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ABSTRACT

Diadromous fish species have a complex life cycle during which they migrate between marine and freshwater habitats. They experience multiple human-induced pressures in both environments, likely exacerbated by climate change, leading to dramatic population declines across their distribution ranges. Currently Species Distribution Models (SDMs) have been applied separately in both their continental and marine habitats to improve our understanding of their lifecycles and help with species management. Integrating the freshwater-sea continuum into the decisions would now be a step further in improving their management. With this objective, we developed a decision tree that links marine and freshwater SDM outputs with current observations of population functionality and suggested management guidance options for the viability of these species. Potential effects of climate change were included through future SDM projections to guide integrative and long-term management. Several criteria were proposed to assess the SDM validity considering the main sources of SDM uncertainties and local expert knowledge on habitat and population status. The framework was applied to approximately one hundred catchments from southern Portugal to southern Scandinavia for four diadromous species. At the European level, management guidance options differed between the two anadromous and two catadromous species. *Platichthys flesus* and *Chelon ramada* European populations seemed in better state than those of *Alosa alosa* and *A. fallax*. Finally, with the help of national diadromous species experts, we focused on four catchments distributed along the European latitudinal gradient to test the proposed methodology and demonstrate local management challenges in terms of freshwater-sea continuity.

1. Introduction

Diadromous species are fish that share their life cycle between marine and freshwater habitats (McDowall, 1988). Thus, they experience multiple human-induced pressures in each environment and at different life stages, which make them highly vulnerable to local and global change (Costa-Dias et al., 2009; Wilson and Veneranta, 2019). Most of these species are facing dramatic population declines across their distribution ranges. Many are listed in the EU Habitats Directives, the Bern convention and the IUCN Red List at both national and European levels (Waldman and Quinn, 2022; Elliott et al., 2023), but their conservation remains challenging, mainly because their seasonal migrations conflict with multiple human uses of their environment (e.g., Verhelst et al., 2021). Management measures on stocks and habitats have been implemented in various catchments across Europe (e.g., artificial reproduction with stocking, fish ways improvements, dam removals,

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fisheries restrictions and closures, spawning habitat restoration, and improvement in overall water quality). However, no significant European recovery has been observed to date, despite all these efforts. Focussing on their marine environment and its connections with continental habitats has been identified as the next obvious progression towards more effective management of these migratory species (Friedman et al., 2019; Ouellet et al., 2022; Elliott et al., 2023).

The marine distribution of some European diadromous species has already been studied using statistical modelling approaches (e.g. Trancart et al., 2014; Elliott et al., 2023; Charbonnel et al., 2023). The main limitation of these approaches remains the scarcity of presence data in the marine environment along with true absences. Today, diadromous species are seldom targeted by marine fisheries (except for Salmonidae within coastal waters and the European flounder in the Baltic Sea) or scientific surveys at sea. One of the best sources of available data comes from a French bycatch at-sea-monitoring programme, which was put in place following the Data Collection Framework - to Protected, Endangered and Threatened Species incidental catches (PETS; ICES, 2022).

In freshwaters, regular monitoring is conducted on various rivers, sometimes with long time series, but data collection and archival over a significant part of the species distribution range remains a complex process to implement (e.g., DATAPOMI initiative in France; Legrand et al., 2021). In this context, large-scale modelling approaches have been developed to predict the current and future habitat suitability of European catchments for diadromous species using historical distributional data and environmental predictors (Lassalle et al., 2008; Lassalle et al., 2010; Barber-O'Malley et al., 2022a; Duarte et al., 2022).

The next step would be to move from these single-domain approaches, where freshwater and marine ecosystems are considered as independent parts, to a more integrative framework that combines continental and marine habitat suitability assessments in a joint evaluation. Even though methods have been applied to marine birds (Häkkinen et al., 2021) and mammals (Frans et al., 2018) to account for the use of different habitats during their lifecycle, their application to diadromous fish is not straightforward. Indeed, the method used for marine birds relied on one Species Distribution Model (SDM) with co-variables from the different habitats inhabited by the species. However, birds are using both terrestrial and marine domains in the same day, contrary to diadromous species that spend prolonged periods of time (days up to years) in one environment before moving to the other. The other method applied to mammals is a "multi-state species distribution modelling" framework that allows for the combination of multiple SDMs constructed based on the temporal or behavioural use of each habitat by the species. Given the scarcity of marine occurrences for diadromous species, connecting different models with this method requires an improved characterisation of their marine habitats first. Further, their at-sea seasonal migrations, dispersal distance, population mixing, or social life-history behaviour remain largely unknown. Thus, in this study, we propose a semi-quantitative framework to combine single-domain SDMs into broad strategic guidelines to manage diadromous fish populations.

The combination of present and future single-domain SDMs has two objectives: (1) evaluate the freshwater-sea continuity in terms of environmental quality between marine and continental (freshwater and estuary) environments inhabited by diadromous species and (2) study the evolution of this continuity with regard to climate change. From this combination, the proposed framework gives insights in effective management guidance options for a more integrative management, by means of combining information from the two previous objectives. A decision tree, informed by the current population functionality along with the current and future suitability of the continental and marine environments, was designed to assess the overall status of the population. Different approaches to classify the population functionality exist such as the IUCN Red List of Threatened Species, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) or the categories used by Barber-O'Malley et al. (2022b); they vary in their level of details, criteria used and objectives. This decision tree considered connections across systems and climate change impacts, and it proposes management guidance options accordingly. The methodology was applied to four diadromous species for approximately one hundred catchments from southern Portugal to southern Scandinavia. Firstly, we identified potential management challenges linked with habitat continuity and its interconnections with climate change at the species biogeographic scale to evaluate the common management guidance options at the European level. Then, we focused on four catchments to discuss and complement the framework classification with the support of diadromous fish management specialists from these basins. Using a latitudinal gradient along the Atlantic coast, we wanted to analyse if management guidance options for those species were varying from south to north.

2. Material and methods

2.1. Design of a decision tree for management guidance options

2.1.1. Decision tree rationale

The proposed framework that combines data from marine and continental domains to guide for diadromous species management follows a decision tree approach (Fig. 1). Each management guidance options were designed to be implemented at the catchment scale.

The current functionality of the population, based on expert knowledge, comes first in the decision tree, coming from expert-knowledge; it serves as the baseline for the management guidance options, followed by the continuity in terms of habitat suitability across systems through time. It starts with the joint assessment of the continental and marine environment suitability for the current period, and it ends with future suitability projections under climate change (e.g., next management plan timeline) in both environments. SDMs are advised considering the large spatial and temporal scales of such analyses. The path taken through all steps leads to the main management guidance option for the species of interest in a given catchment.

2.1.2. Check model validity

As the framework uses statistical models to inform the decision process, their evaluation comes first and conditions the confidence in their outputs and thus, in the application of the selected management guidance option. We identified two main sources of uncertainties to be evaluated during this check of model validity: the choices made to build the model (mainly linked to the data quality and availability) and the statistical model performances. We designed Table 1 as a checklist for users to evaluate how relevant is a species distribution model for the use of the decision tree. Table 1 is an adaptation of the works of Sofaer et al. (2019) and Araújo et al. (2019). If a model receives at least one box in the "very cautious" or "cautious" column, users should be circumspect when applying the decision tree. This evaluation does not judge global validity of models but only informs on model's adequacy within our framework. When using the decision-tree for large-scale applications covering numerous catchments for which population functionality and model outputs cannot be verified, this assessment helps with the level of confidence users may have on the management guidance options emerging for the species of interest.

For an application on a single or restricted list of catchments, we encourage users to integrate expert knowledge in the model evaluation (Table 2) in addition to the criteria listed above. When experts disagree with population functionality, we recommend avoiding the use of the decision tree as the continental SDM was probably undertaken using the "wrong" or, at least, controversial entry. On the contrary, when experts disagree with model outputs, we recommend using the decision tree as an "exploratory" tool where users can follow branches not with the modelling outcomes but also with their expectations and discuss the differences in management options.

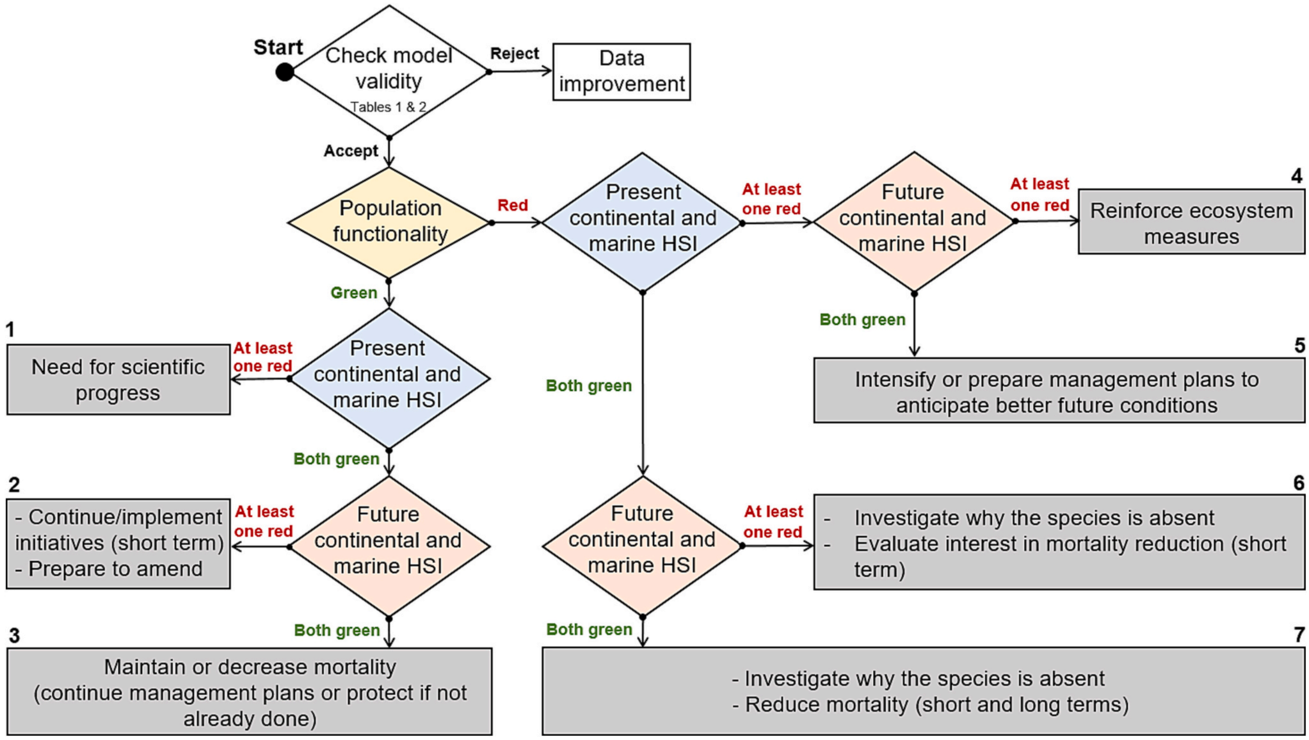

Fig. 1. Decision tree linking the marine and continental life phases of diadromous species to identify management guidance options that integrate interconnections between the environments used by the species in time. Grey rectangles detail the proposed management guidance options while coloured diamonds depict the decision variables used (see Sections 2.1.2 and 2.2.1 for the application). HSI = "Habitat Suitability Index", which is the species distribution model output, ranges from 0 to 1. "Green" refers to abundant population or suitable habitat and "Red" to species absence or unsuitable habitat (see 2.1.2 and 2.2.1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.1.3. Data needs and preparation, and user choices

Five decision variables are required for the decision tree framework to be applied to a species or group of species. The first decision variable informs on the current population functionality in the catchment. Here, we chose the definitions of Barber-O'Malley et al. (2022b) which evaluate the sustainability of a population on two broad criteria. The first one estimates the number of individuals in a catchment over the last years. The second one focuses on the regularity of the reproduction. The EuroDiad 4.0 database (Barber-O'Malley et al., 2022b), based on this approach, gives the population functionality of diadromous species for many European catchments. Following these criteria, the designation of population functionality for anadromous species (i.e., reproducing in rivers and growing at sea) relies on the observations of reproduction events in the last few years and for catadromous species (i.e., reproducing at sea and growing in rivers), on the actual size of the population and its prominence in the community (see 2.2.1). The four other decision variables are species distribution models simulating the continental and marine present suitability (decision variables 2 and 3; Table 3) and projected environmental suitability for the species of interest (decision variables 4 and 5; Table 3).

The decision variables are a mix of continuous and categorical variables. The first step for comparison is to define two categories with a colour code: present or suitable ("Green") and absent or unsuitable ("Red") (Table 3). The thresholds applied on model outputs to indicate between suitable and unsuitable habitat should be made explicit by the framework users.

In addition, defining the zone of suitability of the marine environment associated with a given catchment and species needs to be set by the framework users. When at sea, if the species of interest is suspected to remain close to its catchment of origin to grow (anadromous) or to reproduce (catadromous), the marine suitability should be assessed in a zone around the catchment's mouth, with a radius defined by existing knowledge of the species movements at sea and whether the species is known to return to rivers of origin or not. However, if the species is known to migrate and reproduce or grow in specific areas (e.g., salmon in the Norwegian waters and Greenland, and the European eel in the Sargasso Sea), the suitability for this "destination" area would be more appropriate.

2.1.4. Management guidance options

In the first three management guidance options [1–3], the current population was classified as functional in the catchment while, for the four remaining options [4–7], the current population was assessed as non-functional. From here on, the terms "Green" and "Red" are used (see the definitions for categorical and continuous decision variables in Section 2.1.3).

The first management guidance option [1] is "Need for scientific progress" when there is a discrepancy between the actual current functionality of the population recorded as"Green" in the catchment and the predicted current suitability of one or two of the environments calculated as "Red". First, scientific investigations as to why the population functionality is high in the catchment despite a "Red" marine and/or freshwater environment should be considered. In many cases, it may require a better understanding of the area where the species inhabits at sea through scientific or fishery-based monitoring surveys. Subsequently, additional or new measures to support the species would be envisaged.

The second management guidance option [2] is "Continue/implement initiatives (short-term) and prepare to amend". In this case, the population functionality is "Green" as is the current environmental conditions for the species in both freshwater and at-sea environments. Due to this coherency, the management strategy adopted (if any) seemed efficient. However, at least one habitat domain was set to turn "Red" in the future, thus climate change may modify the environmental

Table 1
Checklist to evaluate the validity of Species Distribution Models that drive the decision tree adapted from Sofaer et al. (2019) and Araújo et al. (2019).

Modelling choices	Data format		Presence only (check the way pseudo-absences were generated and the prevalence between the two categories)	Presence only (check the way pseudo-absences were generated and the prevalence between the two categories)	Presence/absence or Abundance
	Data coverage		A small part (<25 %) of the species distribution area or only one season covered	Subregions (≥25 %) of the species distribution area or under-representation of some seasons	The entire species distribution area and covering all the seasons
	Number of occurrences		<30 (Wisz et al., 2008; van Proosdij et al., 2016)	≥30	Hundreds to thousands depending on spatial scale, presence distribution and absences
	Environmental variables	No climatic variable[a] tested during the calibration for climate change effects	No climatic variable[a] selected during the calibration process for climate change effects	At least one climatic variable[a] selected during the calibration process for climate change effects	All variables, including climatic ones[a], with known underlying biological mechanisms with the distributions of the species
	Spatial and temporal resolutions of the environmental variables		Loss of ≥25 % of occurrences or no temporal alignment with the biological response being modelled	Loss of <25 % of occurrences and temporal alignment with the biological response being modelled	No significant loss of occurrences and temporal alignment with the biological response being modelled
	Climate change modelling		A global climate model	Multiple global climate models	Multiple regionalised climate models
Model performances	Model building limits		Acknowledgment of uncertainties in model outputs without statistical evaluation	Acknowledgement of uncertainties in model outputs with a formal uncertainties analysis	Full exploration of uncertainties in model outputs
	Evaluation metrics adapted to the data and models and predictive capacities evaluated		Very low (relative to its scale and ratio of presence to absence; Landis and Koch, 1977)	Low (relative to its scale and ratio of presence to absence; Landis and Koch, 1977)	High (relative to its scale and ratio of presence to absence; Landis and Koch, 1977)
	Model validation		No attempt to validate the model	Simple techniques to validate the model such as validating the model on a subset of the initial dataset	Intense techniques to validate the model such as n-fold cross-validation or use of independent dataset
	Model extrapolation		High (Mesgaran et al., 2014)	Low (Mesgaran et al., 2014)	Low (Mesgaran et al., 2014)
Decision tree option		Avoid using	Be very cautious	Be cautious	Be confident

[a] Climatic variables refer here to physical and biological variables that will evolve with climate change (e.g. temperature, salinity, or primary production). Fixed variables (e.g. sediment, depth or slope) can explain species distributions as habitat filters supposedly considered as time-independent. Note that climatic biological variables (e.g. primary or secondary productions) are derived from climatic physical variables (i.e. temperature and salinity) and thus, less trustworthy in terms of projections.

Table 2
Integration of expert knowledge in the evaluation of the Species Distribution Models that drives the decision tree.

		Agreement with present model outputs		
		No – for one or two SDM(s)	Difficulties to express an opinion for one or two SDM(s)	Yes
Agreement with the population functionality	No	Avoid using the decision tree	Avoid using the decision tree	Avoid using the decision tree
	Lack of information	Be very cautious with the decision tree	Be cautious with the decision tree	Be cautious with the decision tree
	Yes	Be very cautious with the decision tree	Be cautious with the decision tree	Confident application

Table 3
Mandatory decision variables for the framework on the selected diadromous fish over the study area. The sources for the present work and the 'abundance categorisation' in "Green" / "Red" are presented and detailed in Section 2.2.1.

Decision variable	Definition	Source for the present work
1. Current population functionality	Expert knowledge/database entries about the number of individuals and the level of reproduction in the catchments during the last decade	**EuroDiad 4.0** "Green": abundant, common "Red": rare, absent
2. Current continental distribution model	SDM outputs informing the quality of the continental environment for the species over the last decade	**HyDiaD's BRT** "Green" > 0.5 "Red" ≤ 0.5
3. Current marine distribution model	SDM outputs informing the quality of the marine environment for the species over the last decade	**SO iCAR** "Green" > 0.4 "Red" ≤ 0.4
4. Future continental distribution model	SDM outputs informing the quality of the continental environment for the species in future decades	**HyDiaD's BRT** "Green" > 0.5 "Red" ≤ 0.5
5. Future marine distribution model	SDM outputs informing the quality of the marine environment for the species In future decades	**SO iCAR** "Green" > 0.4 "Red" ≤ 0.4

suitability, and adaptations in the management practices may be needed. In the case of no particular current management, the catchment will need more strategic measures.

The third management guidance option [3] is "Maintain or decrease mortality". There is coherence in the present, but contrary to the previous case [2], the environmental conditions were predicted to persist as "Green" for the species even with climate change effects. Management measures should be continued with options to increase protection given the suitability of the area. Preferably, the area should be listed as a "climate refuge" zone for the species.

The fourth management guidance option [4] is "Reinforce ecosystem measures". This option is not specific to the species of interest. The species has little possibility to colonise or recolonise the catchment, with "Red", current, and future habitat suitability lead to a low coherency between domains in both periods. Managers should focus on measures for other species or on the ecosystem that could also benefit the focal species.

The fifth management guidance option [5] is "Intensify or prepare management plans to anticipate better future conditions". If the species was "Red" in the catchment, with "Red" current habitat suitability but the environments are predicted as "Green" and in the future, measures can be discussed to assist species' returning or new colonisation in the catchment.

The sixth management guidance option [6] is "Investigate why the species is absent and evaluate the interest in mortality reduction (short term)". Here, the population functionality is "Red", but marine and freshwater present environments were "Green". A reduction in anthropogenic impacts could probably allow the species to colonise or recolonise this catchment. Nonetheless, in this scenario, climate change reduced the environmental suitability and continuity between domains. As such, mitigation measures to reduce climate change impacts on species and habitats should be integrated into the management plans.

The final management guidance option [7] is "Investigate why the species is absent and reduce mortality (short and long terms)". The species is categorised as "Red" whereas both environments (current and future) are "Green". The first step would be to identify the reasons why the species is classified as "Red" in the catchment. If anthropogenic pressures were the main issue, the management plans can be implemented or intensified to reduce their impact and allow for the species (re-) settlement in the catchment. In this specific scenario, re-introducing the species (if the species occurred in the catchment in the past) or undertaking assisted migration (if the species has never been recorded in the catchment before but present in the general region) should be considered.

The decision tree and its associated management guidance option are proposed as a tool to support consensus with many types of stakeholders on diadromous species management. Therefore, this framework should be used as a first step before any local assessment of political, social, and institutional factors involved in such decisions.

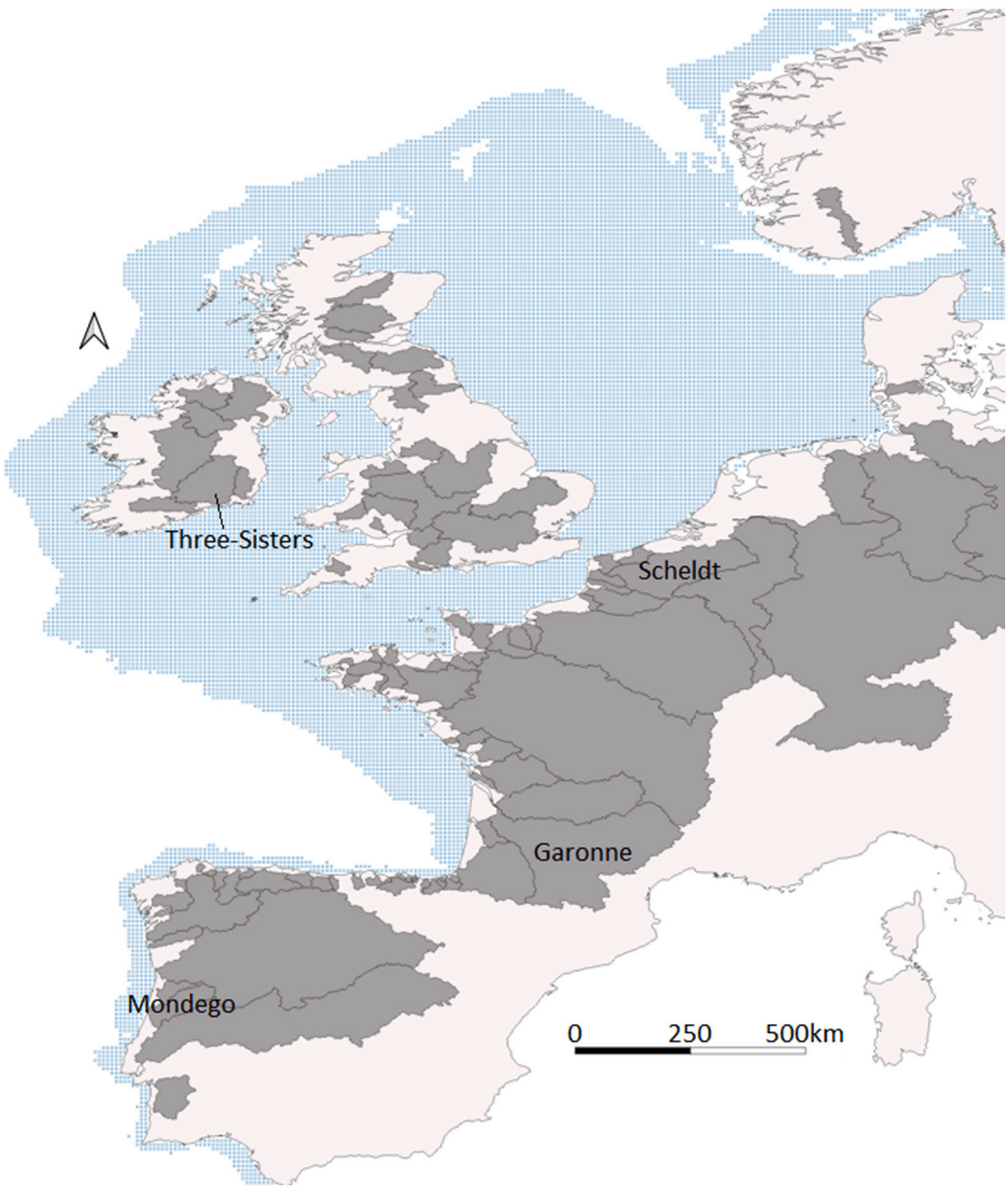

Fig. 2. Map of the study area. All European catchments present in the EuroDiad 4.0 database and used for the analysis at the European level (depicted as dark grey polygons). The four catchments to which the framework was applied following discussions with local experts are indicated (i.e., Mondego, Garonne, Scheldt, and Three-Sisters). The 0.1° × 0.1° grid cells used to model the marine environment suitability are represented in blue. For the latter, grid cells with depths >300 m were not studied as the four species of interest are primarily coastal species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Applying the methodology to four diadromous species in Western Europe

2.2.1. Gathering freshwater-sea information in Western Europe

For the current population functionality decision variable, the EuroDiad 4.0 database (Barber-O'Malley et al., 2022b) was used (Table 3). Population functionality was available for catchments in Europe, the Middle East and North Africa in four abundance categories for the 2011-present time period. The categories are abundant (i.e., a present and numerically dominant functional population in the freshwater community), common (i.e., a present functional population in the catchment), rare (i.e., occasional vagrants were recorded in the basin) and absent (i.e., the species has never been recorded in the catchment or disappeared from the freshwater community). Categories "abundant" and "common" were classified as "Green" whereas the two others were grouped under "Red" (see definitions in Section 2.1.1).

The Habitat Suitability Index (HSI) for the continental environment (estuary and freshwater) was extracted from the HyDiaD model (Barber-O'Malley et al., 2022b), which is a hybrid species distribution model for diadromous species mixing a population dynamics module (i.e., mortality and dispersal processes) with a habitat suitability module. Here, we only used the outputs from the habitat suitability module (Table 3), which used seven environmental variables from both marine and continental habitats (sea surface temperature, surface salinity, mixed layer depth, precipitation, surface area of the catchment, length of the main watercourse and altitude at the source). It was calibrated with occurrences from the pre-industrial revolution period (i.e., 1851–1950) found in EuroDiad 4.0. The module was then used to calculate the continental suitability at the catchment scale with an annual time step from 1950 up to present day, for catchments flowing in the North-eastern Atlantic Ocean (Fig. 2). The habitat suitability from HyDiaD reflects the quality of the continental environment without any anthropogenic pressure (i.e., calibration process with data before the pre-industrial revolution). Mean HSI values for the periods 2011–2021 and 2050–2060 above 0.5 were considered as "Green". This threshold is commonly used in SDMs to binarize the probability of occurrence into presence/absence (Liu et al., 2005).

For the marine environment, a Bayesian hierarchical SDM (i.e., a site occupancy intrinsic conditional autoregressive model (SO iCAR)) framework (Elliott et al., 2023a) implemented using data from Elliott et al. (2023) (Table 3). This spatially explicit distribution model incorporates imperfect detection from the different gear types. It provides the marine distribution for eleven diadromous species between 2006 and 2019 using marine environmental variables (see Elliott et al., 2023). For the present work, we used the same environmental variables (i.e., surface salinity, surface net primary production, sediments and depth or distance to the coast) as Elliott et al. (2023) but extracted from another model (Holt and James, 2001; Butenschön et al., 2016). We, then recalibrated the model and extrapolated it into a wider area (i.e., inclusion of the Cantabrian and Portuguese Seas) and projected for the period 2050–2060 (see Annex 1). The spatial grid resolution of predictions was 0.1°x 0.1° (Fig. 2). To binarize the variable into presence/absence, we used the threshold defined by Elliott et al. (2023). HSI above 0.4 probability of presence was considered as "Green".

2.2.2. Species with contrasting marine and continental habitat use

From the eleven diadromous species for which the five sources of information were available, four species were selected, chosen to illustrate contrasting habitat uses as synthesized in Table S1 with key life-history traits. Two anadromous species (reproducing in rivers and growing at sea) were selected: *Alosa alosa* and *A. fallax*. These species hatch in freshwater, then migrate to grow at sea for several years before returning to freshwater to reproduce (once for *A. alosa* and several times for *A. fallax*). Two catadromous species (reproducing at sea and growing in rivers) were chosen: *Platichthys flesus* and *Chelon ramada*. These species, on the contrary, hatch at sea, grow in freshwater/ transitional waters and return to reproduce several times at sea. Although they have contrasting life histories, the selected species show different levels of conservation status, with *A. alosa* being the most threatened according to the European IUCN Red List. *Chelon ramada* was included in this study since it is an undervalued species as it may become important in the near future for local economies (Pereira et al., 2023). As all four species are thought to stay in the vicinity of the catchment of origin, a buffer zone around the catchment's mouths was defined to study the marine suitability related to a catchment in the study area. The size of the buffer zone was calculated from experts' opinion of the mean distance each species is likely to disperse between its catchment of origin and a new destination catchment (see supplementary material in Barber-O'Malley et al. (2022a) for information related to dispersal for anadromous and catadromous species). This distance was then used as a proxy of how the species was using the marine environment. According to these authors, the buffer radius for *A. alosa* was 50 km, 30 km for *A. fallax* and *P. flesus*, and 60 km for *C. ramada* (Barber-O'Malley et al., 2022a).

2.2.3. Management guidance options at the European and species levels

To investigate differences in the proposed management guidance options between species, the decision tree was applied to all catchments with population functionality entries which were present in EuroDiad 4.0 between southern Portugal and southern Scandinavia (Fig. 2). Results were summarised in a contingency table in which a Chi2-test was applied to evaluate the significance of the relationship between the management guidance options and the species at the European level.

2.2.4. Management guidance options at the catchment and population levels

2.2.4.1. Pilot catchment descriptions. Four catchments along a latitudinal gradient were selected to test the management guidance options at the catchment level against expert knowledge: the Mondego (Portugal), Garonne (France), Scheldt (Belgium), and Three-Sisters (Barrow, Nore and Suir; Ireland) (see Table S2 for main characteristics and Fig. 2). These catchments were located within the distribution area of the four studied species. Historically, all four species to which the framework was applied were known to be present in the four pilot catchments.

2.2.4.2. Expert-knowledge elicitation. The objectives of this local analysis were to: (i) validate the current population functioning extracted from EuroDiad 4.0, (ii) challenge the proposed management guidance options following the decision tree application with the current management strategy in place in the catchment, and (iii) highlight new opportunities in terms of diadromous species management considering freshwater-sea connectivity and climate change impacts. Regional experts were gathered during a two-hour interview and went through the three points listed above. For the first point, we cross-tabulated the agreement between expert knowledge and model outputs for each of the four studied catchments. This outcome was integrated as an evaluation criterion in the model validity check (see Section 2.1.2).

3. Results

3.1. Check model validity

The evaluation of both SDMs for their use within this framework was estimated as "Be very cautious" (Tables 1 & 2). For HyDiaD, we judged the "building model limits" criterion as weak, and for the SOiCAR, we judged the "climate change modelling" criterion as weak. Criteria related to agreement with expert opinions did not change the level of confidence in model outcomes as we were already advised to be critical with model outputs. Following Table 2, for the four case studies, the advice was to "Be cautious" as no explicit disagreements with the model were expressed during the meetings, only some reservations due to knowledge gaps (Table 4).

3.2. Management guidance options for the four diadromous species at the European and species levels

The Chi2-test on the contingency table (Table S3 and Fig. 3) revealed differences among the frequencies of management guidance applied to each species (*p*-value <0.05) over 100 (*A. alosa*), 95 (*A. fallax*), 98 (*P. flesus*) and 86 (*C. ramada*) European catchments for which EuroDiad 4.0 had information on population functionality over the period "2011 to present time".

Along the European Atlantic coast, recommendations for anadromous species were mainly for "#4 - Reinforce climate mitigating for other species" (Table S3; Fig. 3). For *A. alosa*, it reached 72.0 % of the studied catchments and 36.8 % for *A. fallax*. Followed by "#1 - Need for scientific progress" (i.e., 16.0 % for *A. alosa* and 16.9 % for *A. fallax*) recommendations, which revealed inconsistencies between population functionality and suitability of continental and/or marine environments.

For catadromous species, "#1 - Need for scientific progress" was mostly recommended (Table S3; Fig. 3) when considering the overall options at the Atlantic area scale. For *P. flesus*, it reached 60.2 % of the studied catchments and 45.3 % for *C. ramada*. Then, "#3 - Maintain or decrease mortality" represented 30.6 % of the management guidance options for *P. flesus* that revealed the functionality of the populations in many European catchments and the constant coherency in habitat suitability. For *C. ramada*, "#4 - Reinforce climate mitigating for other species" reached nonetheless 27.9 %.

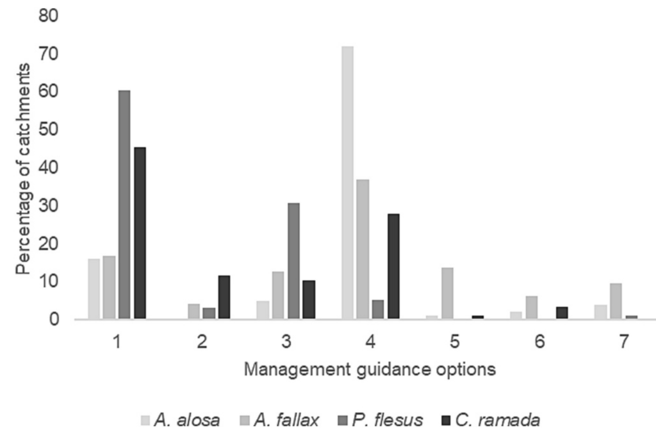

Fig. 3. Summary of the management guidance options categories' distribution by species. The management guidance options were as follows: (1) Need for scientific progress, (2) Continue/implement initiatives (short term) and prepare to amend, (3) Maintain or decrease mortality, (4) Reinforce climate mitigating for other species, (5) Intensify or prepare management plans to anticipate better future conditions, (6) Investigate why the species is absent and evaluate interest in mortality reduction (short term), and (7) Investigate why the species is absent and reduce mortality (short and long terms).

3.3. Management guidance options for the four diadromous species at the catchment and population levels

Meetings with experts to evaluate models' confidence revealed an

Table 4

Management guidance options in four pilot catchments for the four diadromous species (see Table 3 for"Green"/"Red" categorisation). 0, 1 and ? refer to the agreement between models' outputs and experts' knowledge. 1 means agreement, 0 disagreement and ? difficulty to express an opinion. A value between brackets after a question mark means that experts are not sure but would instinctively go for this value.

		Alosa alosa	*Alosa fallax*	*Platichthys flesus*	*Chelon ramada*
Mondego	Current population functionality	1	1	1	1
	Current continental suitability	? (0)	1	1	1
	Current marine suitability	? (1)	? (0)	?	?
	Future continental suitability	?	1	1	1
	Future marine suitability	?	?	?	?
	Management guidance options	*Need for scientific progress*	*Need for scientific progress*	*Need for scientific progress*	*Need for scientific progress*
Garonne	Current population functionality	1	1	1	1
	Current continental suitability	1	1	1	1
	Current marine suitability	1	1	1	1
	Future continental suitability	1	1	1	1
	Future marine suitability	1	1	1	1
	Management guidance options	*Maintain or decrease mortality*	*Maintain or decrease mortality*	*Maintain or decrease mortality*	*Maintain or decrease mortality*
Scheldt	Current population functionality	1	1	1	1
	Current continental suitability	? (1)	1	1	1
	Current marine suitability	?	?	?	?
	Future continental suitability	?	1	1	1
	Future marine suitability	?	?	?	?
	Management guidance options	*Reinforce climate mitigating for other species*	*Maintain or decrease mortality*	*Continue initiatives (short term) and prepare to amend*	*Need for scientific progress*
Three-Sis-ters	Current population functionality	1	1	1	? (1)
	Current continental suitability	? (0)	1	1	1
	Current marine suitability	?	1	? (0)	?
	Future continental suitability	?	1	1	1
	Future marine suitability	?	?	?	?
	Management guidance options	*Reinforce climate mitigating for other species*	*Continue initia-tives (short term) and prepare to amend*	*Need for scientific progress*	*Need for scientific progress*

overall consistency between model predictions and experts' expectations (Table 4). Explicit disagreements between models and experts were not registered. Nonetheless, experts expressed more difficulties in assessing the suitability of the marine environment for diadromous species (i.e., interrogation marks in Table 4). This comparison also reveals difficulties for experts to anticipate climate change effects (mainly because of the lack of knowledge on the effects of environmental factors on species and of their potential interactions).

In the Mondego and Garonne rivers, management guidance options were consistent across the four species. In the Mondego River, the management guidance option was "#1 - Need for scientific progress". For *A. fallax*, *P. flesus,* and *C. ramada*, the current marine environment was calculated as "Red" and for *A. alosa*, the current continental environment was also classed as "Red" by the model, despite functioning populations in the catchment for the four species. The experts were too uncertain to firmly disagree with these model outcomes, but they would have classified the continental habitat suitability of the Mondego "Green" for *A. alosa* and the marine one "Green" for *A. fallax*. The reasons for these inconsistencies might be important to be understood before planning further management measures as the counter-intuitive outcomes of the models may reflect important biological or environmental features to decipher. For the Garonne River, as both current and future marine and continental environments were calculated as "Green" without any disagreements or doubts from experts, the management guidance option was "Maintain or decrease mortality". The current management strategy seemed to be appropriate in terms of habitat coherency for the four species of interest and climate change did not appear to be a major threat for the diadromous species habitats.

In the Scheldt River, management guidance options differed between species. For *A. alosa*, which was absent from the catchment (i.e., the species disappeared in the early 20th century; Pauwels pers. comm.), with current and future continental environments without anthropogenic pressures that were "Green" associated to "Red" current and future marine environments, the option was "#4 - Reinforce climate mitigating for other species". Actions to favour specific species recolonisation were discussed as less of a priority since mitigation measures may be more beneficial to other species of interest in the region. For *A. fallax*, a functioning population with "Green" current and future marine and continental environments led to the management guidance option "#3 - Maintain or decrease mortality". For *P. flesus*, the management guidance option was "#2 – Continue/implement initiatives (short term) and prepare to amend" as the population was recorded as presently functioning with "Green" current continental and marine environments, but a marine environment that could become "Red" with climate. Thus, measures should anticipate this potential deterioration of habitat for the species. For *C. ramada* in both time periods, the marine environment was "Red" despite a functioning population and a "Green" continental environment without anthropogenic pressures. This inconsistency should be investigated before starting any new measure, the management guidance option was thus "#1 - Need for scientific progress". Contrary to the Mondego catchments, experts expressed doubts without raising any alternative hypothesis of habitat suitability for the Scheldt River.

Finally, management guidance options for the Three-Sisters River depended on the species. For *A. alosa*, all five categories were deemed "Red" for the species, the management guidance option was "#4 - Reinforce climate mitigating for other species". Without certainty, the experts would have classified the continental habitat suitability of *A. alosa* as "Green". For *A. fallax*, the option was "#2 – Continue/implement initiatives (short term) and prepare to amend" as the marine environment could become "Red" with climate and this possibility needs to be anticipated. For the two catadromous species, the option was "#1 - Need for scientific progress" as the population was recorded as functioning in the catchments, whereas the marine environment was indicated to be "Red". Again, with some uncertainty, the experts would have evaluated the marine suitability for *P. flesus* "Green".

4. Discussion

4.1. A tool supporting a change of perception on diadromous species management

Our approach demonstrates how the combination of information from literature, expert knowledge, and model outputs could improve the management of diadromous species in changing environments. By combining continental population functionality with continental and marine habitat suitability, in the present and the future, our framework integrates two main factors influencing species management that are not easily approached with "standard" methods. The complexity for applying spatio-temporal modelling frameworks (Thorson, 2019) to diadromous species resides mostly in how to take into account the physical connectivity between domains (Charsley et al., 2023). To our knowledge, our approach tries for the first time to join semi-quantitatively existing continental and marine habitat suitability outputs into a single framework for diadromous species. Hermoso et al. (2021) also highlighted the importance to study multiple realms including estuaries for conservation purpose. Note that applications without any information in transitional waters weaken the relevance of the framework, as this area in an essential habitat for migration and growth, especially for diadromous species. Furthermore, merging outputs from different sources to promote the debate on the management of species with a complex life cycle or in conflicting situations has occurred before. For example, to help managers in weighing up the pros and cons of conducting assisted migrations, Peterson and Bode (2021), proposed a decision tree using ensemble-modelling outputs to evaluate the impact of this management measure on recipient ecosystems.

Our framework uses outputs from marine and continental models generated separately to incorporate freshwater-sea interdependencies and potential impacts of climate change. In doing so, we wanted to facilitate collective learning in these growing research areas. As the proposed framework relies on large-scale species distribution models for data-poor species, their relevance needs to be assessed before an application at a large scale. Using the checklist as proposed in Table 1, could help users that are not modellers in evaluating how cautious they should be with model outputs. Moreover, at a local scale, a validation by regional experts during focus group meetings included as an evaluation criterion of model validity in Table 2 could also re-align the framework classification. The statistical outputs presented in this work may evolve with the collection of new biological data and progress in modelling techniques, leading to possible changes in modelled outputs, and therefore management guidance options, in a targeted catchment. Population functionality can be debated when human actions are required for population sustainability (e.g. restocking programs; Lennox et al., 2021) and/or when it evolves thanks to the with actual management plan (e.g. Twaite shad in the Scheldt River). Consequently, the framework should be considered as a tool to generate debates/discussions on how best to locally manage diadromous species when considering climate change and oceanic dimensions, two topics often not associated in conservation studies. The framework was thus designed as a tool to gather the actors committed to diadromous species management and encourage them to integrate plural perspectives and representations of the same system.

4.2. A tool revealing a need for more evidence to support integrative management of diadromous species

The application of our framework on four specific catchments was debated with regional experts, both on the decision variable values used for their catchment and the management guidance options obtained. By this process, in the Scheldt River, the population status of *A. fallax* in the EuroDiad database was reviewed from « rare » to « common », leading to a population functionality classified as "Green". The Scheldt River is a great example of fish (Van den Bergh, pers. Comm.) and hyperbenthic community recovery (De Neve et al., 2020) in response to local management measures targeting water quality improvement (Van den Bergh et al., 2005). In this first stage of the decision tree, no other conflict between database entries and expert knowledge were noted. In cases where every decision variables had the same colors, almost no discussions arose among participants (e.g., in the Garonne River case study). When discrepancies occurred among decision variables, debates focused on methodological/technical aspects rather than ecological interpretations. Potential discrepancies between a « Green » population functionality and « Red » model output (e.g., all species in the Mondego River) raised questions about why the models turned the habitat to « Red », and particularly on which variables were included in the model. A need for identifying the "driver" variable(s) in a « Red » classification was highlighted by experts to support discussions (Table S4 summarises the suitability of each variable included in the marine model for each species). Except for *A. alosa* in the Mondego River, potential discrepancies occurred for the marine environment only. Elliott et al. (2023) noted the overall paucity of marine occurrences to calibrate the models and the potential problem of misidentifications (e.g. *P. flesus* with the *Pleuronectes platessa* or *A. fallax* with *A. alosa*) that could lead to weak estimations in some part of the species ranges. Along with other weaknesses listed in Tables 1 & 2, this lack of confidence in marine model outputs emphasizes the necessity of taking multiple paths in the decision tree for local analyses.

Environmental variables used to model the distribution of the marine environment and the buffer applied to calculate the suitability of the marine environment were also raised as critical methodological choices that could explain differences between experts' expectations and models outputs. Indeed, even where some recent studies have tracked diadromous species at sea (Davies et al., 2020), the use of the marine environment by diadromous species remains poorly understood (ICES, 2014; Wilson and Veneranta, 2019). This lack of knowledge in the marine phase was confirmed when asking the local experts to validate the models (Table 4). It showed that, in future applications, expanding the list of participants to include actors, not specialized in diadromous species but with a global understanding of the marine coastal environment dynamics (e.g., marine fishermen, marine protected area managers) might be relevant. As shown by Clarke et al. (2021), it is essential to identify the marine habitats used by diadromous species to limit anthropogenic impacts at sea. Distribution models are a tool for a better understanding of their distribution at sea and for anticipating the impacts of climate change, but it is important to assess the explanatory and predictive capacities of the models before their use in this framework. Thus, to be more intelligible, colour combinations between the different decision variables obtained from models should be presented as « the most likely scenario » for a given catchment and the starting point for discussions and debates around the freshwater-sea continuum and the impacts of climate change on the overall habitat suitability. To circumvent this issue around data paucity at sea, gathering an international database on diadromous catches and by-catches at sea could be a good solution but it would require strong transnational cooperation and data management plans. Other protocols for the collection of marine distributional data could be considered (e.g. tagging, telemetry and/or eDNA). It would be helpful to apply these methods at a local level to inform on catadromous spawning areas and on growth aggregations for anadromous species at sea.

4.3. A tool to be deployed for other diadromous species and contexts

For the four case study species, a high level of discrepancies between current habitat suitability emerged at the Atlantic Area scale (i.e., the categories "#1 - Need for scientific progress" and "#4 - Reinforce climate mitigating for other species" had the highest percentages). When decision variables agreed, it reveals a low impact of climate change for the four species (i.e., the categories "#2 – Continue/implement initiatives (short-term) and prepare to amend" and "#6 - Implement or intensify short-term management plans" showed low scores). Those broad insights at the European level could be used in ICES Working Groups (e.g. WGDIAD for diadromous species; Wilson and Veneranta, 2019), future species status assessments at ICES (WKLS; Almeida & Rochard, 2015) and OSPAR (https://oap.ospar.org/en/ospar-assessments/), for improved understanding of climate change impacts and highlighting the need for more studies/interest on the freshwater-sea continuum for these species. The present work was limited to four species but the rest of the North-Western Atlantic assemblage of diadromous species could be analysed using the proposed framework (i.e., Atlantic salmon, sea trout, river lamprey, sea lamprey, Atlantic sturgeon, European smelt, European eel). On the other side of the Atlantic, our framework could be used for the ASMFC American Shad Benchmark Stock Assessment (ASMFC, 2020) as all the required data and parameters are available for *Alosa sapidissima*, including continental and marine models (Poulet et al., Under review; Lynch et al., 2015). Given the general interest of the U.S. scientific community on upscaling the species management to regional levels, including climate change impacts (Ouellet et al., 2022; Kritzer et al., 2022), our framework could be adapted to existing data or match ongoing work on diadromous fish distributions.

CRediT authorship contribution statement

CD, PL and GL conceived the research idea; CD ran data analyses and wrote the manuscript; and CD, PL, GL, SE, JB-P, CM, CO, IP, RP, WR, EVdB, JV, GC participated in discussions of the results and critically reviewed the manuscript.

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

The authors do not have permission to share data.

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Appendix A. Supplementary data

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