudo-absences × 10 replications)
Env_filter_PCA Environmentally filtered using the first two axes of a PCA including the 5 final variables at presence cells: 74 (model I)/69 (model II)	Random: 2000	Random with 20 iterations (i.e. 2 sets of pseudo-absences × 10 replications)
Env_filter_VAR Environmentally filtered using the distMOUTH variable and the distance to the coast: 72 (model I)/73 (model II)	Random: 2000	Random with 20 iterations (i.e. 2 sets of pseudo-absences × 10 replications)
Spat_filter Spatially filtered: 62 (model I)/ 63 (model II)	Random: 2000	Random with 20 iterations (i.e. 2 sets of pseudo-absences × 10 replications)
Block_CV All: 107 (model I)/110 (model II)	Random: 2000	Non-random and blocked with 5 replications (selected in 15 × 15 blocks)
PA_target_group All: 107 (model I)/110 (model II)	Inventoried from target-group species: 1770	Random with 10 iterations (i.e. 1 set of pseudo-absences × 10 replications)

(*Env_filter_PCA* method), the first two axes of a principal component analysis (PCA), including the five most influential variables at presence cells, were used to represent the environmental space. Hence, each filtering treatment led to a pool of unique presence cells (Supplementary Figs. S3a and S4a).

Random cross-validation can produce the same spatial autocorrelation structure between calibration and validation datasets (de Oliveira et al., 2014; Pottier et al., 2013). This issue can be reduced by partitioning the datasets using a block cross-validation approach (Valavi et al., 2019) which increases the degree of independence of both datasets. The study area was divided into 15 × 15 blocks that were partitioned randomly (Supplementary Figs. S3c and S4c). The presence and pseudo-absence cells contained in blocks selected for the calibration dataset were assigned to it, and similarly for the validation dataset. We applied this approach (*Block_CV* method) using 5 replications and the *blockCV* R package.

Then, the use of target-group pseudo-absences instead of random pseudo-absences considers that a site with a similar species observed but not the targeted one can be considered as an inventoried absence. Models using target-group pseudo-absences can have better predictive performance than those using random pseudo-absences (Mateo et al., 2010) if areas that are unfavourable for the targeted species are correctly represented (Brotons et al., 2004) or have the same bias as the presence dataset (Phillips et al., 2009). We adapted that method (*PA_target_group* method) by extracting pseudo-absences from the MigrenMer database (Elliott et al., 2021). This database contains capture records of diadromous species from French fisheries observers and scientific surveys (downloaded from ICES DATRAS and French scientific surveys). These data have been filtered to coincide with the spatio-temporal extent of this study and consider only fishing gears than can catch *A. sturio*. In this

subsample, all cells with at least one site surveyed and without detection of *A. sturio* were considered as pseudo-absence cells (Supplementary Figs. S3b and S4b). The Supplementary Table S3 gave a more complete description of the advantages and limits for each method used.

2.6. Comparison of modelling methods

To determine the extent of change in predicted HSI between the different modelling methods and to select the most robust one, we compared (i) the obtained evaluation metrics (i.e. Boyce, AUC, MaxTSS, MaxKappa); (ii) anomaly maps; (iii) Schoener's D statistics (Schoener, 1968) and (iv) percentage of HSI values among 4 classes of HSI (i.e. 0-250/250-500/500–750/750-1000). Anomaly maps were pairwise calculation of differences in HSI values between predictions with the basic method and those with the alternative methods. An increase in HSI corresponded to negative values on anomaly maps while a decrease in HSI corresponded to positive values (Castellanos et al., 2019). The pairwise Schoener's D statistic compared habitat suitability maps on a scale from 0 (no similarity between predictions) to 1 (identical predictions) by using the *ENMeval* package in R (Muscarella et al., 2014).

2.7. Building the final habitat suitability map

For the most robust final ensemble models I and II, we converted the 20 mean continuous predictions (i.e. 2 sets of pseudo-absence × 10 replications) of HSI into binary predictions according to the threshold that maximizes sensitivity (i.e. ratio of correctly predicted presences to their total number) plus specificity (i.e. ratio of correctly predicted absences to their total number). Then, the 20 binary maps of both final ensemble models were summed to build the final habitat suitability map. Values of this map range from 0 (i.e. the 40 predictions agreed that the HSI of the given cells were low) to 40 (i.e. the 40 predictions agreed that the HSI of the given cells were high) while intermediate values indicated variability between predictions.

3. Results

The reduction from 10 to 5 variables in the models resulted in the selection of the following variables: TEMP_MEAN_10km, VEL_MEAN_10km and OXY_RANGE_10km for both models as well as BATHY_10km and distMOUTH for model I and SAL_MEAN_10km and DISP_MEAN_10km for model II (Fig. 2). The application of spatial and environmental filters resulted in the reduction of 107/110 (model I/ model II) presence cells to 62/63 for the *Spat_filter* method, 72/73 for the *Env_filter_VAR* method and 69/74 for the *Env_filter_PCA* method. For the latter method, the first two axes of PCA explained 75% and 71% of the total variance for models I and II, respectively. The NNI values increased

from 0.67/0.67 (p-value < 0.01) to 0.91/0.92 (p-value < 0.01) following the application of the *Spat_filter* method, which allowed getting closer to a random distribution (Supplementary Figs. S3a and S4a). The *PA_target_group* method resulted in 1770 pseudo-absence cells (Supplementary Figs. S3b and S4b).

Basic and alternative methods applied on both final ensemble models resulted in satisfying evaluations according to AUC (ranging from (mean ± SD) 0.87 ± 0.04 for the *Spat_filter* method applied to model I to 0.93 ± 0.03 for the *Basic* method applied to model II), MaxTSS (ranging from 0.67 ± 0.08 for the *Spat_filter* method applied to model I to 0.77 ± 0.07 for the *Basic* method applied to model II), MaxKappa (ranging from 0.30 ± 0.06 for the *Spat_filter* method applied to model I to 0.55 ± 0.07 for the *Basic* method applied to model II) and Boyce Index (ranging from 0.82 ± 0.12 for the *Block_CV* method applied to model II to 0.89 ± 0.06 for the *Basic* method applied to model II; Fig. 3). While predictive capacities were relatively similar among methods, they were still slightly better for the *Basic* method whereas the *Spat_filter* method had always the least good predictive capacities, except with the Boyce index.

Predictive and anomaly maps as well as Schoener's D statistics confirmed similar results among methods for both final ensemble models (Fig. 4). Predictive maps for both models and all methods showed very high HSI on the French Atlantic coast and more intermediate HSI on the southern coasts of the English Channel and the North Sea, and around the Thames estuary in the United-Kingdom (Fig. 4a to l). Schoener's D statistic values were always greater than 0.90 and anomaly maps were dominated by cells with values close to 0 (Fig. 4a–b to 4g-l), meaning small differences between predictions of the basic method and those of alternative methods. However, little variations were observed depending on the method used for the model I. With the three filter methods (i.e. *Spat_filter*, *Env_filter_VAR*, *Env_filter_PCA*), a slight decrease of HSI was observed along the French Atlantic coast as well as a minimal increase of HSI on the rest of the study area (Fig. 4a-b to 4a-d). The *Env_filter_PCA* method also caused a slight increase of HSI in the Iroise Sea and in the Bay of Seine (Fig. 4a–b). The *Block_CV* and *PA_target_group* methods gave nearly identical results to the basic one (Fig. 4a–e to 4a-f). Still for the model I, alternative methods tended to slightly decrease the percentage of cells with very high (i.e. 750-1000 class; except for *Block_CV* and *PA_target_group* methods where an increase was observed) and very low HSI (i.e. 0- 250 class), and to slightly increase the percentage of cells with moderately low and strong HSI (i.e. 250-500 and 500–750 classes respectively; Supplementary Table S4). For model II, same trends were observed as with model I. However, new sectors appeared with a decrease in HSI following the application of filters, such as the English coasts (*Env_filter_PCA*; Fig. 4g–h), or the Belgian and Dutch coasts (*Env_filter_VAR*; Fig. 4g-i). A slightly more pronounced decline in HSI appeared on the French Brittany coast for the
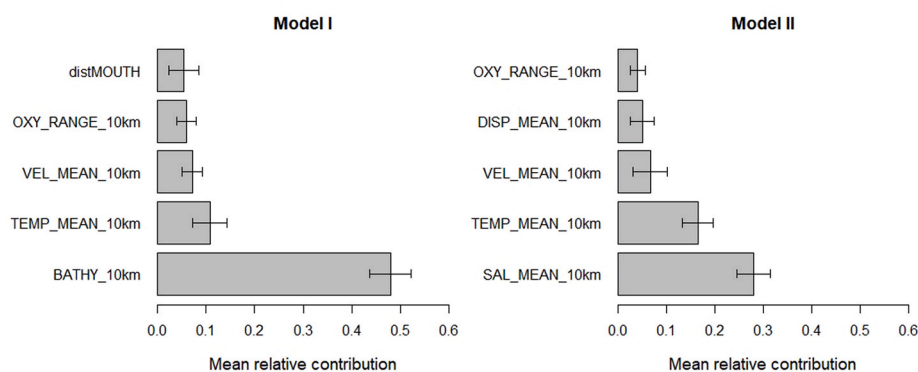

Fig. 2. Mean relative contribution across the 20 iterations (i.e. 2 sets of pseudo-absences × 10 replications) of ensemble modelling for the 5 most important variables selected in the final ensemble models I (left) and II (right) for the basic method. Variables were listed in increasing order of mean relative contribution. Error bars represented standard deviation (SD).

Abbreviations: BATHY_10km, bathymetry; TEMP_MEAN_10km, mean annual temperature on the seabed (2012–2020); VEL_MEAN_10km, mean current speed on the seabed (2012–2020); OXY_RANGE_10km, inter-monthly mean range of dissolved oxygen on the seabed (2012–2020); distMOUTH, distance to the river origin (i.e. Gironde estuary); SAL_MEAN_10km, mean annual salinity on the seabed (2012–2020); DISP_MEAN_10km, mean amplitude of sediment displacement on the seabed (2012–2020).
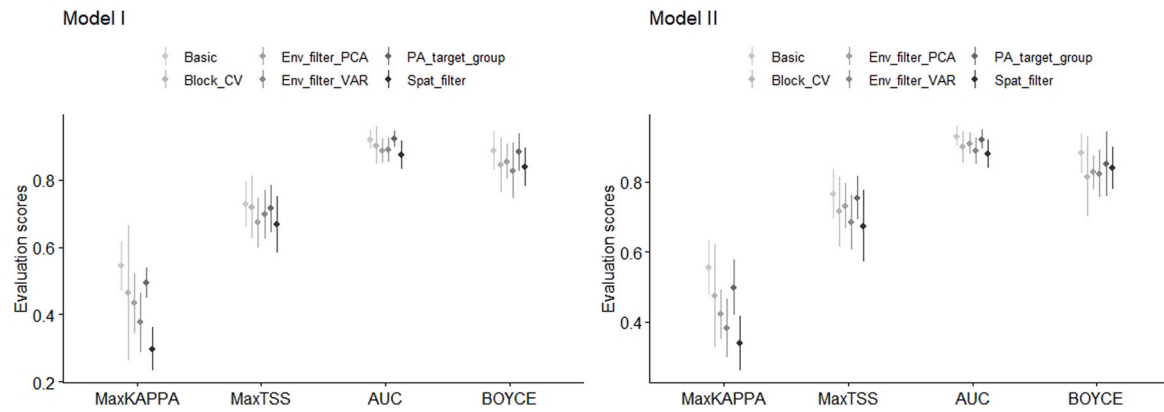
Fig. 3. Plots of the results of the evaluation metrics obtained for the basic and the alternative methods tested for final ensemble models I (left) and II (right). The results shown were MaxKappa, MaxTSS, AUC and Boyce metrics. Each point is the average value across the 20 iterations with the standard deviation displayed as an error bar. The grey gradient allowed the distinction between the methods used.

Abbreviations: *Basic*, basic method; *Spat_filter*, spatial filtering of presence cells; *Env_filter_PCA*, environmental filtering of presence cells using the first two axes of a PCA including the 5 final variables at presence cells; *Env_filter_VAR*, environmental filtering of presence cells using the distMOUTH variable and the distance to the coast; *PA_target_group*, inventoried pseudo-absences from target-group species; *Block_CV*, block cross-validation approach.
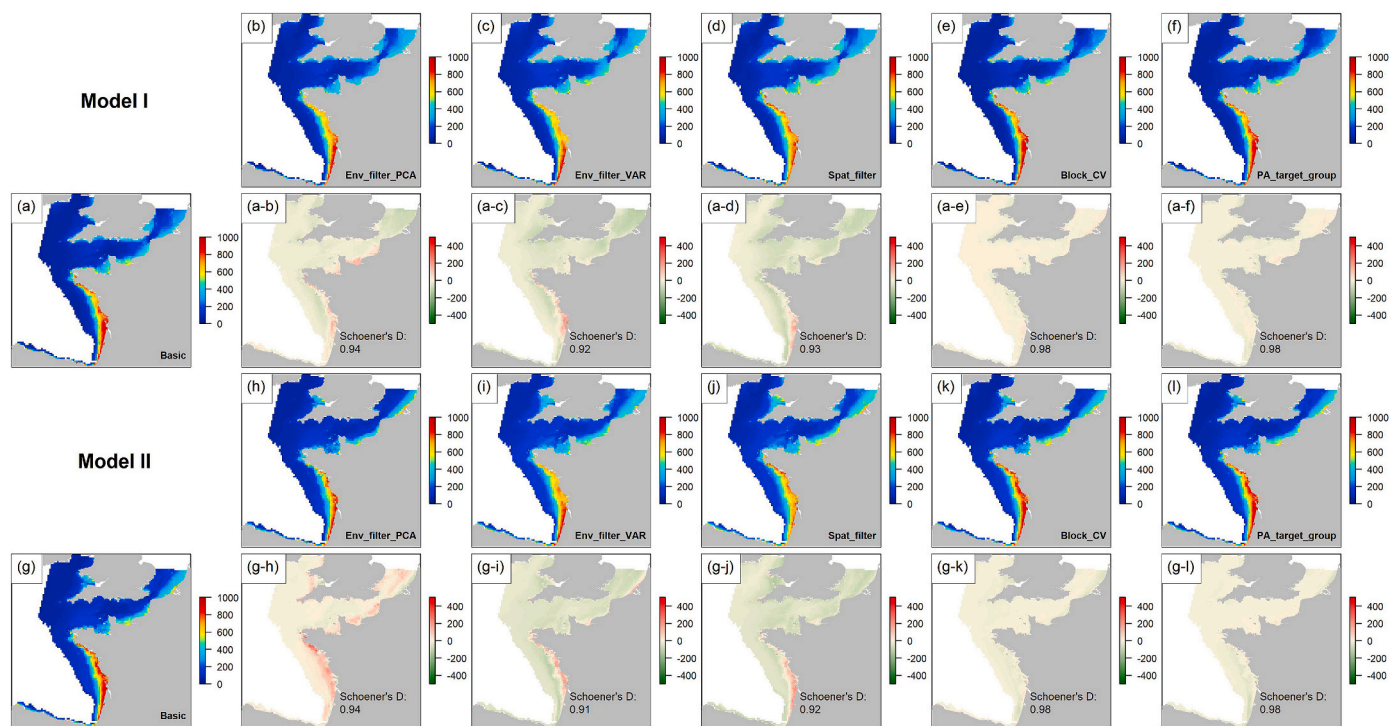

Fig. 4. Habitat suitability index (HSI) predictions for the final ensemble models I (top) and II (bottom) with the basic (a, g) and the alternative methods (b to f & h to l). Anomaly maps (a–b to a–f & g–h to g–l) facilitated the pairwise comparison between the basic method and each alternative method. The map (a–b) represented the values of map (a) from which the values of map (b) were subtracted. Increases in HSI for alternative methods were shown in shades of green, while decreases in HSI were depicted in shades of red. The other anomaly maps should be interpreted in the same way. Schoener's D statistic was also displayed on each anomaly map.

Abbreviations: *Basic*, basic method; *Spat_filter*, spatial filtering of presence cells; *Env_filter_PCA*, environmental filtering of presence cells using the first two axes of a PCA including the 5 final variables at presence cells; *Env_filter_VAR*, environmental filtering of presence cells using the distMOUTH variable and the distance to the coast; *PA_target_group*, inventoried pseudo-absences from target-group species; *Block_CV*, block cross-validation approach. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Env_filter_PCA method (Fig. 4g-h). Hence, comparison of results from different modelling methods associated with their known limits and advantages (Supplementary Table S3) led to the selection of the basic method for the next analyses.

For model I, BATHY_10km had the best relative contribution (0.48 ± 0.04) followed by TEMP_MEAN_10km (0.11 ± 0.04), VEL_-MEAN_10km (0.07 ± 0.02), OXY_RANGE_10km (0.06 ± 0.02) and then distMOUTH (0.05 ± 0.03; Fig. 2). Concerning model II,

SAL_MEAN_10km had the greatest relative contribution (0.28 ± 0.03) followed by TEMP_MEAN_10km (0.17 ± 0.03) while VEL_MEAN_10km (0.07 ± 0.04), DISP_MEAN_10km (0.05 ± 0.02) and OXY_RANGE_10km (0.04 ± 0.01) contributed less. The more BATHY_10km, VEL_-MEAN_10km and distMOUTH values increased, the more the HSI decreased (Fig. 5). HSI appeared to increase up to TEMP_MEAN_10km values between 14 and 15 °C, and to increase also very slightly when DISP_MEAN_10km and OXY_RANGE_10km values increased.
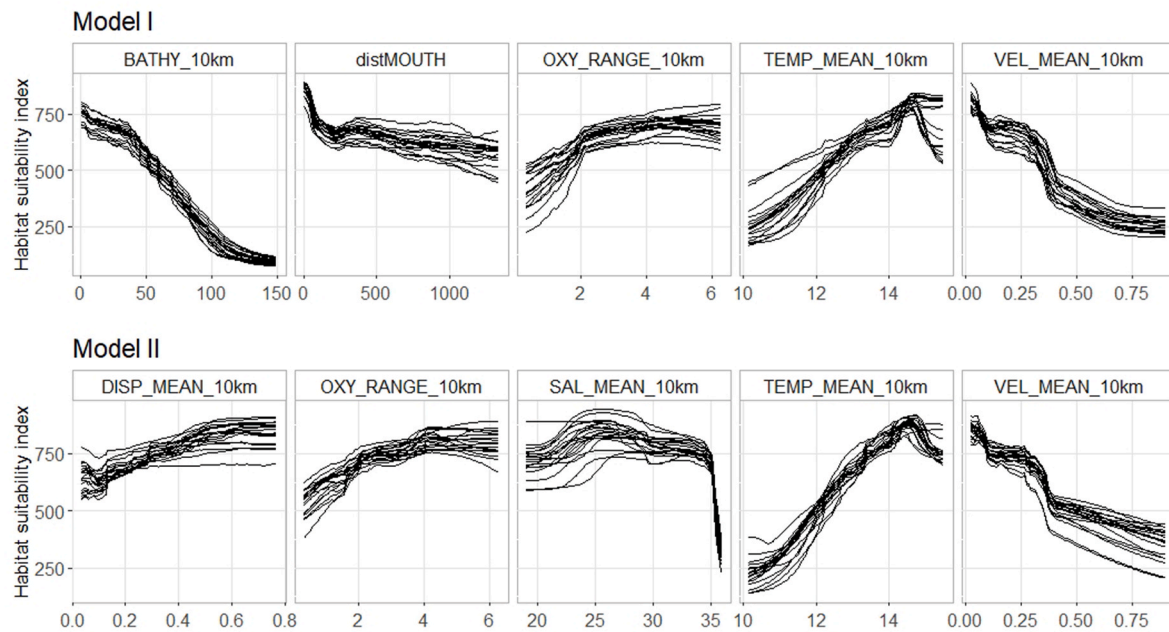
Fig. 5. Mean response curves among the seven algorithms for the five most important variables of models I (top) and II (bottom) applied on the selected method (i.e. the basic method). The y-axes represented the habitat suitability index (HSI) while the x-axes represented the values of the variables. Response curves demonstrated how HSI differed as variables varied, whilst all other variables were kept constant at their average values. There were 20 mean response curves for each variable, as one response curve corresponded to one iteration.
Abbreviations: BATHY_10km, bathymetry; TEMP_MEAN_10km, mean annual temperature on the seabed (2012–2020); VEL_MEAN_10km, mean current speed on the seabed (2012–2020); OXY_RANGE_10km, inter-monthly mean range of dissolved oxygen on the seabed (2012–2020); distMOUTH, distance to the river origin (i.e. Gironde estuary); SAL_MEAN_10km, mean annual salinity on the seabed (2012–2020); DISP_MEAN_10km, mean amplitude of sediment displacement on the seabed (2012–2020).

Concerning SAL_MEAN_10km, HSI values seemed maximum around 25–30 and dropped quickly and drastically from 35.

Looking at the final habitat suitability map, the most suitable marine areas for *A. sturio*, with a strong consensus of both final ensemble models, were distributed along the French Atlantic coast, the Seine and Somme bays, around the Rhine delta and in some coastal areas in Northern Spain (Fig. 6). The least suitable areas with a strong consensus of both final ensemble models were mainly located offshore from France, Belgium and Netherlands while they were closer to the coasts in Spain, the United-Kingdom and Ireland. Some sectors were characterized by high variability among final ensemble models and iterations, such as the bays of the Mont Saint-Michel in France and the Thames and sectors along the Dutch coast.

4. Discussion

For the first time, this study draws a map of *A. sturio* marine habitat in coastal European waters, a key starting point to understand complex, wide-ranging distribution patterns and mechanisms driving the species ecological requirements. We acknowledge that *A. sturio* observations used in this study were collected from participatory declarations. This type of approach is vital for gaining information on this species that is difficult to access and to promote cooperative management between fishermen and researchers (Giareta et al., 2021). Our results showed that regardless the aim of the modelling method used (i.e. to remove the biases in presence data, to generate pseudo-absences, to perform cross-validation), the predictions were very similar which brings more confidence in the results. Along the same lines, the study of Pennino et al. (2016) highlighted that spatial patterns of suitable habitat predicted for elasmobranchs were similar whatever the source of data used, fishery-independent (i.e. scientific surveys) or -dependent data (i.e. surveys by observers in commercial vessels). In the course of our study, having removed duplicate observations within each 10 × 10 km cell
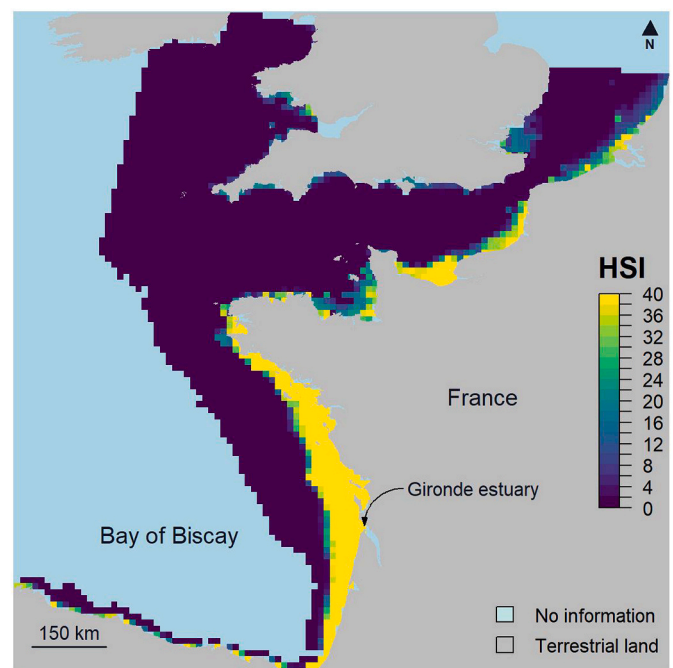

Fig. 6. Final habitat suitability map summing binary predictions of both final ensemble models I and II, using the basic method. Values of this map ranged from 0 (i.e. the 40 binary predictions of both final ensemble models I and II agreed that the HSI of the cells were low) to 40 (i.e. the 40 binary predictions of both final ensemble models I and II agreed that the HSI of the cells were high) while intermediate values indicated variability between predictions.
Abbreviations: HSI, habitat suitability index.

before the application of further thinning and statistical modelling, which is already a kind of spatial thinning (Aiello-Lammens et al., 2015), may have reduced biases inherent in the dataset.

Another important consideration suggested by Pennino et al. (2016) is that fishing data can be an unbiased indicator of species occurrences in case that their locations have been chosen independently of the known distribution of the interest species. This hypothesis seems plausible for *A. sturio* as this is a non-target species for commercial fishing with a fishing ban in France since 1982. Yet, given the paucity of data available, we are confident that citizen science was essential to model *A. sturio* distribution along the European Western coast with the best-available data.

The strong influence observed for the bathymetry, temperature and salinity is in agreement with Bradie and Leung (2017) meta-analysis, which showed these variables as the most important drivers of marine species distribution. The strong negative influence of the bathymetry is consistent with previous studies conducted on *A. sturio* in marine and estuarine environments (Acolas et al., 2017; Rochard et al., 1997), as well as on other sturgeon species such as *A. medirostris* (Huff et al., 2012, 2011) and *A. oxyrinchus* (Breece et al., 2018; Stein et al., 2004). Since bathymetry is known to indirectly drive the species distribution (Bosch et al., 2018), we hypothesize that this variable, in association with the seabed chlorophyll-a concentration (negatively correlated to the bathymetry, r = -0.74), can be linked to the benthic macrofauna abundance (Karakassis and Eleftheriou, 1997) on which *A. sturio* feeds in estuaries (Brosse et al., 2000). On the continental shelf of Portugal for example, a decrease in abundance of polychaetes with depth has been observed (Martins et al., 2013). Highest abundances were found between 30 and 60 m depth, which are depth levels highly suitable to *A. sturio*. However, the lack of studies in our study area does not allow confirming the trend observed in Portugal between the abundance of polychaetes and depth. Moreover, the diet at sea of the species is unknown. The bathymetry was also strongly correlated with the distance to the coast (i.e. r = 0.73), and coastal waters can offer more food resources favouring the growth of individuals, as observed for sharks (Speed et al., 2010).

The temperature is a limiting factor that directly influences the species physiology (Pörtner, 2002) and this being even more true for fish that are poikilotherms (Doudoroff, 1938). In this study, the optimum in the response curve is around 14–15 °C mean annual temperatures and the coldest temperatures around 10–11 °C seem to limit *A. sturio* occurrence. However, the coldest areas are mainly located in the northern part of the study area, far from the GGD system (i.e. the natal river). The energy cost of moving away from GGD spawning sites (Jonsson and Jonsson, 2006) may result in fewer individuals being observed in the northern and coldest parts of the study area. In addition, the extent of the study area was constrained by the availability of environmental variables, and did not consider the northern part of the species range. This limitation may have underestimated habitat suitability at colder temperatures (Sánchez-Fernández et al., 2011).

Sectors with high suitability regarding the mean salinity (i.e. maximal suitability between 27 and 34) correspond to narrow coastal margins mainly located around estuaries and bays, and therefore under the influence of river flows (Trimoreau et al., 2013). Sea outlets with high productivity could serve as nursery areas, as already observed for the common sole (*Solea solea)* in the Seine estuary (Rochette et al., 2010).

The observed negative influence of the average current velocity on the seabed is contrary to our expectations. Sea currents provide energetic advantages to cover long-migration distances at lower cost for the green sturgeon (*A. medirostris*) (Huff et al., 2012; Kelly and Klimley, 2012). However, average current velocity on the seabed may be globally too slow or poorly oriented, to provide energetic advantages for individuals during their migration or their coastal movements, as it has been observed for the plaice (*Pleuronectes platessa* L.) (Hunter et al., 2003). The present result suggests that rather than migrating or moving,

the individuals observed in the study area would have selected habitats with low average current speeds, probably for feeding.

Habitat suitability also decreases as the distance to the Gironde estuary increases. This result supported the hypothesis that observed sturgeons originate from a single natal river (i.e. the GGD system) and display a homing behaviour, which may drive the species marine distribution. This constraint, linked with the need to be close to the natal river for reproduction through the life span, would lead to an increase in energetic costs caused by repeated long-distance movements at sea (Jonsson and Jonsson, 2006). An influence of the river origin on the marine spatial distribution of chinook salmon (*Oncorhynchus tshawytscha*) stocks has also been observed (Shelton et al., 2021). The sharp drop in habitat suitability in the first 200 km from the GGD system may also be explained by two migratory tactics within the population: some individuals would remain around the estuary while some would travel greater distances, the two tactics could be alternatively used by individuals. Moreover, the estuarine plume of the GGD system is a mandatory transition zone between the marine environment for growth and the breeding basin. Nonetheless, the importance of this variable can be challenged since the model without the distance to the Gironde estuary provides similar predictions to the one including this predictor.

Surprisingly, all substrate variables are less relevant in explaining the marine distribution of *A. sturio*, but this conclusion remains consistent with the results of Rochard et al. (1997) for *A. sturio* and Stein et al. (2004) for *A. oxyrinchus*. However, substrate type is known to directly influence benthic invertebrate prey (Levin, 1982; McBreen et al., 2008). Future studies with more precise data on *A. sturio* marine distribution and looking further into its diet and associated prey availability are needed to provide knowledge on its fine-scale habitat choices.

Predictions in the present work provide a static image, irrespective of potential migratory events (e.g. Wisz et al., 2015) or seasonal changes in distribution. Given the paucity of observation data, it was not possible to make seasonal models for which the relevance has been demonstrated for *A. medirostris* (Huff et al., 2012) and *A. oxyrinchus* (Breece et al., 2018). Hence, our approach provides global estimates and general trends, most of the variables being annual averages over 9 years in calibration and validation. Correlative SDM approaches give information on where a species actually or potentially lives across a landscape according to the physical/environmental features (Sillero et al., 2021). They do not rely on an explicit mechanistic understanding (i.e. causal relationships) of how different environmental factors interact with the target species to affect its key biological processes such as growth, survival and reproduction (i.e. its fitness) (Kearney, 2006). In addition, they do not provide information on how the habitat is used nor how the organism experiences that habitat (e.g. for food, rest, movement). Indeed, correlative SDM studies should be considered as a first step in generating hypotheses about mechanistic links between a species and its surroundings (Kearney, 2006). Relationships and hypotheses proposed in this study will have to be confirmed at finer scales thanks to specific studies, such as through real-time tracking of individual movements (e. g. Huff et al., 2011). Then, shifts in environmental requirements throughout ontogeny is common in mobile marine species (Dahlgren and Eggleston, 2000) and can result in shifts in spatial distributions (e.g. Camiolo et al., 2021; Wisz et al., 2015). Concerning the stocked *A. sturio*, individuals start to leave the Gironde estuary to grow at sea at the age of 3 and later acquire sexual maturity (Acolas et al., 2011). We can therefore assume that habitats at sea modelled in this study concern mainly immature juveniles from stocking, from 3 to 14 years old, since no natural reproduction was observed over the period considered.

Model predictions confirm a potential near-shore distribution and also more coastal habitats for *A. sturio*. Hence, this species is potentially vulnerable to anthropogenic stresses which are increasingly accumulating in coastal areas (Bugnot et al., 2021; Davidson et al., 2012). The benthic behaviour of *A. sturio* (Brosse et al., 2000) and the use of electromagnetic fields for orientation (Lohmann et al., 2008) can make the species sensitive to actions that physically and directly impact the

seabed (e.g. substrate and minerals extraction, bottom trawling, underwater constructions) (Bugnot et al., 2021; Kaikkonen et al., 2018; Taormina et al., 2018) or marine structures that emit electromagnetic fields (Taormina et al., 2018). Sectors identified as highly suitable for *A. sturio* are subject to exploitation of shell or siliceous sands and gravels (Pichon et al., 2017), installation of submarine cables (RTE, 2018) or construction of wind energy developments (Creocean, 2021). Further specific studies would help to assess the potential impacts of these human activities on *A. sturio* and the need for compromises to optimize the species conservation with the maintenance of socio-economic activities. By overlapping the habitat suitability map with the existing marine protected area (MPA) network, conservation gap analyses (Jennings, 2000) will also help environmental managers to evaluate the amount of suitable habitats for *A. sturio* within the MPA network (e.g. Hooker et al., 2011). Furthermore, as the species spends most of its life span at sea, the existence of suitable areas in this environment is essential for the population to be functional. Nevertheless, this modelling attempt at sea remains disconnected from information on habitat suitability for *A. sturio* in the Gironde estuary and in the Garonne and Dordogne rivers. A future challenge would be the application of SDM combining information from riverine, estuarine and marine environments to ensure the availability and the preservation of the global longitudinal connectivity between the different living environments of this diadromous fish (Brevé et al., 2014). This kind of approach would make it possible to consider the ecological requirements of *A. sturio* at different stages of its life cycle (Frans et al., 2018; Häkkinen et al., 2021).

CRediT authorship contribution statement

Anaïs Charbonnel: Conceptualization, Software, Validation, Formal analysis, Writing - Original Draft, Visualization, **Patrick Lambert:** Conceptualization, Methodology, Validation, Writing - Review & Editing, **Géraldine Lassalle:** Conceptualization, Methodology, Validation, Writing - Review & Editing, **Eric Quinton:** Methodology, Software, Writing - Review & Editing **Antoine Guisan:** Conceptualization, Methodology, Validation, Writing - Review & Editing, **Lise Mas:** Methodology, Writing - Review & Editing, **Guillaume Paquignon:** Conceptualization, Supervision, Project administration, Funding acquisition, **Marie Lecomte:** Methodology, Writing - Review & Editing, **Marie-Laure Acolas:** Conceptualization, Software, Methodology, Validation, Resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition

Declaration of competing interest

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

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2022.108136.

References

Acolas, M.L., Castelnaud, G., Lepage, M., Rochard, E., 2011. Chapter 10 biological cycles and migrations of *Acipenser sturio*. In: Williot, P., Rochard, E., Desse-Berset, N., Kirschbaum, F., Gessner, J. (Eds.), Biology and Conservation of the Atlantic European Sturgeon *Acipenser sturio* L., 1758. Springer, Berlin Heidelberg, pp. 147–152. https://doi.org/10.1007/978-3-642-20611-5_10.

Acolas, M.L., Le Pichon, C., Rochard, E., 2017. Spring habitat use by stocked one year old European sturgeon *Acipenser sturio* in the freshwater-oligohaline area of the Gironde estuary. Estuar. Coast Shelf Sci. 196, 58–69. https://doi.org/10.1016/j.ecss.2017.06.029.

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B., Anderson, R.P., 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38, 541–545. https://doi.org/10.1111/ecog.01132.

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43, 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22, 42–47. https://doi.org/10.1016/j.tree.2006.09.010.

Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol. Evol. 3, 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x.

Bemis, W.E., Kynard, B., 1997. Sturgeon rivers: an introduction to acipenseriform biogeography and life history. Environ. Biol. Fish. 48, 167–183. https://doi.org/10.1023/A:1007312524792.

Bemis, W.E., Findeis, E.K., Grande, L., 1997. An overview of Acipenseriformes. Environ. Biol. Fish. 48, 25–71. https://doi.org/10.1023/A:1007370213924.

Borja, A., Amouroux, D., Anschutz, P., Gómez-Gesteira, M., Uyarra, M.C., Valdés, L., 2019. Chapter 5 - the bay of Biscay. In: Sheppard, C. (Ed.), World Seas: an Environmental Evaluation, second ed. Academic Press, pp. 113–152. https://doi.org/10.1016/B978-0-12-805068-2.00006-1.

Bosch, S., Tyberghein, L., Deneudt, K., Hernandez, F., De Clerck, O., 2018. In search of relevant predictors for marine species distribution modelling using the MarineSPEED benchmark dataset. Divers. Distrib. 24, 144–157. https://doi.org/10.1111/ddi.12668.

Bradie, J., Leung, B., 2017. A quantitative synthesis of the importance of variables used in MaxEnt species distribution models. J. Biogeogr. 44, 1344–1361. https://doi.org/10.1111/jbi.12894.

Bradley, M., Nagelkerken, I., Baker, R., Sheaves, M., 2020. Context dependence: a conceptual approach for understanding the habitat relationships of coastal marine Fauna. Bioscience 70, 986–1004. https://doi.org/10.1093/biosci/biaa100.

Bradter, U., Mair, L., Jönsson, M., Knape, J., Singer, A., Snäll, T., 2018. Can opportunistically collected Citizen Science data fill a data gap for habitat suitability models of less common species? Methods Ecol. Evol. 9, 1667–1678. https://doi.org/10.1111/2041-210X.13012.

Breece, M.W., Fox, D.A., Haulsee, D.E., Wirgin, I.I., Oliver, M.J., 2018. Satellite driven distribution models of endangered Atlantic sturgeon occurrence in the mid-Atlantic Bight. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 75, 562–571. https://doi.org/10.1093/icesjms/fsx187.

Brevé, N.W.P., Buijse, A.D., Kroes, M.J., Wanningen, H., Vriese, F.T., 2014. Supporting decision-making for improving longitudinal connectivity for diadromous and potamodromous fishes in complex catchments. Sci. Total Environ. 496, 206–218. https://doi.org/10.1016/j.scitotenv.2014.07.043.

Brosse, L., Rochard, E., Dumont, P., Lepage, M., 2000. Premiers résultats sur l'alimentation de l'esturgeon européen, *Acipenser sturio* Linnaeus, 1758 dans l'estuaire de la Gironde et comparaison avec la macrofaune estuarienne présente. Cybium 24, 49–61.

Brotons, L., Thuiller, W., Araujo, M.B., Hirzel, A.H., 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. Ecography 27, 437–448. https://doi.org/10.1111/j.0906-7590.2004.03764.x.

Bugnot, A.B., Mayer-Pinto, M., Airoldi, L., Heery, E.C., Johnston, E.L., Critchley, L.P., Strain, E.M.A., Morris, R.L., Loke, L.H.L., Bishop, M.J., Sheehan, E.V., Coleman, R.A.,

Dafforn, K.A., 2021. Current and projected global extent of marine built structures. Nat. Sustain. 4, 33–41. https://doi.org/10.1038/s41893-020-00595-1.

Camiolo, M.D., Cozzolino, E., Jaureguizar, A.J., 2021. Suspended particulate matter is a key factor shaping the spatial arrangement of *Micropogonias furnieri* (sciaenidae) population in a Southwestern Atlantic temperate estuary. Regional Studies in Marine Science 43, 101667. https://doi.org/10.1016/j.rsma.2021.101667.

Carrera-García, E., Rochard, E., Acolas, M.L., 2017. Effects of rearing practice on post-release young-of-the-year behavior: *Acipenser sturio* early life in freshwater. Endanger. Species Res. 34, 269–281. https://doi.org/10.3354/esr00854.

Castellanos, A., Huntley, J.W., Voelker, G., Lawing, A.M., 2019. Environmental filtering improves ecological niche models across multiple scales. Methods Ecol. Evol. 10, 481–492. https://doi.org/10.1111/2041-210X.13142.

Clark, P.J., Evans, F.C., 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35, 445–453. https://doi.org/10.2307/1931034.

Cornou, A., Quinio-scavinner, M., Sagan, J., Cloâtre, T., Dubroca, L., Billet, N., 2021. Captures et rejets des métiers de pêche Français. Résultats des observations à bord des navires de pêche professionnelle en 2019. Obsmer. https://doi.org/10.13155/79198.

Crain, C.M., Halpern, B.S., Beck, M.W., Kappel, C.V., 2009. Understanding and managing human threats to the coastal marine environment. Ann. N. Y. Acad. Sci. 1162, 39–62. https://doi.org/10.1111/j.1749-6632.2009.04496.x.

Creocean, 2021. Projet de parc éolien en Sud-Atlantique. Etude bibliographique sur l'environnement marin, Rapport, p. 177. https://www.debatpublic.fr/sites/default/files/2021-11/EtudeBiblio_EnviroMarin_AO7_vf-3%20%281%29.pdf.

Dahlgren, C.P., Eggleston, D.B., 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology 81, 2227–2240. https://doi.org/10.2307/177110.

Davidson, A.D., Boyer, A.G., Kim, H., Pompa-Mansilla, S., Hamilton, M.J., Costa, D.P., Ceballos, G., Brown, J.H., 2012. Drivers and hotspots of extinction risk in marine mammals. Proc. Natl. Acad. Sci. USA 109, 3395–3400. https://doi.org/10.1073/pnas.1121469109.

de Oliveira, G., Rangel, T.F., Lima-Ribeiro, M.S., Terribile, L.C., Diniz-Filho, J.A.F., 2014. Evaluating, partitioning, and mapping the spatial autocorrelation component in ecological niche modeling: a new approach based on environmentally equidistant records. Ecography 37, 637–647. https://doi.org/10.1111/j.1600-0587.2013.00564.x.

Doudoroff, P., 1938. Reactions of marine fishes to temperature gradients. Biol. Bull. 75, 494–509. https://doi.org/10.2307/1537576.

Eble, J.A., Daly-Engel, T.S., DiBattista, J.D., Koziol, A., Gaither, M.R., 2020. Chapter two - marine environmental DNA: approaches, applications, and opportunities. In: Sheppard, C. (Ed.), Advances in Marine Biology. Academic Press, pp. 141–169. https://doi.org/10.1016/bs.amb.2020.01.001.

Elith, J., Graham, H., C. P. Anderson, M., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., Lohmann, G., Loiselle, L.A., B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC, M., Overton, J., Townsend Peterson, A., J. Phillips, S., Richardson, K., Scachetti-Pereira, R., E. Schapire, R., Soberón, J., Williams, S., Wisz, S., M., E. Zimmermann, N., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x.

Elliott, S.A.M., Deleys, N., Rivot, E., Acou, A., Réveillac, E., Beaulaton, L., 2021. Shedding light on the river and sea lamprey in western European marine waters. Endanger. Species Res. 44, 409419 https://doi.org/10.3354/esr01113.

Fernández-Pasquier, V., 1999. *Acipenser sturio* L. in the Guadalquivir river, Spain. Water regulation and fishery as factors in stock decline from 1932 to 1967. J. Appl. Ichthyol. 15, 133–135. https://doi.org/10.1111/j.1439-0426.1999.tb00222.x.

Folk, R.L., 1954. The distinction between grain size and mineral composition in sedimentary-rock nomenclature. J. Geol. 62, 344–359. https://doi.org/10.1086/626171.

Frans, V.F., Augé, A.A., Edelhoff, H., Erasmi, S., Balkenhol, N., Engler, J.O., 2018. Quantifying apart what belongs together: a multi-state species distribution modelling framework for species using distinct habitats. Methods Ecol. Evol. 9, 98–108. https://doi.org/10.1111/2041-210X.12847.

Gessner, J., Tautenhahn, M., Von Nordheim, H., Borchers, T., 2010a. Plan national d'actions pour la protection et la conservation de l'Esturgeon européen (*Acipenser sturio*), Gesellschaft zur Rettung des Störes Acipenser sturio L, p. 86. Rostock. https://belinra.inrae.fr/index.php?lvl=notice_display&id=242164.

Gessner, J., Williot, P., Rochard, E., Freyhof, J., Kottelat, M., 2010b. *Acipenser sturio*: the IUCN Red List of Threatened Species 2010: e.T230A13040963. https://doi.org/10.2305/IUCN.UK.2010-1.RLTS.T230A13040963.en.

Giareta, E.P., Prado, A.C., Leite, R.D., Padilha, É., Santos, I.H. dos, Wosiak, C.D.C.D.L., Wosnick, N., 2021. Fishermen's participation in research and conservation of coastal elasmobranchs. Ocean Coast Manag. 199, 105421 https://doi.org/10.1016/j.ocecoaman.2020.105421.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H. P., Buckley, Y.M., 2013. Predicting species distributions for conservation decisions. Ecol. Lett. 16, 1424–1435. https://doi.org/10.1111/ele.12189.

Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. Habitat Suitability and Distribution Models: with Applications in R. Cambridge University Press, Cambridge. https://doi.org/10.1017/9781139028271.

Häkkinen, H., Petrovan, S.O., Sutherland, W.J., Pettorelli, N., 2021. Terrestrial or marine species distribution model: why not both? A case study with seabirds. Ecol. Evol. 11, 16634–16646. https://doi.org/10.1002/ece3.8272.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. Science 319, 948–952. https://doi.org/10.1126/science.1149345.

Hardisty, J., 1990. The British Seas: an Introduction to the Oceanography and Resources of the North-west European Continental Shelf. Routledge, London, p. 272p. http://geoprodig.cnrs.fr/items/show/82500.

Hijmans, R.J., 2012. Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. Ecology 93, 679–688. https://doi.org/10.1890/11-0826.1.

Hijmans, R.J., 2019. Introduction to the "Geosphere" Package, Version 1.5-10. https://cran.r-project.org/web/packages/geosphere/vignettes/geosphere.pdf.

Hijmans, R.J., 2020. Geographic Data Analysis and Modeling. R Package Raster Version 3, pp. 4–5. https://cran.r-project.org/web/packages/raster/index.html.

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C., Guisan, A., 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecol. Model. 199, 142–152. https://doi.org/10.1016/j.ecolmodel.2006.05.017.

Hooker, S., Cañadas, A., Hyrenbach, K., Corrigan, C., Polovina, J., Reeves, R., 2011. Making protected area networks effective for marine top predators. Endanger. Species Res. 13, 203–218. https://doi.org/10.3354/esr00322.

Huff, D.D., Lindley, S.T., Rankin, P.S., Mora, E.A., 2011. Green sturgeon physical habitat use in the coastal Pacific ocean. PLoS One 6, e25156. https://doi.org/10.1371/journal.pone.0025156.

Huff, D.D., Lindley, S.T., Wells, B.K., Chai, F., 2012. Green sturgeon distribution in the Pacific ocean estimated from modeled oceanographic features and migration behavior. PLoS One 7, e45852. https://doi.org/10.1371/journal.pone.0045852.

Hunter, E., Metcalfe, J.D., Reynolds, J.D., 2003. Migration route and spawning area fidelity by North Sea plaice. Proc. R. Soc. Lond. Ser. B Biol. Sci. 270, 2097–2103. https://doi.org/10.1098/rspb.2003.2473.

Inman, R., Franklin, J., Esque, T., Nussear, K., 2021. Comparing sample bias correction methods for species distribution modeling using virtual species. Ecosphere 12, e03422. https://doi.org/10.1002/ecs2.3422.

Jennings, M.D., 2000. Gap analysis: concepts, methods, and recent results. Landsc. Ecol. 15, 5–20. https://doi.org/10.1023/A:1008184408300.

Jiménez-Valverde, A., Lobo, J.M., 2006. The ghost of unbalanced species distribution data in geographical model predictions. Divers. Distrib. 12, 521–524. https://doi.org/10.1111/j.1366-9516.2006.00267.x.

Jonsson, B., Jonsson, N., 2006. Life-history effects of migratory costs in anadromous brown trout. J. Fish. Biol. 69, 860–869. https://doi.org/10.1111/j.1095-8649.2006.01160.x.

Kaikkonen, L., Venesjärvi, R., Nygård, H., Kuikka, S., 2018. Assessing the impacts of seabed mineral extraction in the deep sea and coastal marine environments: current methods and recommendations for environmental risk assessment. Mar. Pollut. Bull. 135, 1183–1197. https://doi.org/10.1016/j.marpolbul.2018.08.055.

Karakassis, I., Eleftheriou, A., 1997. The continental shelf of Crete: structure of macrobenthic communities. Mar. Ecol. Prog. Ser. 160, 185–196. https://doi.org/10.3354/meps160185.

Kearney, M., 2006. Habitat, environment and niche: what are we modelling? Oikos 115, 186–191. https://doi.org/10.1111/j.2006.0030-1299.14908.x.

Kelly, J.T., Klimley, A.P., 2012. Relating the swimming movements of green sturgeon to the movement of water currents. Environ. Biol. Fish. 93, 151–167. https://doi.org/10.1007/s10641-011-9898-8.

Koutsikopoulos, C., Le Cann, B., 1996. Physical processes and hydrological structures related to the Bay of Biscay anchovy. Sci. Mar. 60, 9–19. In: https://www.semanticscholar.org/paper/Physical-processes-and-hydrological-structures-to-Koutsikopoulos-Cann/335803dfe67ff259954433a7cad9d8c688800d09.

Lassalle, G., Béguer, M., Rochard, E., 2011. Chapter 6 an overview on geographical distribution from Past descriptions. In: Williot, P., Rochard, E., Desse-Berset, N., Kirschbaum, F., Gessner, J. (Eds.), Biology and Conservation of the Atlantic European Sturgeon *Acipenser sturio* L., 1758. Springer, Berlin Heidelberg, pp. 81–90. https://doi.org/10.1007/978-3-642-20611-5_6.

Letaconnoux, R., 1961. Note sur la fréquence de la distribution des captures d'esturgeons (*Acipenser sturio* L.) dans le Golfe de Gascogne. Rev. Trav. Inst. Peches Marit. 25, 253–261. Open Access version : https://archimer.ifremer.fr/doc/00000/4255/.

Levin, A.V., 1982. Substrate selection, daily rhythm of vertical distribution and swimming speed of juvenile Russian sturgeon, *Acipenser gueldenstaedti*. J. Ichthyol. 22, 130–136. https://scholarworks.umass.edu/fishpassage_journal_articles/742/.

Lobo, J.M., Jiménez-Valverde, A., Real, R., 2008. AUC: a misleading measure of the performance of predictive distribution models. Global Ecol. Biogeogr. 17, 145–151. https://doi.org/10.1111/j.1466-8238.2007.00358.x.

Lohmann, K.J., Putman, N.F., Lohmann, C.M.F., 2008. Geomagnetic imprinting: a unifying hypothesis of long-distance natal homing in salmon and sea turtles. Proc. Natl. Acad. Sci. U. S. A 105, 19096–19101. https://doi.org/10.1073/pnas.0801859105.

Lorance, P., Bertrand, J.A., Brind'Amour, A., Rochet, M.-J., Trenkel, V.M., 2009. Assessment of impacts from human activities on ecosystem components in the Bay of Biscay in the early 1990s. Aquat. Living Resour. 22, 409–431. https://doi.org/10.1051/alr/2009049.

Martins, R., Sampaio, L., Rodrigues, A.M., Quintino, V., 2013. Soft-bottom Portuguese continental shelf polychaetes: diversity and distribution. J. Mar. Syst. 123–124, 41–54. https://doi.org/10.1016/j.jmarsys.2013.04.008.

Mateo, R.G., Croat, T.B., Felicísimo, Á.M., Muñoz, J., 2010. Profile or group discriminative techniques? Generating reliable species distribution models using pseudo-absences and target-group absences from natural history collections. Divers. Distrib. 16, 84–94. https://doi.org/10.1111/j.1472-4642.2009.00617.x.

McBreen, F., Wilson, J.G., Mackie, A.S.Y., Aonghusa, C.N., 2008. Seabed mapping in the southern Irish Sea: predicting benthic biological communities based on sediment characteristics. In: Davenport, J., Burnell, G.M., Cross, T., Emmerson, M., McAllen, R., Ramsay, R., Rogan, E. (Eds.), Challenges to Marine Ecosystems. Springer Netherlands, Dordrecht, pp. 93–103. https://doi.org/10.1007/978-1-4020-8808-7_9.

McDowall, R.M., 1997. The evolution of diadromy in fishes (revisited) and its place in phylogenetic analysis. Rev. Fish Biol. Fish. 443–462. https://doi.org/10.1023/A:1018404331601.

McKinley, D.C., Miller-Rushing, A.J., Ballard, H.L., Bonney, R., Brown, H., Cook-Patton, S.C., Evans, D.M., French, R.A., Parrish, J.K., Phillips, T.B., Ryan, S.F., Shanley, L.A., Shirk, J.L., Stepenuck, K.F., Weltzin, J.F., Wiggins, A., Boyle, O.D., Briggs, R.D., Chapin, S.F., Hewitt, D.A., Preuss, P.W., Soukup, M.A., 2017. Citizen science can improve conservation science, natural resource management, and environmental protection. Biol. Conserv. 208, 15–28. https://doi.org/10.1016/j.biocon.2016.05.015.

McShea, W.J., 2014. What are the roles of species distribution models in conservation planning? Environ. Conserv. 41, 93–96. https://doi.org/10.1017/S0376892913000581.

Melo-Merino, S.M., Reyes-Bonilla, H., Lira-Noriega, A., 2020. Ecological niche models and species distribution models in marine environments: a literature review and spatial analysis of evidence. Ecol. Model. 415, 108837 https://doi.org/10.1016/j.ecolmodel.2019.108837.

Ministère de l'écologie du développement durable des transports et du logement, 2011. Plan national d'actions en faveur de l'esturgeon européen *Acipenser sturio* 2011-2015, p. 69.

Ministère de la Transition Ecologique et Solidaire, 2020. Plan national d'actions en faveur de l'esturgeon européen *Acipenser sturio* 2020-2029, p. 89. https://www.nouvelle-aquitaine.developpement-durable.gouv.fr/IMG/pdf/pna-esturgeon-2020-2029-complet-high-quality-v101120.pdf.

Murphy, H.M., Jenkins, G.P., 2010. Observational methods used in marine spatial monitoring of fishes and associated habitats: a review. Mar. Freshw. Res. 61, 236. https://doi.org/10.1071/MF09068.

Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P., 2014. ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods Ecol. Evol. 5, 1198–1205. https://doi.org/10.1111/2041-210X.12261.

Noviello, N., McGonigle, C., Jacoby, D.M.P., Meyers, E.K.M., Jiménez-Alvarado, D., Barker, J., 2021. Modelling Critically Endangered marine species: bias-corrected citizen science data inform habitat suitability for the angelshark (*Squatina squatina*). Aquat. Conserv. 31, 3451–3465. https://doi.org/10.1002/aqc.3711.

Pennino, M.G., Conesa, D., López-Quílez, A., Muñoz, F., Fernández, A., Bellido, J.M., 2016. Fishery-dependent and -independent data lead to consistent estimations of essential habitats. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 73, 2302–2310. https://doi.org/10.1093/icesjms/fsw062.

Pennino, M.G., Paradinas, I., Illian, J.B., Muñoz, F., Bellido, J.M., López-Quílez, A., Conesa, D., 2019. Accounting for preferential sampling in species distribution models. Ecol. Evol. 9, 653–663. https://doi.org/10.1002/ece3.4789.

Peter, M., Diekötter, T., Kremer, K., 2019. Participant outcomes of biodiversity citizen science projects: a systematic literature review. Sustainability 11, 2780. https://doi.org/10.3390/su11102780.

Peterson, A., Soberón, J., 2012. Species distribution modeling and ecological niche modeling: getting the concepts right. Natureza & Conservação 10, 102–107. https://doi.org/10.4322/NATCON.2012.019.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol. Appl. 19, 181–197. https://doi.org/10.1890/07-2153.1.

Pichon, A., Lavarde, P., Avezard, C., Legait, B., Wallard, I., 2017. Impact environnemental et économique des activités d'exploration ou d'exploitation des ressources minérales marines, p. 70. https://igedd.documentation.developpement-durable.gouv.fr/notice?id=Affaires-0010311.

Pörtner, H.O., 2002. Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. Comp. Biochem. Physiol. Mol. Integr. Physiol. 132, 739–761. https://doi.org/10.1016/s1095-6433(02)00045-4.

Pottier, J., Dubuis, A., Pellissier, L., Maiorano, L., Rossier, L., Randin, C.F., Vittoz, P., Guisan, A., 2013. The accuracy of plant assemblage prediction from species distribution models varies along environmental gradients. Global Ecol. Biogeogr. 22, 52–63. https://doi.org/10.1111/j.1466-8238.2012.00790.x.

Rochard, E., Castelnaud, G., Lepage, M., 1990. Sturgeons (Pisces: Acipenseridae); threats and prospects. J. Fish. Biol. 37, 123–132. https://doi.org/10.1111/j.1095-8649.1990.tb05028.x.

Rochard, E., Lepage, M., Meauzé, L., 1997. Identification et caractérisation de l'aire de répartition marine de l'esturgeon européen *Acipenser sturio* à partir de déclarations de captures. Aquat. Living Resour. 10, 101–109. https://doi.org/10.1051/alr:1997011.

Rochette, S., Rivot, E., Morin, J., Mackinson, S., Riou, P., Le Pape, O., 2010. Effect of nursery habitat degradation on flatfish population: application to *Solea solea* in the Eastern channel (western Europe). J. Sea Res. 64, 34–44. https://doi.org/10.1016/j.seares.2009.08.003.

Rönnbäck, P., Kautsky, N., Pihl, L., Troell, M., Söderqvist, T., Wennhage, H., 2007. Ecosystem goods and services from Swedish coastal habitats: identification, valuation, and implications of ecosystem shifts. Ambio 36, 534–544. https://doi.org/10.1579/0044-7447(2007)36[534:EGASFS]2.0.CO;2.

Roques, S., Berrebi, P., Rochard, E., Acolas, M.L., 2018. Genetic monitoring for the successful re-stocking of a critically endangered diadromous fish with low diversity. Biol. Conserv. 221, 91–102. https://doi.org/10.1016/J.BIOCON.2018.02.032.

Rosenthal, H., Bronzi, P., Moreau, D., Rochard, E., Lasen, C., 2007. Draft Action Plan for the Conservation and Restoration of the European Sturgeon (*Acipenser sturio*), p. 47. Council of Europe, Convention on the conservation of European wildlife and natural habitats, Strasbourg. https://rm.coe.int/090000168074689b.

RTE, 2018. Interconnexion électrique France-Espagne par le golfe de Gascogne. Dossier de concertation. détermination du fuseau de moindre impact, p. 136. https://www.inelfe.eu/sites/default/files/2020-09/Dossier%20de%20concertation%20Fuseau%20de%20Moindre%20Impact_0.pdf.

Sánchez-Fernández, D., Lobo, J.M., Hernández-Manrique, O.L., 2011. Species distribution models that do not incorporate global data misrepresent potential distributions: a case study using Iberian diving beetles: regional data misrepresent potential distributions. Divers. Distrib. 17, 163–171. https://doi.org/10.1111/j.1472-4642.2010.00716.x.

Schoener, T.W., 1968. The Anolis Lizards of Bimini: resource partitioning in a complex Fauna. Ecology 49, 704–726. https://doi.org/10.2307/1935534.

Shelton, A.O., Sullaway, G.H., Ward, E.J., Feist, B.E., Somers, K.A., Tuttle, V.J., Watson, J.T., Satterthwaite, W.H., 2021. Redistribution of salmon populations in the northeast Pacific ocean in response to climate. Fish Fish. 22, 503–517. https://doi.org/10.1111/faf.12530.

Sillero, N., Arenas-Castro, S., Enriquez-Urzelai, U., Vale, C.G., Sousa-Guedes, D., Martínez-Freiría, F., Real, R., Barbosa, A.M., 2021. Want to model a species niche? A step-by-step guideline on correlative ecological niche modelling. Ecol. Model. 456, 109671 https://doi.org/10.1016/j.ecolmodel.2021.109671.

Speed, C.W., Field, I.C., Meekan, M.G., Bradshaw, C.J.A., 2010. Complexities of coastal shark movements and their implications for management. Mar. Ecol. Prog. Ser. 408, 275–293. https://doi.org/10.3354/meps08581.

Steen, V.A., Tingley, M.W., Paton, P.W.C., Elphick, C.S., 2021. Spatial thinning and class balancing: key choices lead to variation in the performance of species distribution models with citizen science data. Methods Ecol. Evol. 12, 216–226. https://doi.org/10.1111/2041-210X.13525.

Stein, A.B., Friedland, K.D., Sutherland, M., 2004. Atlantic sturgeon marine distribution and habitat use along the northeastern coast of the United States. Trans. Am. Fish. Soc. 133, 527–537. https://doi.org/10.1577/T02-151.1.

Taormina, B., Bald, J., Want, A., Thouzeau, G., Lejart, M., Desroy, N., Carlier, A., 2018. A review of potential impacts of submarine power cables on the marine environment: knowledge gaps, recommendations and future directions. Renew. Sustain. Energy Rev. 96, 380–391. https://doi.org/10.1016/j.rser.2018.07.026.

Taverny, C., Lepage, M., Piefort, S., Dumont, P., Rochard, E., 2002. Habitat selection by juvenile European sturgeon *Acipenser sturio* in the Gironde estuary (France). J. Appl. Ichthyol. 18, 536–541. https://doi.org/10.1046/j.1439-0426.2002.00414.x.

Thuiller, W., Lafourcade, B., Engler, R., Araújo, M.B., 2009. BIOMOD – a platform for ensemble forecasting of species distributions. Ecography 32, 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x.

Trancart, T., Rochette, S., Acou, A., Lasne, E., Feunteun, E., 2014. Modeling marine shad distribution using data from French bycatch fishery surveys. Mar. Ecol. Prog. Ser. 511, 181–192. https://doi.org/10.3354/meps10907.

Trimoreau, E., Archambault, B., Brind'Amour, A., Lepage, M., Guitton, J., Le Pape, O., 2013. A quantitative estimate of the function of soft-bottom sheltered coastal areas as essential flatfish nursery habitat. Estuarine. Coastal and Shelf Science 133, 193–205. https://doi.org/10.1016/j.ecss.2013.08.027.

Valavi, R., Elith, J., Lahoz-Monfort, J.J., Guillera-Arroita, G., 2019. blockCV: an r package for generating spatially or environmentally separated folds for k-fold cross-validation of species distribution models. Methods Ecol. Evol. 10, 225–232. https://doi.org/10.1111/2041-210X.13107.

van Puijenbroek, P.J.T.M., Buijse, A.D., Kraak, M.H.S., Verdonschot, P.F.M., 2019. Species and river specific effects of river fragmentation on European anadromous fish species. River Res. Appl. 35, 68–77. https://doi.org/10.1002/rra.3386.

Varela, S., Anderson, R.P., García-Valdés, R., Fernández-González, F., 2014. Environmental filters reduce the effects of sampling bias and improve predictions of ecological niche models. Ecography 37, 1084–1091. https://doi.org/10.1111/j.1600-0587.2013.00441.x.

Vasquez, M., Allen, H., Manca, E., Castle, L., Lillis, H., Agnesi, S., Al Hamdani, Z., Annunziatellis, A., Askew, N., Bekkby, T., Bentes, L., Doncheva, V., Drakopoulou, V., Duncan, G., Gonçalves, J., Inghilesi, R., Laamanen, L., Loukaidi, V., Martin, S., McGrath, F., Mo, G., Monteiro, P., Muresan, M., Nikilova, C., O'Keeffe, E., Pesch, R., Pinder, J., Populus, J., Ridgeway, A., Sakellariou, D., Teaca, A., Tempera, F., Todorova, V., Tunesi, L., Virtanen, E., 2021. EU-SeaMap 2021. A European Broad-Scale Seabed Habitat Map. https://doi.org/10.13155/83528.

Williot, P., Castelnaud, G., 2011. Chapter 20 Historic overview of the European sturgeon *Acipenser sturio* in France: surveys, regulations, reasons for the decline, conservation, and analysis. In: Williot, P., Rochard, E., Desse-Berset, N., Kirschbaum, F., Gessner, J. (Eds.), Biology and Conservation of the Atlantic European Sturgeon *Acipenser sturio* L., 1758. Springer, Berlin Heidelberg, pp. 285–308. https://link.springer.com/chapter/10.1007/978-3-642-20611-5_20.

Williot, P., Rochard, E., Desse-Berset, J., Gessner, J., Kirschbaum, F., 2011a. Chapter 1 Brief introduction to sturgeon with a special focus on the European sturgeon, *Acipenser sturio* L. 1758. In: Williot, P., Rochard, E., Desse-Berset, N., Kirschbaum, F., Gessner, J. (Eds.), Biology and Conservation of the Atlantic European Sturgeon

Acipenser sturio L., 1758. Springer, Berlin Heidelberg, pp. 3–11. https://link.springer.com/chapter/10.1007/978-3-642-20611-5_1.

Williot, P., Rouault, T., Brun, R., Pelard, M., Mercier, D., Jacobs, L., Kirschbaum, F., 2011b. Chapter 31 building a brood stock of *Acipenser sturio* in France. In: Williot, P., Rochard, E., Desse-Berset, N., Kirschbaum, F., Gessner, J. (Eds.), Biology and

Conservation of the Atlantic European Sturgeon *Acipenser sturio* L., 1758. Springer, Berlin Heidelberg, pp. 425–438. https://doi.org/10.1007/978-3-642-20611-5_31.

Wisz, M.S., Broennimann, O., Grønkjær, P., Møller, P.R., Olsen, S.M., Swingedouw, D., Hedeholm, R.B., Nielsen, E.E., Guisan, A., Pellissier, L., 2015. Arctic warming will promote Atlantic–Pacific fish interchange. Nat. Clim. Change 5, 261–265. https://doi.org/10.1038/nclimate2500.