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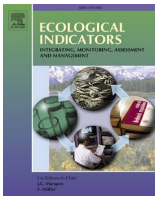

Travelling away from home? Joining global change and recovery scenarios to anticipate the marine distribution of diadromous fish

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ABSTRACT

Species Distribution Models (SDM) are useful tools providing results that can be extrapolated to anticipate species range shifts, under climate change scenarios. SDM studies integrating spatial constraints are significantly lacking in the marine environment, leading to optimistic predictions. This is particularly true for anadromous species in which marine distributions can be driven by their affinity to their natal rivers. *Acipenser sturio* is a critically endangered anadromous fish for which two stocked populations are currently maintained in the Gironde-Garonne-Dordogne (France) and Elbe (Germany) river systems. Benefiting from bycatch reports of *A. sturio*, we applied a SDM process that explicitly considers distance to home when evaluating habitat suitability. More precisely, we included the variable 'distance to mouth of the natal river system' into SDM inputs to test and characterize its influence on the marine distribution of *A. sturio*. We used this model to obtain the marine distribution under current climatic conditions with the two source populations and under population recovery scenarios (functional populations hypothesized to exist in ten currently unoccupied river systems). We projected the model under future conditions with two climatic scenarios (RCP 4.5 and 8.5) and three time slices over the 2023–2099 period. Constrained-ranges of both existing and hypothetical populations are projected to expand in the future. We observed an overall increase of habitat suitability, with new suitable sectors localized further from natal river mouths. By informing on the suitable marine surface that each hypothetical population holds and adds to the existing ones, our approach aims at informing about the feasibility of species recovery and marine habitats protection strategies. Our findings highlight the need for including dispersal information in marine SDM. The application of our dispersal-constrained approach may be considered for other less-well-known species for which dispersal point sources are identifiable, such as other diadromous species in different study areas.

1. Introduction

Many species are shifting their ranges to adapt to environmental modifications and persist in suitable habitats, in response to global change (Maureaud et al., 2021). Understanding these spatial displacements, expansions or contractions is crucial to allow successful conservation of biodiversity, particularly of endangered species (Kerr, 2020). Species Distribution Models (SDM) are useful tools that predict suitability of habitats for species, for research and management purposes (McShea, 2014). They can help to define suitable areas for population reinforcement, stocking, natural or assisted recolonization (McShea, 2014; Seddon et al., 2014) in restoration contexts. They can also be used with future climatic scenarios to anticipate species range shifts under new environmental conditions (Yates et al., 2010).

Species rarely occupy all environmentally suitable areas due to historical or geographical factors that prevent their accessibility (e.g. remote locations, geographical barriers; Barve et al., 2011). Species dispersion ability is one of the most important factors influencing their distributions (Kokko and López-Sepulcre, 2006; Di Musciano et al., 2020), their opportunities to colonize new areas and, thus, to establish

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viable populations (Baur, 2014). Despite its relevance, species dispersal movements and their drivers are ignored in many SDM studies (Allouche et al., 2008). Colonization capacity of species is then implicitly considered as unlimited inside the studied area, which can lead to overpredictions and unrealistic estimation of species range shifts (Della Rocca and Milanesi, 2020; Mendes et al., 2020; Velazco et al., 2020).

Several approaches have nevertheless emerged during the last decades to include spatial constraints when modelling species distributions. Some methods use the same presence records required to build SDM, whereas others rely on additional information on species distribution (e.g. dispersal history, geographical barriers) or even on species biology (e.g. dispersal ability, life cycle, population growth, species interactions; Allouche et al., 2008; Barve et al., 2011). Moreover, three main groups of strategies exist to include dispersal in SDM: (i) delimiting reachable areas inside the suitable habitats by overlapping accessibility and distribution maps after the SDM process (e.g. exclusion of suitable areas outside a convex polygon enclosing all presence records; Kremen et al., 2008; Mendes et al., 2020); (ii) inserting explicitly spatial explanatory variables during the SDM calibration (e.g. geographical coordinates, variable calculated from density of presence records or distance between them; Mendes et al., 2020); and (iii) generating dynamic movement models (Barber-O'Malley et al., 2022) to simulate dispersal through evolutionary time, resulting in accessibility maps that can be overlapped with suitability maps (Barve et al., 2011; Holloway et al., 2016). These existing methods differ according to their complexity, the amount of information needed to be conducted and their stage of application during analyses (Mendes et al., 2020; Velazco et al., 2020).

SDM studies integrating spatial constraints are even more scarce in the marine environment. Yet, species movement restrictions also occur (Bradbury et al., 2008; Waters et al., 2020) even if oceans are more dynamic than terrestrial ecosystems (Fernandez et al., 2017). For example, anadromous fish migrate over long distances in marine systems (i.e. migratory behavior; McDowall, 1992; Pess et al., 2014). They have however strong tendency to return to their natal rivers to spawn, which is called the homing behavior (Cury, 1994). The degree of natal homing varies according to species. It is, for example, very strong in salmonids (Keefer and Caudill, 2014) and suspected to be very low in lamprey species (Bergstedt and Seelye, 1995). These behaviors can lead to more restricted ranges compared to holobiotic marine fish and limited options to respond to changing environments (Limburg and Waldman, 2009). Moreover, the migration strategy of anadromous fish is associated with significant energetic costs (i.e. extensive movements) and mortality risks (e.g. travelling through areas with high predator densities, higher risks of incidental captures and ship collisions; Lucas et al., 1994; Bonte et al., 2012) that increase with the traveled distance. At the same time, these behaviors open additional feed resources and may reduce intraspecific competition (McDowall, 2001).

As species with complex life cycles, diadromous fish can be more vulnerable than exclusively marine or freshwater fish (McDowall, 1992), as they experience stressors and threats from multiple environments (e.g. hydrology alteration, pollution, habitat degradation, invasive species, loss of connectivity along the watershed-ocean continuum, overfishing; Verhelst et al., 2021; Waldman and Quinn, 2022). The combined effects of these pressures have resulted in a decline by at least 90 % in abundance of diadromous species native to the northern Atlantic Ocean, since the end of the 19th century (Limburg and Waldman, 2009; Drouineau et al., 2018). The management and the conservation of diadromous species suffer from a lack of knowledge about their marine life (but see Barber-O'Malley et al., 2022; Elliott et al., 2023a), while many of them are now threatened and protected (Limburg and Waldman, 2009). One reason is that collecting spatial data to evaluate species ranges is especially challenging and costly in marine systems and relies on oceanic surveys not targeting diadromous species, but other stocks. Important mismatches occur such as lack of data availability, disparate biological observations and gap between data collected and true species distributions (Maureaud et al., 2021). Many oceanic species are consequently data-limited (Aylesworth et al., 2017), hindering effective conservation measures.

The most common strategies of dispersal-constrained SDM have the advantage to be simple to apply and use the same data needed to build a SDM (i.e. presence records), even if those data are of low quality. But, these methods do not provide much information about the biological mechanisms underlying species dispersal patterns. In the present study, we proposed a novel and straightforward method adapted for homing species, for which natal sites are known. We also showed how SDM outputs can be used for conservation targets by providing perspectives to anticipate recovery strategies (natural or human-assisted). We focused on the critically endangered and anadromous European sturgeon *Acipenser sturio* (Gessner et al., 2022), which is a perfect case study to apply this approach as: (i) this is a long-lived fish displaying homing behavior; (ii) more than 90 % of its life-span takes place at sea (Williot et al., 2011a); (iii) we have a good knowledge of the natal river system of fish caught at sea; and (iv) this species has a high public attention, which allow to gather citizen observations.

The species was very close to global extinction, remaining in only one river system (i.e. the Gironde-Garonne-Dordogne system, called Gironde system hereafter; Gessner et al., 2022). *A. sturio* is now maintained thanks to restoration programs in France and Germany (Gessner et al., 2010; MEDDTL, 2011; MTES, 2020). These programs rely on a captive stock in France (Williot and Chèvre, 2011) and on stocking events (Roques et al., 2018), since no natural reproduction was observed since 1994.

Benefiting from participatory data (i.e. incidental bycatch reports) of this rare species (Rochard et al., 1997; Charbonnel et al., 2023), the objectives of this study were to:

(i) analyze the spatial variable ‘distance to home’ that improves our SDM according to *A. sturio* biology and migratory behavior;
(ii) project *A. sturio* marine distribution for the current situation, but also under scenarios of global change (two scenarios and three time slices over the period from 2023 to 2099) and population recovery (ten currently unoccupied river systems considered as potential sources of individuals);
(iii) provide a better understanding of *A. sturio* potential marine habitats, through the calculation of different metrics from SDM outputs, to inform thinking concerning the possible restoration of the species in Western Europe.

2. Materials and methods

The modelling framework employed to project *A. sturio* distribution for the current situation and under global change and recovery scenarios, as well as the different metrics calculated from SDM outputs, are illustrated in Fig. 1. Every step is detailed below, but to summarize Fig. 1, SDM were calibrated with presence and randomly sampled pseudo-absence cells (see Sections 2.2 and 2.5). Eleven variables, including ten environmental and one dispersal variables (i.e. distance to home or to mouth of the natal river systems of fish), were included at the beginning of the SDM process to test their influence on *A. sturio* marine distribution (see Section 2.6). A top-down approach was applied to remove the less influential variables. An ensemble model was used to project the current and the future marine habitat suitability of the two existing populations (i.e. Elbe and Gironde), but also under population recovery scenarios in multiple river systems (see Sections 2.7 and 2.8). Continuous suitability maps from ensemble projections were employed to analyze habitat similarity between existing and hypothetical populations, according to the distance between mouths of their respective natal river systems. Ensemble projections were also binarized to: (i) compute the marine habitat suitability at the multi-population level; (ii) estimate distributional range overlap between existing and hypothetical populations; and (iii) compare the distance to mouth values in suitable

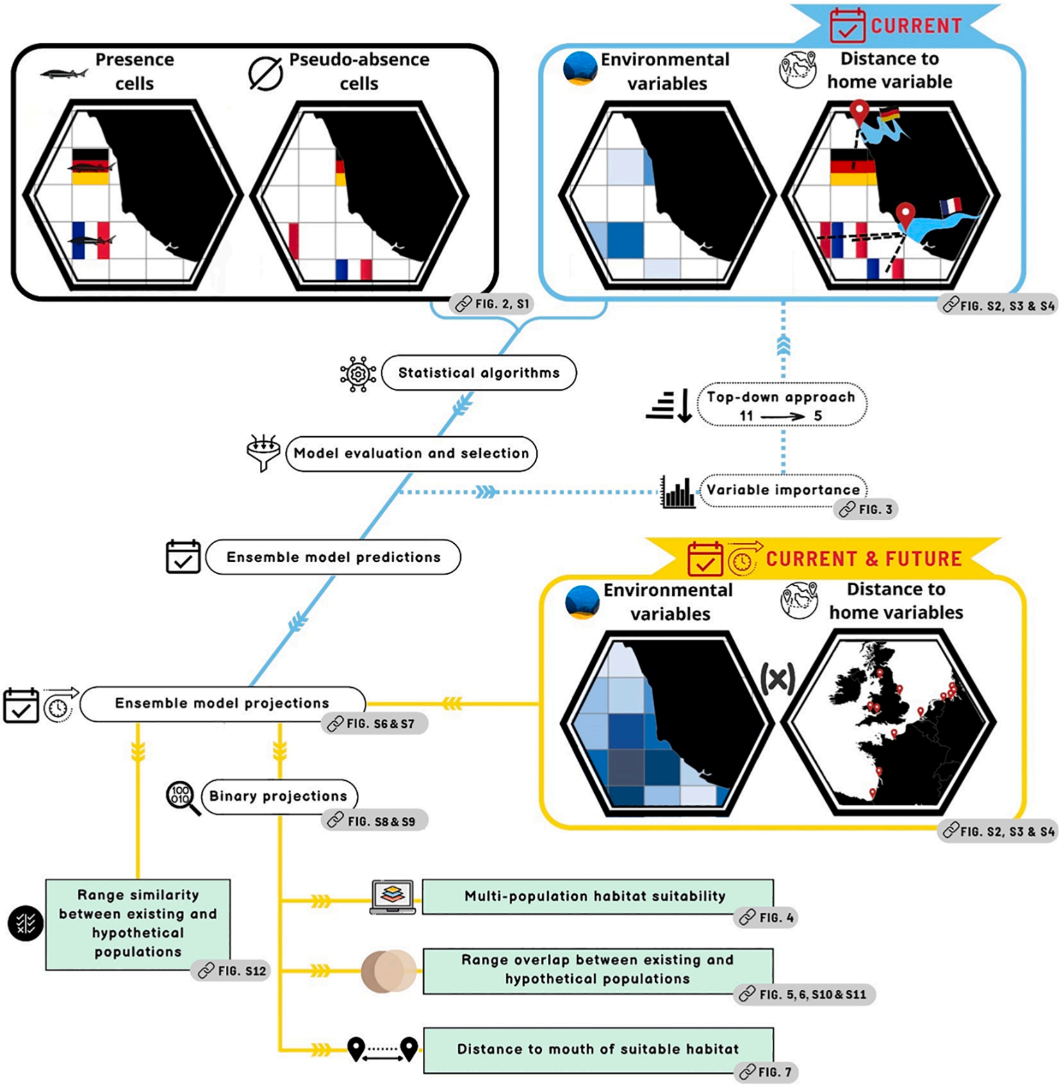

Fig. 1. Workflow process of the species distribution modelling (SDM) approach employed.

habitat for each population, under current conditions and global change scenarios (See Section 2.9).

2.1. Species and study area

The European sturgeon *A. sturio* is a large-bodied fish that accomplishes anadromous migrations through riverine, estuarine and marine habitats (Magnin, 1962; Rochard et al., 1990). Having almost a pan-European distribution a century ago (Lassalle et al., 2011), its marine distribution is today limited to the European coasts of the Atlantic Ocean (Rochard et al., 1997). *A. sturio* is listed as 'critically endangered' in the IUCN Red List (Gessner et al., 2022), listed in Annexes II and IV of the European Habitat Directive (43/92/EWG) since 1992, and protected with a fishing ban in France since 1982. Stocking events have taken place in France and Germany with 1.7 M fish released in the Gironde (2007–2015; France) and 20 000 fish in the Elbe (2008–2015; Germany) systems (Roques et al., 2018), thanks to the *ex-situ* brood stock established during the 1990′s (Williot et al., 2011b).

This study was conducted over the continental shelf of the north-eastern Atlantic Ocean, from the South of Norway to the North of Spain (Fig. 2a). We delimited this spatial area to encompass all known *A. sturio* occurrences since 1990 without extending beyond 150 m depth, as the species was never observed in deeper waters (Letaconnoux, 1961; Rochard et al., 1997). The study area was thus defined to be accessible to the species, based on its dispersal capacity.

2.2. Presence records

Presence records came from incidental bycatch reports, or sightings, by professional and recreational fishermen or citizens available in French, German, Dutch and UK databases (Brevé et al., 2024; McCormick et al., 2022; MEDDTL, 2011; Gessner, *pers. comm.*). Bycatch data were cleaned by removing records: (i) duplicated; (ii) with a doubt about the species identification; (iii) from stranded fish; (iv) from tagged fish originating from the Rhine system where experimental releases were carried out, with a low number of fish released (Brevé et al., 2019); (v) with too imprecise or no geographic coordinates; (vi) located in estuarine or riverine habitats; and (vii) occurring before the year 1990. A total of 530 geo-referenced records (79.2 %, 15.1 %, 5.3 % and 0.4 % from the French, German, Dutch and UK databases, respectively) were compiled for *A. sturio* after this data cleaning phase. Presence records were considered between the years 1990–2022 as this duration: (i) matched the temporal extent of the dynamic environmental variables; and (ii) seems long enough to reduce the risk of niche truncation (Peterson et al., 2018). The study area was then converted into 10 × 10 km grid cells, to deal with the uncertainty of bycatch locations and the spatial resolution of some environmental variables.

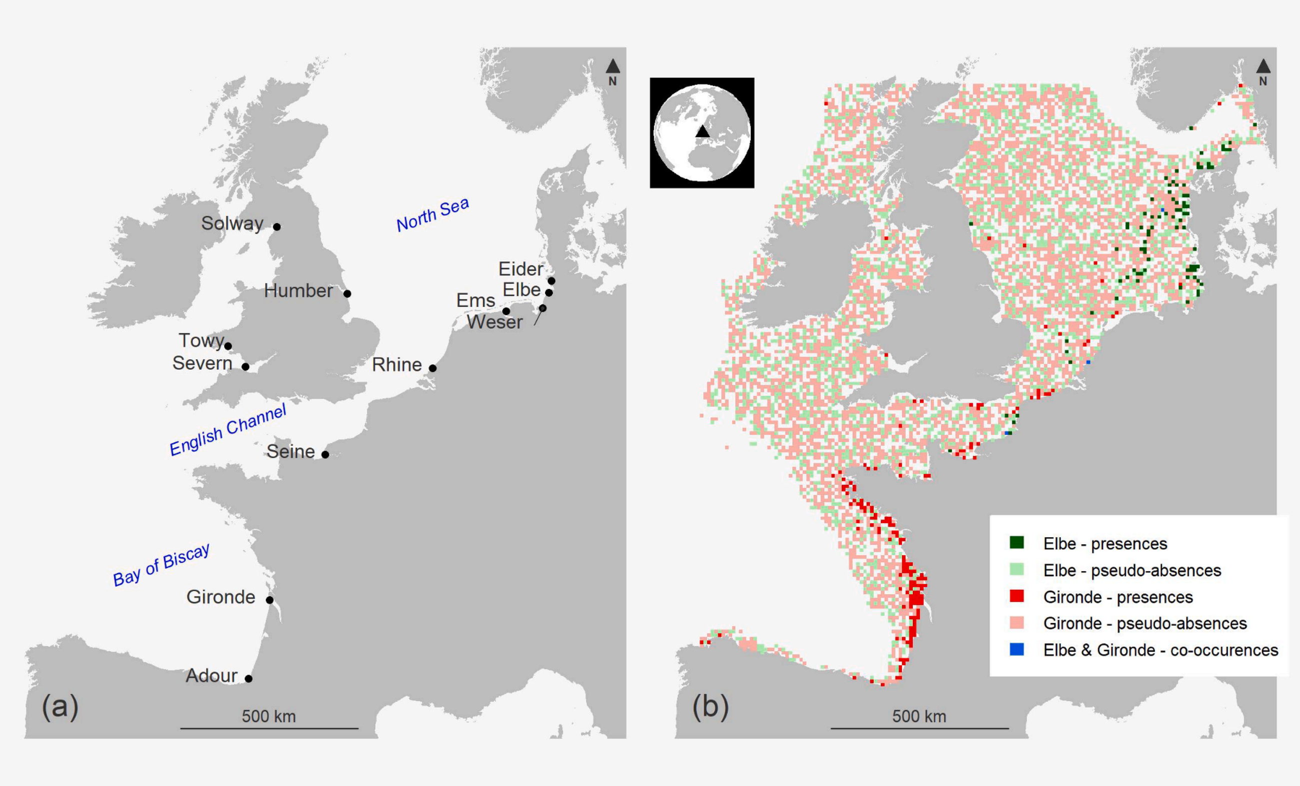

Fig. 2. Maps describing the study area and the species dataset. (a) Location of the main marine regions of the study area, the mouths of the two river systems with existing *A. sturio* stocked populations (i.e. Elbe and Gironde) and the ten other river systems chosen to simulate population recovery scenarios. (b) Location of the presence/pseudo-absence cells (10 × 10 km resolution) with indication of the natal river systems that have been assigned to them.

2.3. Assignment of a natal river system to presence cells

To build the variable ‘distance to home’ or, in other words, ‘distance to mouth of the natal river system’, all presence cells with at least one presence record have been assigned to a natal river system. Different strategies have been used to that end (Fig. S1 in Supplementary Information). First, presence cells with tagged fish have been attributed to their known natal river systems (i.e. Elbe or Gironde; n = 32 and 87, respectively). Secondly, presence cells with fish caught before 2010 have been assigned to the Gironde system as stocking events in the Elbe system started in 2008, and fish go to the sea after 2 years old (n = 18). Then, for fish with unknown origin, tagged fish from the Elbe and Gironde systems, sharing the same time period (i.e. 2010–2022; n = 38 and 38, respectively), have been used to build two kernel density maps (Caha, 2023) at sea, for Elbe and Gironde populations separately (Fig. S1 in Supplementary Information). Density values of both kernel maps have been used to define the two probability weights, in a sampling approach applied to assign remaining bycatch fish to Elbe or Gironde system (n = 66 and 99, respectively). A fish of unknown origin has a higher probability to be assigned to the system with the highest weight in the cell.

2.4. Reduction of the potential sample biases

To reduce the effects of biased sampling (Murphy and Jenkins, 2010), presence records were spatially thinned so that only one record of fish from a specific river system was retained per cell (Aiello-Lammens et al., 2015), resulting in 259 presence cells left for analyses. We did not apply other methods to reduce potential biases as: (i) our recent study (Charbonnel et al., 2023) conducted with a part of our dataset, in part of our studied area, showed that bias-corrected predictions were very similar with those of uncorrected models; (ii) it was not possible to reliably assess the sample biases of our dataset and its effects; and (iii) consequently, the loss of presence records can lead to the loss of crucial ecological information for the species (Sillero et al., 2021).

At the end of the process (i.e. assignment approaches and spatial thinning), 167 cells have been assigned to the Gironde system, 86 to the Elbe system and 3 cells have been assigned to both systems (i.e. co-occurrence cells; Fig. 2b).

2.5. Pseudo-absences selection and natal river assignment

Absence records were not available in our species databases. We thus randomly allocated 5500 cells, as pseudo-absence cells, throughout the study area to sufficiently ‘sample’ the available environment, called the ‘background space’ (Barbet-Massin et al., 2012; Fig. 2b). Consequently, our SDM predicts a habitat suitability index rather than a probability of presence (Guisan et al., 2017).

We assumed that the two populations have the same migratory capacities (i.e. the study area is similarly accessible to them), by randomly assigning a natal river system to pseudo-absences all over the study area. This random assignment respected the presence cells ratio between the two origins (170 for the Gironde *vs* 89 for the Elbe). Thus, over the 5500 pseudo-absences, 3610 cells have been randomly assigned to the Gironde system and 1890 to the Elbe system (Fig. 2b).

2.6. Environmental and dispersal variables

A set of 11 physico-chemical, hydrodynamic, substrate, topographic and dispersal variables were chosen as candidate predictors (Table S1 in Supplementary Information), following the same pre-selection procedure as Charbonnel et al. (2023). Physico-chemical and hydrodynamic variables were calculated from the POLCOM-ERSEM oceanic model (Kay, 2020) and averaged over the 1990–2022 period. The information of the deepest level was used to be consistent with the ecology of

Acipenseridae species (Bemis and Kynard, 1997). For substrate variables, we made four categories following the simplified Folk classification (Folk, 1954): (i) mud to muddy sands; (ii) sands; (iii) coarse-grained and mixed sediments; and (iv) rock and boulders. Then, we computed the shortest distance from each cell to the nearest patch boundary of each substrate category, creating four substrate variables. The distHOME variable (all abbreviations and definitions of variables are given in Table S1 in Supplementary Information) was calculated with the *gridDist* function of the *terra* package in R (Hijmans et al., 2022). For each presence and pseudo-absence cell used for the calibration process, the shortest distance to the mouth of its own natal river system (i.e. Elbe or Gironde) was calculated, excluding terrestrial areas and marine environments deeper than 150 m. The maps of the pre-selected variables are displayed in Supplementary Information (Figs S2–S4).

2.7. Species distribution models

We used an ensemble modelling approach with the *biomod2* package in R (Thuiller et al., 2009) to build the SDM and make projections. Seven algorithms have been used: 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; Araújo and New, 2007; Thuiller et al., 2009). Algorithms were fitted using the default settings of *biomod2*, except the smoothing degree term in GAM models which was set to $k = 4$. The prevalence was fixed to 0.5 to give an equal weight to presence and pseudo-absence cells in the modelling process (Jiménez-Valverde and Lobo, 2006). Models were evaluated using a cross-validation procedure based on repeated split-sampling (80 % for calibration, 20 % for evaluation) with 20 iterations. For each iteration, we assessed model performances using the Boyce index, the true skill statistic (TSS), the area under the ROC curve (AUC) and the Kappa index (Allouche et al., 2006; Hirzel et al., 2006; Lobo et al., 2008), which are complementary evaluation metrics (Fernandes et al., 2019). We excluded models for which the Boyce index was below 0.5, and the remaining models were averaged to build ensemble models. The relative importance of the variables was estimated using the *get_variables_importance* function of *biomod2*.

Reducing the number of variables is generally advisable when projecting distributions under future climatic conditions, to reduce the negative influence of non-analog conditions (Merow et al., 2014). Hence, a top-down approach was applied to remove the less influential variables from the model. To do so, the modelling approach described above was processed with the 11 pre-selected variables. Then, the variable with the lowest mean relative contribution was removed and the modelling process was rerun, and so on until the five most influential variables were left in the final ensemble SDM.

2.8. Model ensemble projections

The final ensemble SDM with the five left variables was projected using current (i.e. 1990–2022) environmental conditions for the two existing populations (i.e. Elbe and Gironde), but also under global change and population recovery scenarios.

Future physico-chemical and hydrodynamic variables were obtained until the horizon 2099, under the Representative Concentration Pathway (RCP) scenarios 4.5 (i.e. climate policies aimed at stabilizing CO_2 concentrations) and 8.5 (i.e. no climate policies), from the POLCOM-ERSEM oceanic model (Kay, 2020). Future variables were averaged for three 30-years overlapping time slices, starting on the years 2023, 2047 and 2070 (Table S1 in Supplementary Information). The maps of these future variables are displayed in Supplementary Information (Fig. S2). The duration of 30 years was chosen to identify an actual global change trend in spite of inter-annual fluctuations. Substrate and topographic variables were assumed to stay constant in the future (Fig. S3 in Supplementary Information).

To project *A. sturio* current and future marine distributions for the two existing stocked populations (i.e. Gironde, Elbe), but also for ten non-existing populations for which their recovery was simulated (called hereafter ‘hypothetical populations’), twelve river systems have been chosen (from South to North): Adour, Gironde, Seine, Rhine, Severn, Towy, Ems, Weser, Humber, Elbe, Eider and Solway (Fig. 2a). The selection of these river systems was based on their current or past spawning functionality for *A. sturio* and their environmental suitability with regard to climate change predictions, from Lassalle et al. (2010; Table S2 in Supplementary Information). In this previous modelling work, these river systems had habitat suitability (considering air temperature, precipitation, slope and drainage surface of the catchment area) that was predicted as medium to high for 2050 and 2100. We relied on the opinion of national experts to choose the river systems in the United Kingdom (McCormick et al., 2022; Colclough, *pers. comm.*). For each river system, a ‘distance to home’ variable was generated calculating the distance of each cell of the study area to the mouth of the river system (see Table S1 and Fig. S4 in Supplementary Information).

Overall, a total of 84 ensemble projections were fitted (1 current period × 12 river systems + 3 future periods × 2 RCP scenarios × 12 river systems) with a habitat suitability index ranging from 0 to 1000. Projections were also reclassified into binary presence-absence maps using the threshold that maximizes TSS scores (Guisan et al., 2017).

To assess SDM potential extrapolation, we evaluated the similarity between current and future environmental conditions. We generated Multivariate Environmental Similarity Surface (MESS) maps (Elith et al., 2010) for each future period, using the *MESS* function of the R package *modEvA* (Barbosa et al., 2013). MESS analyses allow the identification of localities with future novel environments compared to the current period, with respect to a set of environmental variables. The more dissimilar (i.e. non-analog) the localities are, the less reliable the projections are in these localities.

2.9. Metrics calculated from SDM outputs to compare and compile habitat suitability between populations

We should specify that when the distHOME variable is included in SDM, the habitat suitability index estimated by the model incorporates both the habitat suitability and the dispersal ability of *A. sturio*. For a same period, differences in habitat suitability between populations are only due to the distances to natal river mouth, which are specific to each population. Hence, if the habitat is projected suitable to the population A but unsuitable to the population B, it means that this habitat is suitable to all populations but inaccessible to the population B, according to the distance to its natal river. Moreover, for a same population, differences in habitat suitability between periods are only due to abiotic changes, as the distHOME variable remains constant over time.

Continuous suitability maps from ensemble projections were employed to analyze habitat similarity between hypothetical populations and each existing population, in view of the distance between their respective river mouths. The marine habitat similarity between populations was evaluated with the Schoener’s D statistic (Schoener, 1968) which ranges from 0 (no similarity) to 1 (identical projections). We also summed the binary projections of all populations for each time period, to have an overall view of the habitat suitability at the multi-population level. Then, we evaluated the distributional range differences between populations, by examining the geographical overlap of suitable habitats between existing and hypothetical populations (i.e. suitable surface of the hypothetical populations accessible or not to the existing ones). Finally, for each population, the median distances of suitable cells to the mouth of their respective natal river systems were compared, between periods and scenarios, by running Wilcoxon tests with Bonferroni correction.

3. Results

3.1. Model performances and variable contributions

The check for collinearity for the 11 pre-selected variables resulted in Spearman’s correlation coefficients |r| < 0.58 and a variance inflation factor (VIF; Brauner and Shacham, 1998) threshold < 2.3. The reduction from 11 to 5 variables in the ensemble models resulted in the successive removal of the following variables: VEL_MEAN, OXY_RANGE, distMUD_SAND, distSAND, distMIX_COARSE and distROCK. Final ensemble model predictions performed well in characterizing the range of *A. sturio* over the large continental shelf of the northeastern Atlantic Ocean (Boyce = 0.94 ± 0.02; AUC = 0.93 ± 0.02; TSS = 0.77 ± 0.04; Kappa = 0.54 ± 0.05). The bathymetry had the best relative contribution (0.48 ± 0.04; Fig. 3a) and ‘distance to home’ was the second most important variable (0.36 ± 0.03), while dissolved oxygen concentration, salinity and sea temperature showed much lower contributions. The response curves indicated a decline of suitability as distance to home increased, while a slight increase in suitability started from 2000 km to home (but without a total agreement between iterations; Fig. 3b). See Supplementary Information (Text S1) for a more detailed description of the variable influences on *A. sturio* marine distribution.

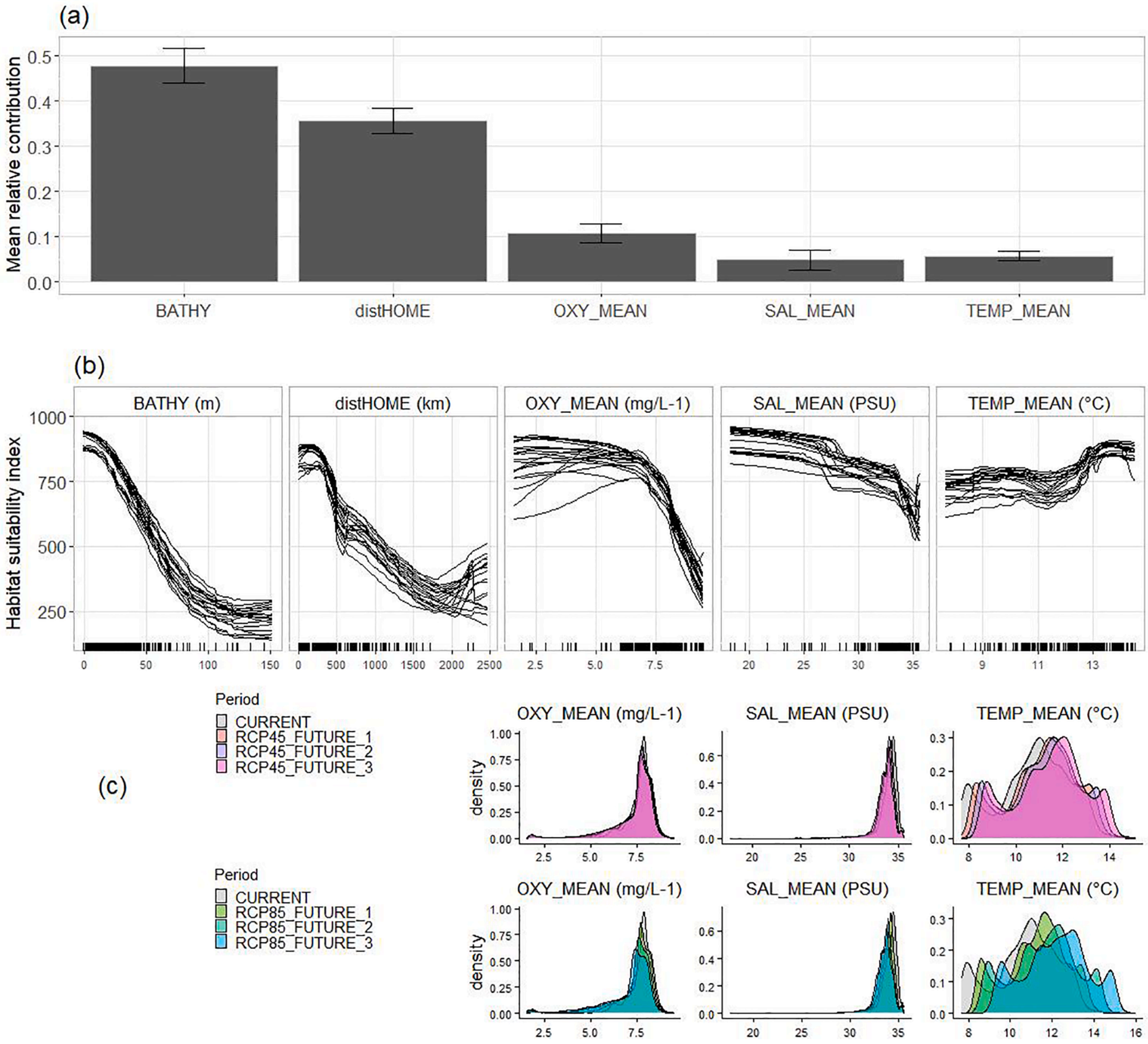

Fig. 3. Relative contribution and response curves of the five variables selected in the final ensemble model. (a) Mean relative contribution across the 20 iterations of ensemble modelling for the five most important variables selected in the final ensemble model. Error bars represent standard deviation (SD). (b) Mean response curves for the five most important variables of the final ensemble model. The y-axes represent the habitat suitability index (ranging from 0 to 1000) while the x-axes represent the range of the variables. Rug plots display distribution of presence cells along the x-axes. We considered that pseudo-absence cells cover the complete range of current environmental conditions in the study area. Response curves show how habitat suitability changes as one variable varied, whilst all the others are kept constant at their mean values. There are 20 mean response curves for each variable, one response curve corresponding to one iteration. (c) Density plots displaying the distribution of the selected physico-chemical variables all over the study area for current and future (FUTURE_1, 2023–2052; FUTURE_2, 2047–2076; FUTURE_3, 2070–2099) periods, with both climatic scenarios RCP 4.5 and RCP 8.5.

3.2. *Habitat suitability at the multi-population level*

Overall, we did not find strong extrapolation localities regardless of the future environmental conditions considered (Fig. 3c, Fig. S5 in Supplementary Information).

Suitable marine sectors currently accessible to -almost- all *A. sturio* populations (i.e. existing and hypothetical) are mainly located along the French and Belgian coasts, the British south coast and, within a smaller extent, within the Severn estuary, the Bristol Channel, the Wadden Sea around the Elbe mouth, and along the southern coastline of the Skagerrak (Fig. 4). Climate change leads to an increasing extent of areas that are suitable to -almost- all populations until the end of the century. Future suitable areas to -almost- all populations are projected to extend over the whole coastal margin of continental Western Europe (except the northern Spanish coast), the English Channel (except its occidental part), the Southern Bight and along the coasts of the southern half of the

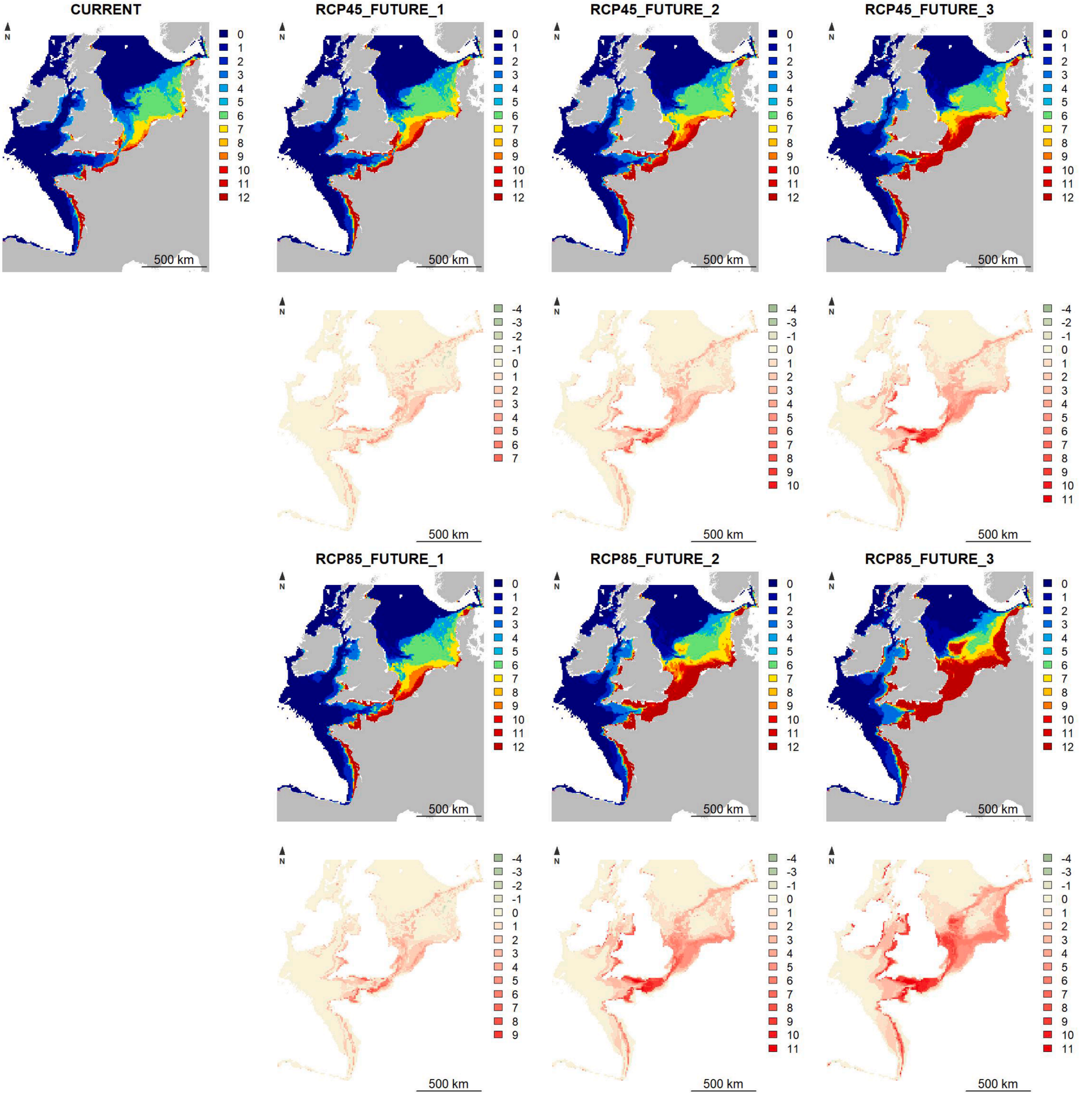
CURRENT
RCP45_FUTURE_1
RCP45_FUTURE_2
RCP45_FUTURE_3
RCP85_FUTURE_1
RCP85_FUTURE_2
RCP85_FUTURE_3

Fig. 4. Habitat suitability combined for existing and hypothetical populations under current conditions and global change scenarios. Maps with color gradients from dark blue to dark red summed the binary predictions of the twelve *A. sturio* populations. Values of these maps ranged from 0 (i.e. unsuitable habitat to all populations) to 12 (i.e. suitable habitat to all populations). Maps with color gradients from green to red are anomaly maps to help pairwise comparisons between each future period (FUTURE_1, 2023–2052; FUTURE_2, 2047–2076; FUTURE_3, 2070–2099) and the current one. They represented the values of the map located just above minus the values of the current map (top left). Values of these anomaly maps ranged from −12 (i.e. the habitat becomes unsuitable to all populations under global change) to 12 (i.e. the habitat becomes suitable for all populations under global change) while 0 means no change over time. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Great Britain (Fig. 4). In Supplementary Information (Figures S6–S9), the continuous and binary projections for each population under current conditions and global change scenarios, are depicted.

3.3. Geographic overlap between existing and hypothetical populations

Suitable habitat inaccessible to existing populations, but accessible to the hypothetical ones, are especially located in the coastal areas of the United Kingdom (except the northern part), along the east coast of Ireland and inside the English Channel (Fig. 5). Under global change, the extent of suitable habitat unreachable to existing populations but accessible to the hypothetical ones, based on the distance from their natal rivers, is predicted to decrease (Fig. 5). More precisely, suitable habitat accessible to the existing populations is projected to increase at sea. Additionally, the gain in terms of surface of marine habitat linked to hypothetical populations is projected to decrease from about 61 % (current period) to 37 % (2070–2099 period with RCP 8.5 scenario). See Supplementary Information (Figures S10 and S11) for maps displaying additional accessible marine habitat for each hypothetical population.

Looking at the current period, some populations have large surfaces of suitable habitat (i.e. $\geq$ 198 000 km^2 for Eider, Elbe, Humber, Weser, Ems and Rhine populations), whereas some others have low extents (i.e. $\leq$ 81 000 km^2 for Gironde, Adour and Solway; Fig. 6). Yet, considering the global change influence, those last populations are projected to increase by more than three times their suitable surfaces at sea, with RCP 8.5 scenario at the end of the century (i.e. 2070–2099 period) based upon temperature, salinity and oxygen concentration changes. Overall, the surface of suitable marine habitat is projected to increase for all populations with global change. Hypothetical populations from Eider, Weser and Adour systems have almost no suitable habitat unreachable by the existing populations (i.e. between 0 and 2.3 % of the total available habitat for all periods included; Fig. 6). Hypothetical populations from Humber, Towy and Severn systems have a lot of suitable habitat inaccessible to the existing populations (i.e. between 12.2 and 41.2 % all periods included) while Seine, Rhine and Ems populations have intermediate overlaps, increasing under future scenarios (1.9–33.1 %).

Finally, the closer the mouth of the natal system of each hypothetical population is to the mouth of the natal systems of existing stocked populations (i.e. Gironde and Elbe), the more similar the projections are to those of the existing populations (Fig. S12 in Supplementary Information). For example, the Adour mouth is distant of 240 km from the Gironde mouth, and projection comparisons display Schoener's D statistics ranging from 0.85 to 0.95 (1 being identical projections), all periods included. Similarly, Elbe and Eider populations have a distance of 35 km between their river mouths and display Schoener's D statistics ranging from 0.92 to 0.99. By contrast, the Eider mouth is 1 689 km away from the Gironde mouth, and projection comparisons of their respective populations display Schoener's D statistics ranging from 0.65 to 0.68, according to periods.

3.4. Distance to home of suitable habitats

For all populations, suitable marine habitats are projected to be, on average, farther from the mouth of their natal rivers under climate change scenarios (Fig. 7). This observed pattern is more evident and significant for the scenario RCP 8.5 and for the most northern and southern populations (i.e. Adour, Gironde and Solway), that have lowest surfaces of current suitable habitat (Fig. 6; Figs. S8 and S9 in Supplementary Information). Hence, global change would lead to broader ranges of suitable marine habitat for all *A. sturio* populations but, in average, farther from the mouth of their natal river systems. For example, suitable habitat accessible to the Gironde population is currently located as an average of 542 km (±466) from the Gironde mouth. Under the effect of temperature, salinity and oxygen concentration changes, it is projected to be located as an average of 952 km (±516) during the period 2070–2099 with the RCP 8.5 scenario (Fig. 7). A detailed description of some metric results (i.e. numerical data) obtained from SDM outputs is given in Supplementary Information (Table S3), to compare accessible suitability between populations.

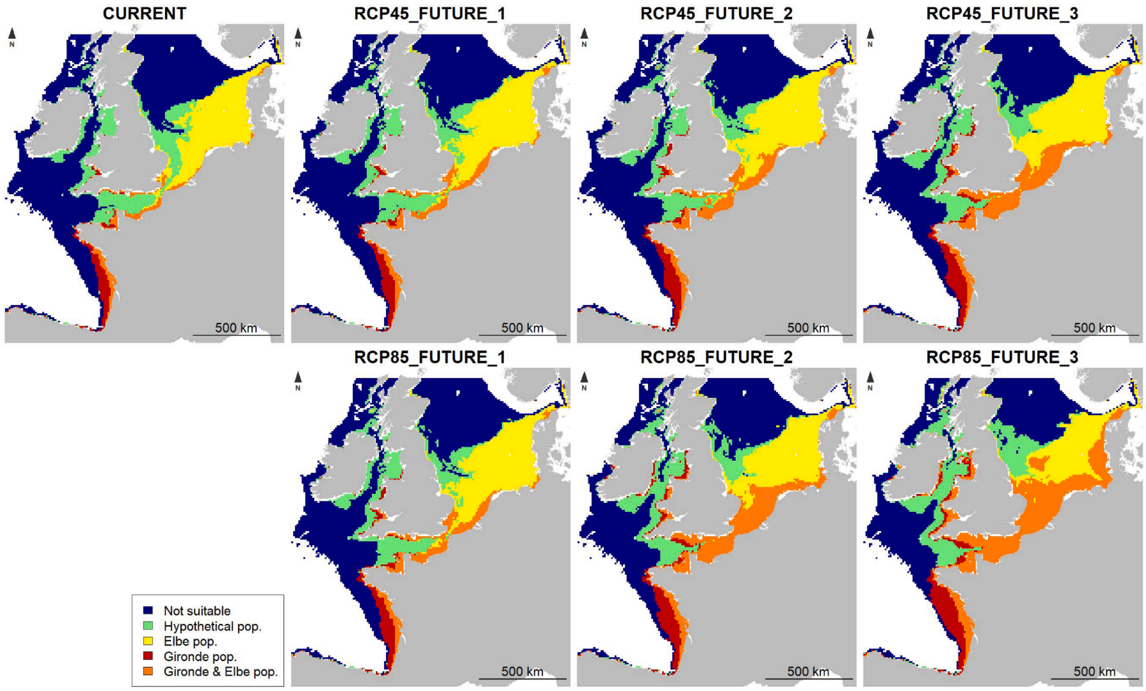

Fig. 5. Maps overlapping the marine habitat accessible to Elbe and/or Gironde population(s) (yellow, orange and red colors) and the remaining marine habitat accessible to the 10 hypothetical populations but not to Elbe and/or Gironde population(s) (green color). Overlaps are displayed under current and future (FUTURE_1, 2023–2052; FUTURE_2, 2047–2076; FUTURE_3, 2070–2099) marine conditions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

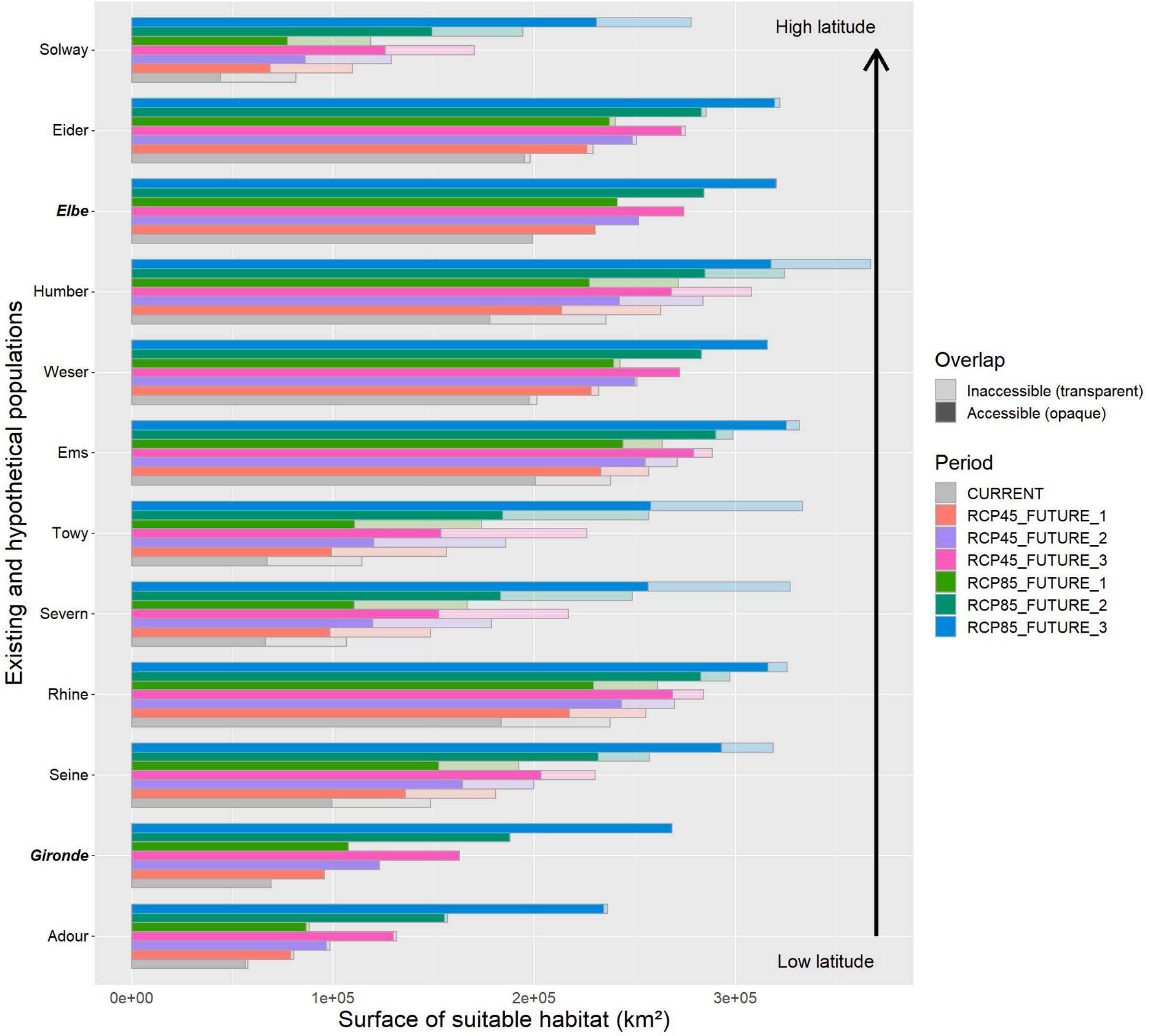

Fig. 6. Bar charts displaying the surfaces of suitable marine habitat, for current and future (FUTURE_1, 2023–2052; FUTURE_2, 2047–2076; FUTURE_3, 2070–2099) periods, and for each *A. sturio* population. The whole surface of suitable habitat for hypothetical populations is differentiated according to whether it is accessible (opaque colors) or not (transparent colors) to the existing populations (i.e. Elbe and Gironde, indicated in bold and italic on the y-axis). Populations are sorted by the latitude of the mouth of their respective natal river systems.

4. Discussion

Developing knowledge on oceanic species responses to global change is the first step towards elaborating international and concerted management actions. To that end, our study was possible thanks to a transboundary cooperation for sharing *A. sturio* national bycatch databases, which is crucial for improving the conservation of migrating species with cross-border ranges (Maureaud et al., 2021).

As participatory data, it was however not possible to check if all environmental combinations where the species occurs have been surveyed (Phillips et al., 2009). Some localities where the species occurs may not have been sampled, just as some bycatch events may not have been reported. The modelled habitat of *A. sturio* may then be biased, by corresponding to a mixture between the true distribution of the species and the distribution of the sampling effort (Sillero et al., 2021). According to the results of Charbonnel et al. (2023), we can nevertheless hypothesize that the presence cells used in our modelling process would be little subject to spatial or environmental biases. In addition, thanks to the ‘diadromous fish at sea’ database (Elliott et al., 2023b), we can assume that all the study area has been fished since 1990, and that *A. sturio* was never mentioned in the catches far from the shore. However, if the marine areas further from the coast have not been sufficiently surveyed, the estimated habitat suitability may have been underestimated offshore for *A. sturio*. This scenario is possible since 67 % of professional fishing vessels have exclusively coastal activities (i.e. maximum distance of 12 miles) on the French Atlantic coast (Daurès et al., 2012). In the context of this study, it was not possible to know the process behind the spatial aggregation of presence cells, because the fishing intensity presents an unquantifiable spatial heterogeneity. Despite the probable existence of biases linked to the opportunistic nature of our bycatch dataset, this latter represents a unique opportunity to improve marine knowledge for *A. sturio*.

Our results suggest an expansion of projected ranges for both existing and hypothetical populations of *A. sturio* under warming climate. The current strategy to stock distant river systems (i.e. Elbe and Gironde), here located close to the north and south ends of the current species repartition, provided access to a majority of marine areas suitable for *A. sturio*. Indeed, habitat surface accessible to both existing populations (i.e. Elbe and Gironde) covers between 62 and 73 % of the suitable habitat to all populations confounded (i.e. existing and hypothetical), throughout the periods investigated (Fig. 5). We suggest that global change is not a major threat for *A. sturio* in the marine environment,

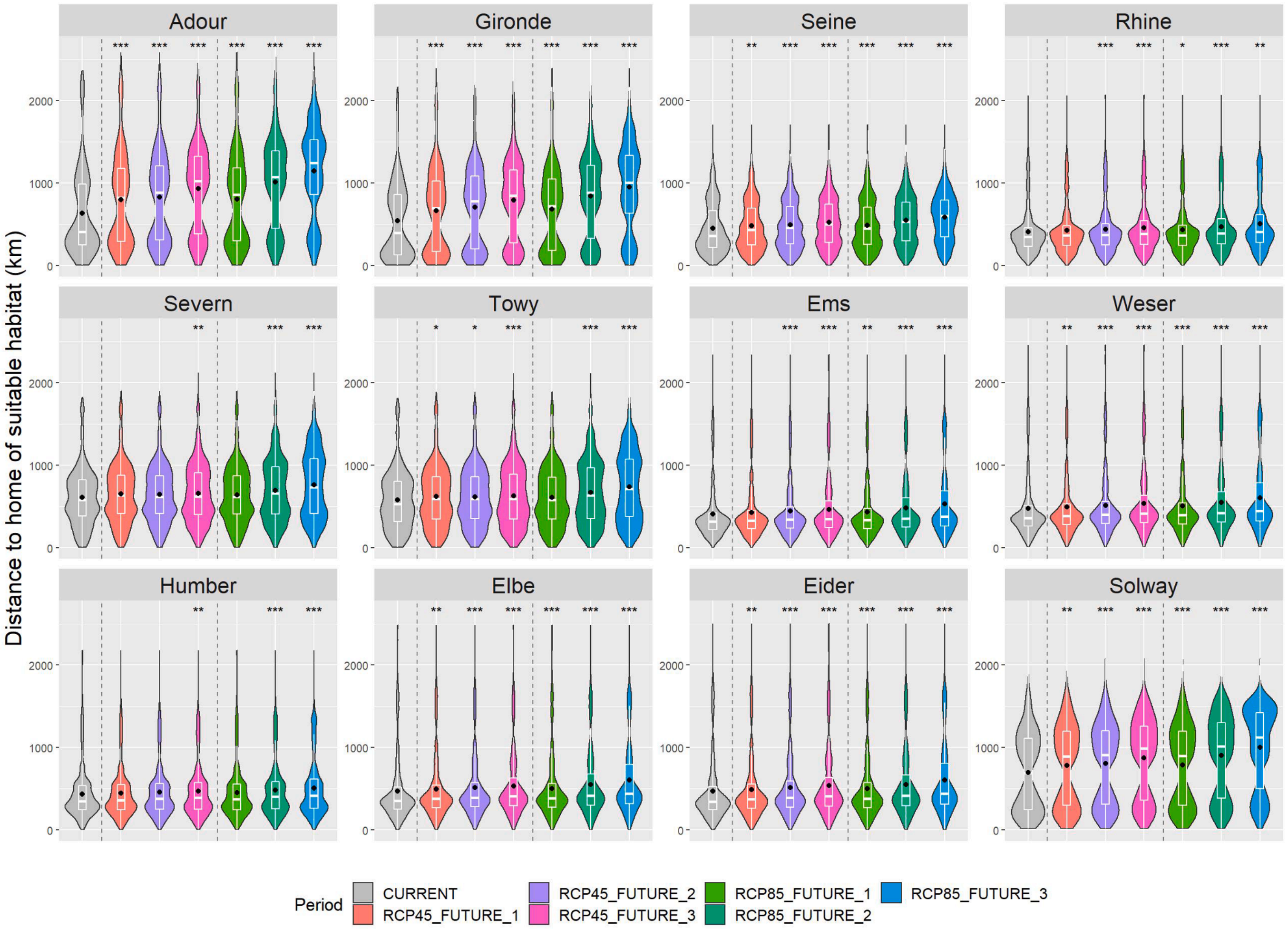

Fig. 7. Violin and box plots displaying the distribution of distance values between suitable marine cells and mouth of the natal river system for each population. Results are shown for current and future (FUTURE_1, 2023–2052; FUTURE_2, 2047–2076; FUTURE_3, 2070–2099) periods and scenarios. Black dots represent means. Box plots with at least one asterisk above them mean that distance values are significantly different from those of the current period, according to Wilcoxon tests with Bonferroni correction (*P < 0.05; **P < 0.005; ***P < 0.0005). Populations are sorted by latitude of the mouth of their natal systems from low (top left) to high (bottom right) latitude.

given the overall gain in habitat suitability projected by SDM (Figs S6–S9 in Supplementary Information). However, a closer look at SDM projections highlights the remoteness of the new suitable marine habitat from natal rivers, with global change. It is perhaps not so worrying for this species with good migratory capacities (Bemis and Kynard, 1997) but it could lead to an increase in distances traveled, with new suitable sectors to be reached, increasing the probability of being accidentally fished and the migration energy costs (Lucas et al., 1994; Jonsson and Jonsson, 2006; Bonte et al., 2012). Moreover, our study only takes into account the marine environment where the species grows and migrates. Climate change impact on freshwater habitats has not be assessed and, for this anadromous species, it is a key-habitat for reproduction and juvenile development. It can also be hypothesized that geographical distance to new future marine habitat may result in a less strict homing behavior for *A. sturio,* in case these remote habitats will be used. Indeed, the attraction to non-natal sites by straying adults is known to increase with the increasing distance from the home site, for anadromous salmonids (Keefer and Caudill, 2014). Returning sturgeons may thus be compelled to enter river systems closer to their new marine habitat, if they are traveling farther away from home. If this happens, straying fish can help natural recolonization of river systems and increase gene flow, as already observed for the Atlantic salmon (*Salmo salar*; Valiente et al., 2010; Perrier et al., 2010).

The low co-occurrence rate (i.e. co-occurrence cells) observed for both existing populations suggests that they do not share the same locations. We can notably report that among the tagged fish (with undoubtedly known origins) there is no co-occurrence cell at all. This pattern can be explained by both the methodological strategies employed for fish river assignment and the particularity of the current situation of *A. sturio*. More specifically, the low co-occurrence rate can be explained by: (i) a high cell resolution for analyses (i.e. 10 × 10 km), as co-occurrence patterns are known to be scale dependent (Araújo and Rozenfeld, 2014); (ii) a large distance (i.e. 1 165 km) between natal river mouths of the two existing populations (i.e. geographical distant populations); (iii) a long period during which the Elbe population was extinct or absent from the sea (i.e. < 2010); (iv) very different population sizes; and (v) a low number of presence cells. Then, we should specify that we implicitly assume a spatial aggregation, based on tagged fish occurrences for each existing population (Ciannelli et al., 2013), by using Kernel maps (Caha, 2023) to assign an origin to individuals for which it was unknown and non-deductible: the more individuals of a given population caught in an area, the greater was the probability that a fish caught in the same area belongs to that population.

The trends observed with the response curves stay consistent with those observed in our previous SDM study (Charbonnel et al., 2023), despite some differences in the amplitude of changes in habitat suitability. The use of shallow coastal waters by the species is still highlighted, with a strong negative influence of the bathymetry (Rochard et al., 1997; Acolas et al., 2017). However, this negative relationship may also reflect a possible sampling bias (i.e. coastal areas more intensively fished; Robinson et al., 2011). The association between high suitability values and very low oxygen concentrations (<2.5 mg/L^{-1}) was nonetheless unexpected (Fig. 3b). A closer look at the map of the dissolved oxygen variable reveals a boundary effect associated to the POLCOM-ERSEM model (i.e. oxygen concentrations predicted unrealistically low; Fig. S2 in Supplementary Information). This can bias dissolved oxygen concentrations towards low values, especially in the deepest sectors around the shelf break. Consequently, a decrease in dissolved oxygen concentrations with global change did not reduce the habitat suitability for *A. sturio* in our work. The impact is certainly negligible in our study, as little change in dissolved oxygen concentrations are calculated with global change (Fig. S2 in Supplementary Information). But, we should still remain cautious regarding the influence of this variable on *A. sturio* marine distribution, knowing that species habitats that may suffer from low oxygen concentrations are in coastal and estuarine areas during summer. See Supplementary Information (Text S1) for more precise interpretations about the ecological results obtained for *A. sturio.* Another source of uncertainty is that physicochemical and hydrodynamic variables used in our analyses were averaged over at least three decades. Hence, our approach provides general trends without considering seasonal changes in distribution. As the distribution of marine migratory species may be influenced with both short- and long-term variability in ocean parameters, multiscale studies or with finer temporal scales are needed to provide more accurate models (Melo-Merino et al., 2020).

Marine ecosystems are commonly accepted to be highly connected, compared to terrestrial ones, owing to fewer impenetrable physical barriers. Species inhabiting marine systems are thus generally perceived as revealing greater dispersal abilities (Cano et al., 2008). Consequently, very few studies integrate dispersal restrictions into marine SDM and when done, this is often with dynamic or process-oriented models difficult to implement (Melo-Merino et al., 2020). Detailed information would be needed, such as yearly dispersal rate (Shipley et al., 2022), which is not available for data-limited species. There is also a general expectation that global warming will drive marine species distributions towards the poles (Perry et al., 2005). In fact, both at sea and on land, many species display potential range shift limitations that may exempt them from broad areas of suitable habitat (Pagel et al., 2020).

In our study, we have chosen to add the ‘distance to home’ variable alongside other environmental variables in the SDM process. Hence, the degree of influence and the response curve of this spatial variable were not fixed beforehand, but evaluated as the other variables. We thus allow the possibility to produce more complex dispersal processes than a negative linear or exponential one, which may represent more realistic patterns for certain species or spatial relations (e.g. species using ocean currents; Mendes et al., 2020). In our case, the results revealed that distance to home is a major determinant of the marine distribution of *A. sturio*, habitat suitability broadly tending to decrease as distance to home increases. More specifically, we obtained an approximately semi-Gaussian curve (Fig. 3b), which is consistent with the general description of the dispersal process in the literature (e.g. Kinlan et al., 2005; Mendes et al., 2020). Looking in greater detail, the response curve observed may reflect two movement tactics inside both existing populations. Some fish would remain close to their specific natal rivers, with a behavior that could be qualified as random dispersal, leading to an exponential decrease of suitability with distance to mouth, until 2000 km. Few other fish would exhibit long-distance dispersal during their migration to find feeding habitat, with a half-dome-shaped response curve from 2000 km. We have yet to remain prudent concerning the trend observed for long ‘distance to home’ values, as model iterations are not unanimous and values higher that 2000 km from home concern very few cells, in our calibration process (i.e. 2 presence and 58 pseudo-absence cells).

Our findings confirm that homing behavior of long-ranged diadromous fish can drive their marine distribution, due to their affinity to natal homing grounds (Lassalle and Rochard, 2009; Hare et al., 2016). Along the same lines, Shelton et al. (2021) find that along California and Alaska coasts, different stocks of the anadromous chinook salmon (*Oncorhynchus tshawytscha*) have different oceanic distributions, driven by the location of the mouth of their natal rivers. If the ‘distance to home’ influence remains accurately stable over time, it means that *A. sturio* populations cannot simply shift their marine range and may be particularly susceptible to climate change. The limits of the most common strategies combining spatial constraints with SDM is that they do not provide an accurate description of species movement (Bruneel et al., 2018). They are nonetheless based on presence records which intrinsically encompass biological information on species evolutionary dispersal mechanisms (Mendes et al., 2020). An asset of our approach taken here is that dispersal behavior from known point sources was explicitly considered for an anadromous fish. We are therefore closer to: (i) quantify *A. sturio* movements; (ii) directly estimate its colonization capacities; and (iii) entail more realistic predictions, especially in light of global change.

We must furthermore state the impossibility of taking into account the route fidelity movements of *A. sturio,* such trajectories being probably more accurate than those based on the shortest path, as we did here. Furthermore, species dispersal can be restricted by directional movements in aquatic systems, such as current flow direction, that are generally asymmetrical movements (i.e. the probability to move in one direction is different from moving in another direction; Acevedo and Fletcher, 2017). Our final model however did not retained information about oceanic currents (i.e. mean current speed on the seabed), while that may be influencing diadromous fish migratory routes (Araújo et al., 2013, Palstra et al., 2008). In our case, *A. sturio* seems to migrate preferentially northward after leaving rivers and estuaries. The Gironde population may probably be influenced by the northward shelf residual circulation (Le Boyer et al., 2013), while the Elbe population may experience the major current that runs from West to North along the Wadden Sea (Seiss and Plüss, 2003). The same pattern of northward movement is also observed for the Green Sturgeon (*Acipenser medirostris*) along the US and Canadian west coasts (Erickson and Hightower, 2007; Huff et al., 2011). Nevertheless, several individuals can be observed to move clockwise against the current (Gessner, *pers. comm.*).

All dispersal-constrained SDM studies are based on symmetrical dispersal or migration rates (Holloway et al., 2016). Hence, the representation of the true complexity of marine currents, as well as the insertion of dispersal routes in SDM, needs to be explored and carried on. It can increase the ecological realism of SDM (Bruneel et al., 2018; Parreira et al., 2023) and help understand the marine spatial patterns of diadromous fish or marine megafauna, for example (Horton et al., 2017). In addition, other factors such as life-history traits, morphological characteristics and ontogeny might also drive the marine behavior of *A. sturio* and the extent of its marine migration. This has already been suggested for others diadromous fish species, such as the brown trout (*Salmo trutta*; del Villar-Guerra et al. 2013). Furthermore, it should be noted that fishing intensity varies spatially and thus, generates various bycatch mortalities risks depending on migratory routes, as observed for the Atlantic Sturgeon (*Acipenser oxyrinchus*; Stein et al., 2004). The integration of these factors was however not achievable with the species investigated here.

Interestingly, the relative importance of the ‘distance to home’ variable is very much more pronounced than observed in our previous study (Charbonnel et al., 2023). This may be explained by the extent of the study area which has more than doubled and has generated a greater number of large ‘distance to home’ values available throughout the study area (means: 1 086 *vs* 653 km, ranges: 5.8–2470 *vs* 5.7–1336 for the current and previous studies, respectively), these large classes of distance having few presence cells. By expanding the spatiotemporal extent to consider all known captures of the species since 1990, we can be relatively sure that we encompass all the current marine range of

A. sturio, and that we have reduced the risk of truncation of its estimated ecological niche (Chevalier et al., 2021). Furthermore, the proper use of this approach is based on a key assumption associated to SDM which is niche conservatism or stability in space and time (Wiens and Graham, 2005). In our case study, this means that we assume that the different *A. sturio* populations have similar dispersal abilities and ecological requirements to the Elbe and Gironde populations (i.e. same response curves), for the current and future periods analyzed. Currently, we suppose they have similar migratory capacity, since all the individuals used for the stocking in the Gironde and the Elbe systems come from the same broodstock. This assumption may not stay true for future populations, but as individuals will still come from the same gene pool, this risk is limited. This hypothesis would be still interesting to verify, as different populations of marine fish species may not have the same ecological requirements (Shelton et al., 2021).

The study of Lassalle et al. (2010) assessed that the continental distribution of *A. sturio* will be affected by climate change, especially river systems localized along the south end of its current range turning less suitable. Globally, they highlighted a tendency with northern river systems becoming more suitable than southern systems. They also indicated that spawning basins that could host medium to high suitable conditions for *A. sturio,* by the end of the century, will be: Adour, Eider, Elbe, Ems, Gironde, Rhine, Seine and Weser basins. We can complete with our results that these river systems are predicted to be surrounded by suitable marine habitat accessible to the majority of populations, with the exception of the Adour. However, we must be cautious considering the suitability of the basins studied by Lassalle et al. (2010) since their study focused on limited variables available at the time: air temperature, slope of the river, annual precipitation and drainage surface. An update of their model using the most recent global change scenarios could be useful before developing additional recovery scenarios.

River systems used to simulate population recovery have been chosen based on the results of Lassalle et al. (2010) and UK expertise (Colclough, *pers. comm.*), especially according to their environmental suitability. However, conservation issues for diadromous fish are multifactorial (Verhelst et al., 2021). Factors of anthropogenic origin occurring in freshwater (e.g. obstacles to migration, river dredging) and in both marine and freshwater environments (e.g. commercial fisheries, exotic species, habitat modification, pollution, ship traffic) were not considered, although they may have a significant impact on diadromous fish population dynamics (Verhelst et al., 2021). In particular, longitudinal connectivity between estuaries and the main channel in large river basins is vital, as fragmentation by dams may prevent diadromous fish from completing their life-cycle (Duarte et al., 2021). We predict habitat suitability at sea, without considering the ecological state of the river systems. Hence, our study provides the basis for a more refined study on the recovery potential of the respective river systems for the species in question. To favor the establishment of *A. sturio*, we recommend to: (i) consider the accessibility to functional spawning grounds (e.g. dam presence, habitat quality); (ii) overall riverine, estuarine and marine habitat suitability under climate change scenarios (Häkkinen et al., 2021; Dambrine et al., 2023); (iii) reevaluate the information of marine habitat suitability considering individual marine trajectories; and (iv) combine multi-factor indices to support management decisions. See Table S2 in Supplementary Information for a description of some factors recommended to take into account in future studies (e.g. connectivity to spawning habitat, ship traffic, exotic species), with a first assessment for the rivers chosen.

Our study still serves as a premise for developing and anticipating management strategies adapted to climate change for *A. sturio*. Natural recolonization of river systems can occur and we do not take sides on those to be favored in the case of future assisted translocation for the species. Our approach aims to provide inputs to drive political decision-making (Beck, 2011) for more effective *A. sturio* recovery strategies and protection of marine habitats in Western Europe. Our results could also be considered for the 2030 Biodiversity Strategy of the European Union (EU) which targets that at least 30 % of the European seas must be protected, with one-third under strict protection (Schultz et al., 2022). We propose a useful guide based upon application tools (Tables S2 and S3 in Supplementary Information) to help in the choice of river systems for recovery of *A. sturio*, depending partly on the marine surface that each population holds and/or adds to the existing ones, under current and future conditions. Several strategies would be possible according to the desired trade-off between the allocation of management resources and the benefits to the species conservation (Marsh et al., 2007). Managers and decision-makers can consider for example: (i) future habitat ranges of each population (Fig. 6), widespread ranges being generally associated with lower risk of extinction (Hoegh-Guldberg et al., 2008); (ii) distance of suitable habitat from natal river systems of each population (Fig. 7), greatest distances implying repeated long-distance movements and thus greater mortality risks (Lucas et al., 1994); or (iii) gain in surface of habitat offered by each new population (Fig. 6), greater gain resulting in larger marine surface colonizable by the species and thus, probably more interactions with human activities (McQuatters-Gollop et al., 2022).

5. Conclusion and perspectives

As far as we know, the influence of the distance to the natal river was never explicitly considered in marine SDM studies (except in Charbonnel et al., 2023) to investigate and predict habitat suitability for anadromous fish species. Our dispersal-constrained SDM approach is feasible without species-specific dispersal data or temporal datasets, and suitable for data-poor species for which natal sites are identified. It may be generalizable to other marine or terrestrial species for which individuals disperse from known or assigned point sources. Hence, its adaptability can be queried for various species, in particular migratory fish (Thorrold et al., 2001), seabirds (Putman, 2020), butterflies (Mouritsen, 2018), marine turtles (Brothers and Lohmann, 2015) or bats (Baerwald et al., 2021), that accomplish natal homing, spawning site fidelity or return migrations.

CRediT authorship contribution statement

Anaïs Charbonnel: Conceptualization, Formal analysis, Methodology, Software, Writing – original draft, Writing – review & editing. **Géraldine Lassalle:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Validation. **Patrick Lambert:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Validation. **Eric Quinton:** Data curation, Software. **Jörn Geßner:** . **Eric Rochard:** Data curation, Software. **Steve Colclough:** Data curation, Validation, Writing – review & editing. **Niels Brevé:** Data curation, Validation, Writing – review & editing. **Marie-Laure Acolas:** Conceptualization, Data curation, Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing.

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 and code used in this research are available on Recherche Data Gouv at https://doi.org/10.57745/YV4CP8.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.111762.

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