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## Modelling the distribution of rare and data-poor diadromous fish at sea for protected area management

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50 Given the coastal distribution of these species, they are exposed to higher  
51 anthropogenic pressures from both terrestrial and marine environments. Risk of  
52 bycatch at sea for most species appears to be low. Nonetheless, for threatened  
53 individuals, even a small amount of bycatch may impact their populations,  
54 especially since misreporting is likely to be high. Differences in catchability  
55 between gears highlight potential benefits of limiting access of certain gears within  
56 protected areas to reduce bycatch.

57  
58 **Key words:** Species Distribution Model, diadromous fish, rare species, imperfect  
59 detection, Marine Protected Areas, bycatch.

60

## 61 1. Introduction

62 Diadromous fish undertake long distance migrations between freshwater and  
63 marine ecosystems during their varying life history stages (Lassalle et al., 2008;  
64 Legrand et al., 2020; Limburg and Waldman, 2009; McDowall, 2009). They are  
65 particularly vulnerable since they are subject to both terrestrial and freshwater  
66 pressures (e.g., terrestrial run-off, pollution, habitat destruction, barriers to  
67 migration, climate change, fishing, etc.) (Costa et al., 2021; Limburg and  
68 Waldman, 2009; Merg et al., 2020; Verhelst et al., 2021). Furthermore, unlike  
69 many marine fish that are geographically widespread, numerous anadromous fish  
70 (e.g., shad and salmonids) form river-specific populations that are more  
71 susceptible to extinction (Limburg and Waldman, 2009; McDowall, 2009). As a  
72 result, most diadromous species native to the northern Atlantic Ocean have  
73 declined in abundance by at least 90% since the end of the late 19<sup>th</sup> century  
74 (Drouineau et al., 2018; Limburg and Waldman, 2009; Waldman and Quinn, 2022).

75  
76 To try and halt the loss of diadromous fish populations, various International  
77 Agreements (e.g., Bern Convention, Convention of Migratory Species) and  
78 legislations (e.g., EU Habitat Directive, EU Marine Strategy Framework Directive  
79 (MSFD)) have been enacted (Table 1). Measures implemented focus principally on  
80 freshwater or estuarine habitats, such as restoration of river continuity as required  
81 by the EU Water Framework Directive (WFD, 2000/60/EC) and freshwater Spatial  
82 Areas of Conservation under the Habitat Directive (HD, 92/43/EEC). However, most  
83 diadromous species remain threatened at a national level  
84 ([www.nationalredlist.org](http://www.nationalredlist.org); Table 1), and the improvements have yet to be attained  
85 throughout their range (Verhelst et al., 2021; Waldman and Quinn, 2022; Wilson  
86 and Veneranta, 2019). The marine life history stages and at-sea distribution of  
87 diadromous fish, largely remain a black box (Elliott et al., 2021), causing difficulty  
88 in evaluating their conservation status required under the various legislations that  
89 protect these species (Table 1; Wilson and Veneranta, 2019). Furthermore, few  
90 Marine Protected Areas (MPAs) have been designated to protect them (e.g.,  
91 <https://mpa.ospar.org>; <https://natura2000.eea.europa.eu>), and at-sea bycatch is  
92 not well understood, even if it is suspected that it could contribute to significant  
93 mortality (Kappel, 2005; Stratoudakis et al., 2016; Verhelst et al., 2021; Wilson and  
94 Veneranta, 2019).

95  
96 Under the EU data collection framework, Member States are required to collect  
97 fisheries bycatch data through an onboard observer program (Cornou et al., 2015).  
98 Fisheries data is a rich set of information which provides year-round catch  
99 information and can be a valuable source of information for data-deficient species  
100 (e.g., Baum et al., 2003; Bisch et al., 2022; Elliott et al., 2020b). Bycatch data for  
101 protected species can be difficult to access, therefore fisheries observer data could  
102 help understand the distribution and bycatch mortality of data-poor species and  
103 meet EU Habitat Directive and MSFD (92/43/EEC; 2008/56/EC) requirements. Use  
104 of fisheries data does, however, require biases from the different gear types, the  
105 targeted nature of fishing, and un-balanced sampling to be taken into consideration  
106 (e.g. Alglave et al., 2022; Bourdaud et al., 2017).

107  
108 Species Distribution Models (SDMs) provide a means to ‘fill in the gaps’ and provide  
109 complete coverage maps on which to base conservation and management decisions  
110 (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000; Leathwick et al.,

111 2005). Modelling the distribution of diadromous fish could help improve protection  
112 measures for threatened and data-poor (insufficient biological information to  
113 determine the current exploitation status (Berkson and Thorson, 2015; Prince and  
114 Hordyk, 2019)) diadromous fish within existing MPAs. SDMs could also be used to  
115 meet Descriptor 1 (Biodiversity - habitat extent) requirements under the MSFD  
116 (2008/56/EC). However, building diadromous fish at sea distribution models  
117 remains challenging because most of these fish are either IUCN red listed at a  
118 national level ([www.nationalredlist.org](http://www.nationalredlist.org)) or data-poor (Limburg and Waldman, 2009;  
119 Merg et al., 2020). Modelling the distribution of data-poor and rare species, can  
120 lead to underestimation of their true distribution due to imperfect detection  
121 (uncertainty in the presence of a species within a site where the data was  
122 recorded) (Guillera-Arroita, 2017; MacKenzie et al., 2002).

123  
124 To model rare and data-poor species' distribution, specific statistical methods are  
125 required to combine several sources of data that may not be initially designed to  
126 study the species distribution (Engler et al., 2004; Lomba et al., 2010; Simmonds et  
127 al., 2020). Using such data requires correction for detection bias arising from  
128 observer error, species rarity and variability in environmental conditions (Guillera-  
129 Arroita, 2017; Kellner and Swihart, 2014; MacKenzie et al., 2002) to help determine  
130 sites where the probability of presence of species is higher (Belmont et al., 2022).  
131 The low detectability of rare species can also result in a high proportion of false  
132 absences (Guillera-Arroita, 2017). Spatial and temporal variation in observation  
133 effort is another important source of heterogeneity in the observations (Guillera-  
134 Arroita, 2017; Kellner and Swihart, 2014; Meyer et al., 2011). Integrated  
135 hierarchical statistical model for species distributions have a great potential to  
136 combine multiple sources of data to infer a single latent field of abundance or  
137 presence/absence, and to enhance rare species distribution models for  
138 conservation and management purposes (Engler et al., 2004; Lomba et al., 2010;  
139 Simmonds et al., 2020). Another common problem which can arise when modelling  
140 species distribution is that data can be autocorrelated (more similar when closer  
141 together). Residual spatial autocorrelation can arise from population demographic  
142 processes or the influence of unobserved variables. Ignoring spatial autocorrelation  
143 can lead to inaccurate parameter estimations (Latimer et al., 2006). Developing  
144 models that explicitly account for spatial autocorrelation in the latent field of  
145 presence/absence is, therefore, necessary for accurate inferences on the  
146 distribution.

147  
148 Given the lack of knowledge on the distribution of most diadromous fish during  
149 their marine life history stages, and the need to ensure they are sufficiently  
150 protected, our objective was to model the current distribution (2003-2019) of  
151 diadromous fish at sea. In addition, we wanted to quantify the risk of bycatch from  
152 different gear types and assess the value of Habitat Directive MPAs for their  
153 conservation. Since at sea targeted surveys do not exist for these species, we  
154 collated a database of 168 904 hauls from fisheries dependent (French fisheries  
155 bycatch observer data) and independent data (scientific survey data undertaken to  
156 assess fish populations) in eastern Atlantic and French Mediterranean waters. A  
157 Bayesian site-occupancy model, taking into account spatial autocorrelation in the  
158 probability of presence, and imperfect detection through gear type, was used for  
159 these data-poor species (Dormann et al., 2007; Latimer et al., 2006; MacKenzie et  
160 al., 2002; Moriarty et al., 2020). From the distribution models we wanted to

161 answer the following questions: 1) Is the distribution of diadromous fish at sea  
162 connected to existing knowledge on their freshwater habitats? 2) Do different gears  
163 have different catchability, and does this provide information on the risk of  
164 bycatch of diadromous fishes? 3) Could existing Habitat Directive MPAs protect  
165 diadromous fish if specific measures are implemented?

166 **Table 1.** Diadromous fish observed within north-eastern Atlantic waters and their IUCN conservation status. A = Anadromous, C =  
 167 Catadromous, - = not listed, CR = Critical, LC = Least Concern, VU = Vulnerable. Demersal species are found near the seabed,  
 168 pelagic species occur in the open sea, demerso-pelagic species are species that migrate between these two water column zones,  
 169 host dependent refers to lampreys that are parasitic species during their marine phase. ✓ = protected under the specific  
 170 convention or Directive, letters specify the specific appendix the species is protected under.

Latin name	Common name	Type	Water column zone <sup>1</sup>	EU IUCN <sup>3</sup>	International conventions and legislation							
					CITES	WFD	HD	MSFD	Bern	Bonn	OSPAR	Barcelona
<i>Acipenser sturio</i>	Atlantic sturgeon	A	Demersal	CR	AI	✓	II, IV	✓	III	I, II	✓	✓
<i>Alosa alosa</i>	Allis shad	A	Pelagic	LC	-	✓	II, V	✓	III	-	✓	-
<i>Alosa fallax</i>	Twait shad	A	Pelagic	LC	-	✓	II, V	✓	III	-	-	-
<i>Alosa agone</i>	Mediterranean twaite shad	A	Pelagic	LC	-		II, V	✓	III	-	-	✓
<i>Anguilla anguilla</i>	European eel	C	Demerso-pelagic	CR	All	✓	-	✓	-	-	✓	✓
<i>Lampetra fluviatilis</i>	River lamprey	A	Host dependent	LC	NA	✓	II, V	✓	III	-	-	✓
<i>Petromyzon marinus</i>	Sea lamprey	A	Host dependent	LC	-	✓	II	✓	III	-	✓	✓
<i>Chelon ramada</i> *	Thinlip mullet	C	Demersal <sup>2</sup>	LC	-	✓	-	-	-	-	-	-
<i>Osmerus eperlanus</i>	Smelt	A	Pelagic	LC	-		-	-	-	-	-	-
<i>Platichthys flesus</i>	European flounder	C	Demersal	LC	-		-	-	-	-	-	-
<i>Salmo salar</i>	Atlantic salmon	A	Pelagic	VU <sup>4</sup>	-	✓	II, V	✓	III	-	✓	-
<i>Salmo trutta</i>	Sea trout	A	Pelagic	LC	-	✓	-		-	-	-	-

171 <sup>1</sup> Elliott and Dewailly, 1995; <sup>2</sup> Almeida, 1996; <sup>3</sup> Freyhof and Brooks, 2011; <sup>4</sup> Nieto et al., 2015 \*previously known as *Lisa ramada*.



## 172 2. Method

### 173 2.1. Combining fisheries independent and dependent surveys

174 Fisheries dependent and independent data from 1965 to 2019 were collated within  
175 eastern Atlantic waters (Greater North Sea, Celtic Sea, Bay of Biscay and the  
176 Iberian coast) and French Mediterranean waters). Scientific bottom trawl surveys  
177 were extracted from the International Council for the Exploration of the Sea (ICES)  
178 Database of Trawl Surveys (DATRAS) portal ([https://www.ices.dk/data/data-  
179 portals/Pages/DATRAS.aspx](https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx); Refer to Elliott et al., 2021 Table S1; Data in brief  
180 Table S1 - S2) and French Metropolitan scientific surveys not submitted to ICES  
181 DATRAS were obtained from the Institut Français de Recherche pour l'Exploitation  
182 de la Mer (IFREMER) (<https://campagnes.flotteoceanographique.fr/campaign>).  
183 Fisheries-dependent data came from French fisheries observer data (ObsMer data;  
184 Cornou et al., 2015) that began in 2003. According to the sampling plan, fisheries  
185 observers sample fishing vessels and fishing operations when on board (Fauconnet  
186 et al., 2015). ObsMer data is held by IFREMER and available on request from the  
187 French Ministry of Fisheries and Aquaculture (Direction des Pêches Maritimes et de  
188 l'Aquaculture; Refer to Elliott et al, 2021 Table S1; Data in brief Table S1).

189  
190 From the database, diadromous fish presence and absence, length, gear type,  
191 spatial location and year and month of capture were extracted (Fig. 1; Fig. S1).  
192 Due to missing data and insufficient information on the length of hauls, size of  
193 vessels, mesh size, etc., effort was not possible to calculate. Details of gear types  
194 and surveys that were used for the analysis can be found within the supplementary  
195 materials of Elliott et al., (2021).

196  
197 Prior to model analysis significant data cleaning was undertaken to standardise the  
198 surveys and extract relevant data to perform statistical analysis (e.g., converting  
199 gear types to gear categories, converting alike variables to the same units, etc.;  
200 see details within the Data in brief; Appendix A). Data from 2003 were used for  
201 spatial analysis, since a large proportion (74%) of the data came from the ObsMer  
202 dataset which started in 2003. In addition, prior to this data few presences were  
203 observed.

204  
205 Since the proportion of zeros to presences was very uneven, which is not ideal for  
206 predictive modelling (Fielding and Bell, 1997), all surveys, gear types, target  
207 species (the intended catch for a particular fishery - from the ObsMer dataset) and  
208 ICES statistical divisions (Fig. 1) without diadromous fish presence, were deleted  
209 before modelling (Fig. S2 contains a spatial map of all hauls per gear type). Depths  
210 outside the ranges the species were observed were also removed. To avoid  
211 targeted fishing bias, all species that were targeted were removed. The latter  
212 included 2 European eels, *Anguilla anguilla*, 33 thinlip mullets, *Chelon ramada* and  
213 41 flat fish which may have included European flounders, *Platichthys flesus*  
214 presences. All species were modelled other than the European sturgeon, *Acipenser*  
215 *sturio* because of too few presences (11 presences from 2003 - 2019). Note, for *L.*  
216 *fluviatilis*, one individual was caught by Set Longline within the Bay of Biscay. Due  
217 to its isolated nature of this capture, this caused problems when modelling (over  
218 detection of the line caught individual). Line gear type was therefore removed  
219 from the hierarchical modelling process.

220

## 221 2.2. Environmental predictor variables

222 Six environmental variables were considered as potential predictors of the  
223 presence of diadromous fish (seabed depth; distance from coast; sediment type;  
224 salinity; net primary production; and sea surface temperature; Table 2; Fig. S3).  
225 Depth and distance from the coast are thought to indicate key diadromous fish  
226 migratory periods (Taverny et al., 2012; Taverny and Elie, 2001; Trancart et al.,  
227 2014). Salinity and temperature are known to have direct physiological effects on  
228 diadromous fish, and their changes can indicate migration timing (Arevalo et al.,  
229 2020; Trancart et al., 2014). Net primary production is the gross primary  
230 production by autotrophs over the rate at which they respire, which is a measure of  
231 marine ecosystem functioning (ERSEM, 2020). Sediment type can be considered a  
232 proxy for food availability and shelter (Elliott et al., 2016; Trancart et al., 2014).  
233 As of result of too few presences and less information on length than the presence  
234 of individuals, distribution changes in length at stage, seasonal life history stage  
235 migration, and changes in habitat occupancy over the years were not considered.

236  
237 To select the model of best fit, variables that were not collinear (Pearson's  
238 correlation coefficient < 0.5 or > -0.5 and a Variance Inflation Factor < 2) (Dormann  
239 et al., 2013) were kept. Depth and distance from coast, and sea surface  
240 temperature and net primary production were collinear. Since most species  
241 occupied a wide latitudinal range and seasonal or yearly temperature effects were  
242 not modelled, net primary production was used instead of sea surface  
243 temperature. To identify the model of best fit a backwards stepwise model  
244 selection process was undertaken, ensuring distance from coast and depth were not  
245 in the same model. The model with the lowest deviance information criterion,  
246 which includes a penalty factor for the number of parameters, was selected  
247 (Spiegelhalter et al., 2002).

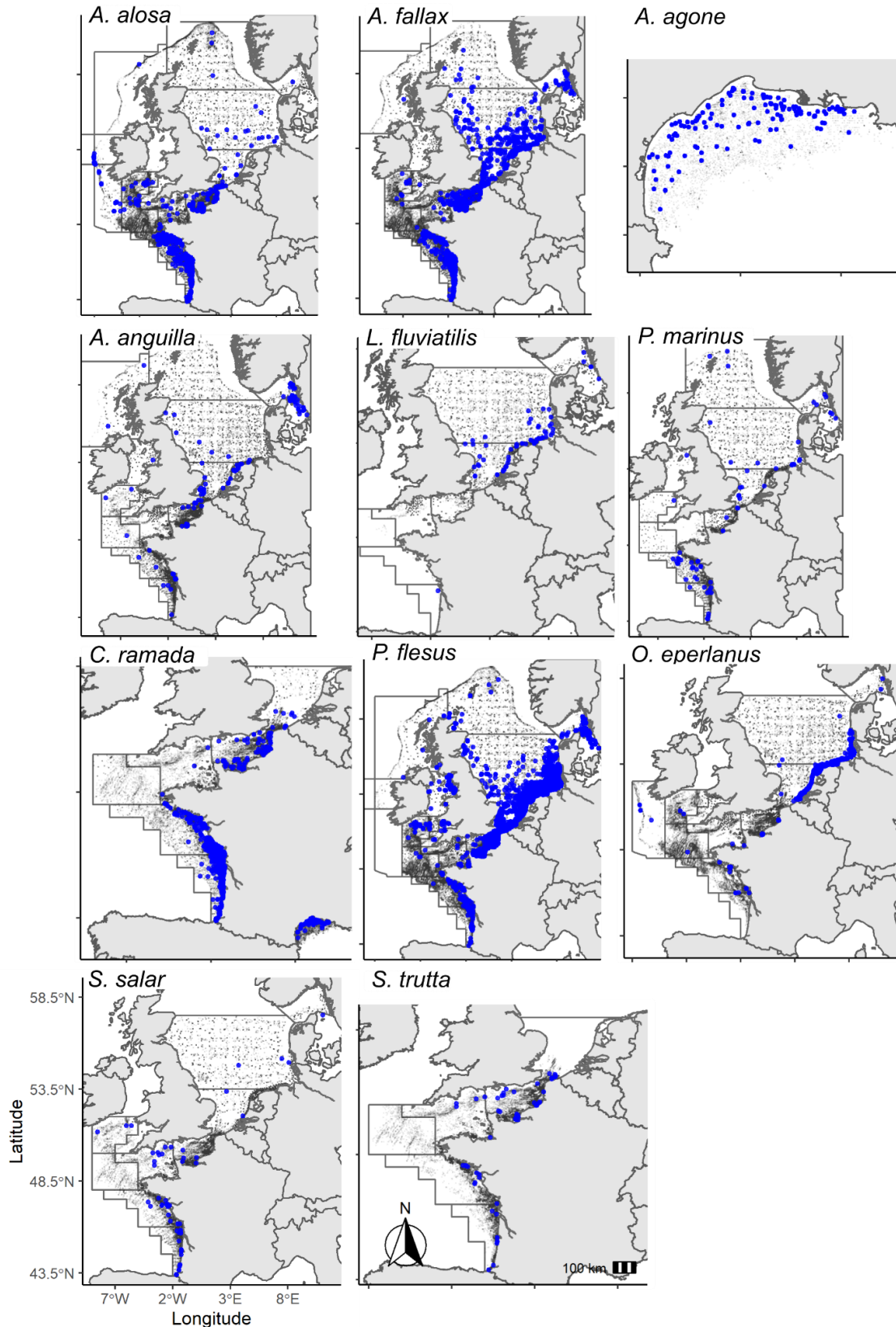
248  
249 **Table 2.** Environmental predictors used to analyse diadromous fish distribution. For  
250 all species except *Alosa agone*, variables were extracted at a 0.1 x 0.1 decimal  
251 degree resolution. *A. agone* environmental variables were extracted at a 0.04  
252 decimal degree resolution.

Variable	Unit	Description / Source
Depth	Meters (m)	Bathymetry data downloaded from National Aeronautics and Space Administration Earth Observations project ( <a href="http://neo.sci.gsfc.nasa.gov">http://neo.sci.gsfc.nasa.gov</a> ) with a 0.1 x 0.1 grid cell resolution by using the General Bathymetric Chart of the Oceans grid.
Distance to coast	Kilometres (km)	Calculated from a continent shape file
Sediment	Categorical	Broad-scale seabed habitat types (EUSeaMap) downloaded from EMODnet. Four classes were used according to grain size: mud ( $\leq 2$ mm), sand ( $> 2$ and $\leq 4$ mm), coarse grain ( $> 4$ mm and $\leq 64$ mm), and rock ( $> 64$ mm).
Salinity	Practical Salinity Units (PSU%)	Modelled sea surface salinity at 0.1 x 0.1 decimal degree resolution downloaded from Copernicus (ERSEM, 2020).

Net primary production	Milligrams of carbon per meters squared (mg C/m <sup>2</sup> )	Modelled at 0.04 x 0.04 decimal degree resolution from Copernicus using Teruzzi et al., (2021). Modelled net primary production at 0.1 x 0.1 decimal degree resolution downloaded from Copernicus (ERSEM, 2020). Modelled at 0.04 x 0.04 decimal degree resolution from Copernicus using Teruzzi et al., (2021).
Sea surface temperature	degrees centigrade (°C)	Modelled Sea surface temperature at 0.1 x 0.1 decimal degree resolution downloaded from Copernicus (ERSEM, 2020). Modelled at 0.04 x 0.04 decimal degree resolution from Copernicus using Teruzzi et al., (2021).

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**Fig. 1.** Diadromous fish presence (blue dots) and absence (light grey dots) data used to model their distribution (2003-2019). Dark grey lines indicate International Council for the Exploration of the Sea statistical divisions.

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### 2.3. Statistical analysis

A Bayesian hierarchical site occupancy Gaussian intrinsic Conditional Autoregressive (iCAR) model was built independently for each species. Hierarchical models have the advantages of separating the ecological process (here, the habitat suitability model, that is the spatial distribution of the probability of presence/absence, including spatial autocorrelation) from the observation process (here, the imperfect detection and its variability among gears or other factors) (Dormann et al., 2007; Isaac et al., 2020; Latimer et al., 2006; MacKenzie et al., 2002). The fundamental concept of the model is that the true presence/absence spatial field (including spatial autocorrelation) is modelled on a grid, each grid cell being associated with multiple observation events with imperfect detection, with detectability that may vary depending upon the fishing gear.

The site occupancy model integrates two processes:

i) Latent ecological process (habitat suitability)

The latent field of probability of presence is modelled on a grid as a function of environmental predictors and by explicitly accounting for spatial autocorrelation:

$$\text{logit}(\theta_j) = X_j\beta + P_j \quad (1)$$

with  $\theta_j$  the latent probability of presence (the habitat suitability) within grid cell  $j$ , modelled in the logit scale as a function of environmental predictors  $X_j$ , with  $\beta$  a vector of fixed effect describing how much the environmental predictor contribute to the suitability process. The spatial autocorrelation  $P_j$  is modelled at the scale of the grid cell as an iCAR random effect (2):

$$\text{iCAR: } P_j \sim \text{Normal}\left(\mu_j, \frac{V_p}{n_j}\right) \quad (2)$$

with  $\mu_j$  the mean of the random effects calculated over the  $n_j$  cells considered in the neighbour of cell  $j$  ( $n_j$  is the number of the neighbours which is 8 in most cases, and <8 when the cell is on the boundary of the spatial domain),  $V_p$  the variance of the spatial random effect. A site is defined here as the area/volume covered during a given sampling/fishing operation. Any site  $i$  within the cell  $j$  as the same latent probability of presence  $\theta_j$ .

ii) Observation process (detection):

Conditionally upon the latent probability of presence/absence in each grid cell  $j$  as describe above, the multiple detection events  $y_{j,i}$  (data 0/1) associated to the same grid cell  $j$  are modelled as mutually independent two steps Bernoulli process with detectability  $\delta_{j,i}$ :

$$y_{j,i} \sim \text{Bernoulli}(z_{j,i} \delta_{j,i}) \quad (2)$$

with

$$z_{j,i} \sim \text{Bernoulli}(\theta_j) \quad (3)$$

and

$$\text{logit}(\delta_{j,i}) = W_{j,i}\gamma$$

where  $\delta_{j,i}$  denotes the probability of detecting the species at site  $i$  within cell  $j$ , modelled as a fixed effect of the gear type associated with observation  $i$ .  $W_{j,i}$  is the raw vector of the design matrix, and  $\gamma$  is the vector of the gear effects, so as  $W_{j,i}\gamma$  is the gear affect associated with observation at site  $i$ .

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306 All SDMs were undertaken using the ‘hSDM’ package (Vieilledent et al., 2014) using  
307 the ‘mod.hSDM.siteocc.iCAR’ function in R version 3.6.3 (R Code Team 2018). The  
308 prior distribution for the variance of the spatial random effect followed weakly  
309 informative uniform distribution. The effect of the detectability from gear and  
310 from the suitability process was modelled as fixed effects drawn from an weakly  
311 informative Gaussian prior centred at zero with a fixed standard deviation of 2  
312 (Gelman et al., 2008; Northrup and Gerber, 2018). Each model was run with 50 000  
313 Gibbs iterations, five Markov chain Monte Carlo simulations and a burn-in phase of  
314 50 000 iterations.

#### 315 316 2.4. Grid size and spatial distribution

317 A critical issue in our modelling framework is the choice of the grid size. Since the  
318 latent field of presence/absence is modelled at the scale of the grid cell (eq. 1),  
319 the larger the grid resolution the higher the probability to get at least one  
320 presence within a grid cell. A finer grid cell will limit the quantity of available  
321 observations falling within each cell, which therefore increases difficulty in model  
322 fitting. We selected the finest grid as possible that allow the model to converge.  
323 For almost all species modelled within Eastern Atlantic waters, a grid of 0.1x0.1  
324 decimal degrees was used. Because of the scarcity of data for Lampreys, the model  
325 did not converge with such a resolution and a coarser resolution of 0.2x0.2 decimal  
326 degrees was therefore used for these species. For *A. agone*, that only occurs within  
327 the Mediterranean, a grid resolution of 0.04 x 0.04 decimal degrees was used  
328 because of the smaller area encompassed. This spatial resolution (0.04 x 0.04  
329 decimal degrees) was not used for other species since it was not available at the  
330 scale required within Eastern Atlantic waters. All environmental variables were  
331 then aggregated and modelled to their relevant spatial resolution. There were  
332 insufficient presences within the Mediterranean for *A. anguilla*, *P. marinus*, *C.*  
333 *ramada*, *P. flesus* predictions (issues with model convergence). Predictions within  
334 the Mediterranean for these were therefore excluded (Fig. 2).

#### 335 336 2.5. Model evaluation

337 The probability of presence was calculated from the mean of the posterior  
338 distribution of the latent field  $\theta_j$ . A threshold of 0.4 was used to bin estimated  
339 probability of presence into binary presence/absence values. A threshold of 0.4  
340 was used as a compromise given the rarity of the species and accuracy following  
341 examining various thresholds and plotting positive predicted values. The model  
342 performance was then evaluated using sensitivity (proportion of correctly classified  
343 presences), specificity (proportion of correctly classified absences) and percent  
344 correct classification (proportion of presences and absences correctly using the R  
345 package ‘PresenceAbsence’ (Freeman and Moisen, 2008a; Fielding and Bell, 1997;  
346 Table 3). Max sensitivity specificity which is often used for rare species distribution  
347 models (Freeman and Moisen, 2008b; Jiménez-Valverde and Lobo, 2007), was not  
348 used since false presences was very high when applying this metric. Additionally,  
349 our SDM objective was to try and minimise false presences and absences within the  
350 distribution models. The threshold independent Area under the receiver operating  
351 curve was also used to evaluate the model performance. These four metrics were  
352 used to better understand the accuracy of the model since, some metrics can be  
353 biased with low prevalence data and where imperfect detection can arise (Allouche  
354 et al., 2006; Fourcade et al., 2018; Guillera-Arroita, 2017; Leroy et al., 2018).

355  
356 So that areas with probabilities of presence above the threshold could be easily  
357 identified for management purposes, all predictions below 0.4 were mapped with a  
358 uniform light blue colour (Fig. 2). Uncertainty maps for each model were also  
359 produced to gauge a better idea of areas of prediction with higher uncertainty  
360 (Loiselle et al., 2003; Spiegelhalter et al., 2002). The uncertainty maps were  
361 calculated by the mean coefficient of variation from the posterior distribution of  
362 spatial parameters in the model of best fit for each species (Lambert et al., 2020;  
363 Latimer et al., 2006). Probabilities of prediction and uncertainty above 0.4 were  
364 classified into 0.2 units to highlight areas of higher and lower probability of  
365 presence more clearly (Fig. 2; Fig. S4). As a result of the low diadromous fish  
366 presence, splitting the data into learning/validation samples led to insufficient  
367 presence in the learning data set. Cross validation was therefore not undertaken.  
368

### 369 *2.6. Diadromous fish river basin presence*

370 The predicted distributions were visually compared to the distribution of  
371 diadromous fish within their freshwater habitats using the EuroDiad database  
372 (version 4; <https://data.inrae.fr/dataset.xhtml?persistentId=doi:10.15454/IVVAIC>;  
373 Barber-O'Malley et al., 2022). From EuroDiad database, migrating diadromous fish  
374 population presence within the study areas our model encompassed, were  
375 extracted using 'recent' literature citing from 1951 to 2020 (see Barber-O'Malley et  
376 al., (2022) and Béguer et al., (2007) for more details on the database) and mapped  
377 with the hierarchical SDM results (Fig. 2). The EuroDiad4 database was used as  
378 opposed to IUCN red list map distribution since it has been peer reviewed and it is  
379 more up to date.  
380

### 381 *2.7. Habitat Directive MPAs of relevance to diadromous fish*

382 'Core areas' with a probability of presence  $>0.4$  were selected and intersected with  
383 European Union Natura 2000 Habitat Directive Sites of Community Importance  
384 (<https://www.eea.europa.eu/data-and-maps/data/natura-12>). A threshold of  $> 0.4$   
385 probability of presence was selected as a result of the low probability of presence  
386 of diadromous fish (particularly Habitat Directive protected species), and to ensure  
387 consistency with the model evaluation threshold. Since only one Site of Community  
388 Importance was submitted to the European Union from the United Kingdom, Special  
389 Areas of Conservation were taken into consideration ([https://jncc.gov.uk/our-  
390 work/special-areas-of-conservation-overview/](https://jncc.gov.uk/our-work/special-areas-of-conservation-overview/)). For each species, the number of  
391 MPAs (Sites of Community Importance and Special Areas of Conservation) and the  
392 proportion of MPAs of relevance to diadromous fish (core areas within an MPA)  
393 were recorded. The extent of the core area within the MPAs was not calculated as  
394 this would be dependent of the model grid used (Table 3). Furthermore, numerous  
395 MPAs were smaller than the grid.  
396

## 397 **3. Results**

### 398 *3.1. Diadromous fish hierarchical SDM*

399 For all species the Area under the receiver operating curve and Percent Correct  
400 Classification performed very well ( $\geq 75\%$ ; Table 3). Correct presence classification  
401 from the confusion matrices was consistently lower ( $<15\%$ ) than that of correct  
402 absence classification ( $\geq 64\%$ ), and false absences were lower ( $\leq 3\%$ ) than false  
403 presences ( $\leq 22\%$ ) because of presence absence imbalance (Table 3; Table S1). The  
404 later led to on average better specificity than sensitivity scores (Table 3).

405

406 *P. flesus* was the most prevalent species modelled (5394 presences), whereas  
407 salmonids the least (*S. salar* = 68 presences and *S. trutta* 63 presences) (Table 3).  
408 SDMs that had lower presences (salmonids and lampreys) did not predict as well  
409 (lower sensitivity and higher uncertainty maps) as species with higher presence  
410 (shads, *C. ramada*, *P. flesus* and *O. eperlanus*). In addition, species that had a  
411 more disperse distribution (e.g., *A. anguilla* and *S. salar*) did not predict as well  
412 (sensitivity  $\leq 0.66$  for both species) as those with a more aggregated distribution  
413 (*O. eperlanus* sensitivity = 0.81) (Table 3; Fig. 1 and 2). Uncertainty maps showed  
414 that in general, areas of high and low predicted probability of presence had lower  
415 uncertainty (Fig. S4).

416

417 All species were observed to have a relatively shallow (<300m depth) coastal  
418 distribution (~<300 km from the coast; Fig. 2 and 3). The main predictor variables  
419 for diadromous fish habitats were depth or distance from coast and salinity (Fig. 3).  
420 Since sufficient *C. ramada* were observed within eastern Atlantic and  
421 Mediterranean waters to model, two salinity peaks are observed corresponding to  
422 the different salinity ranges of the two regions (Fig. 3).

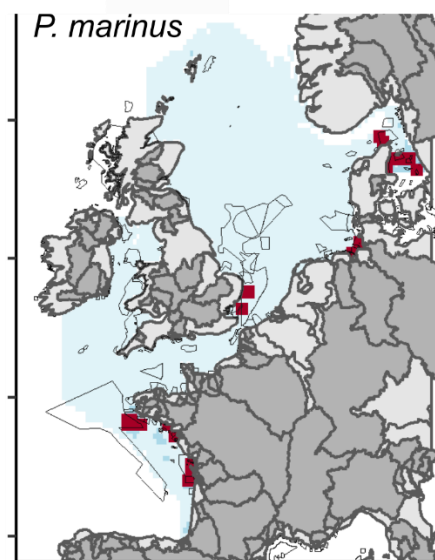
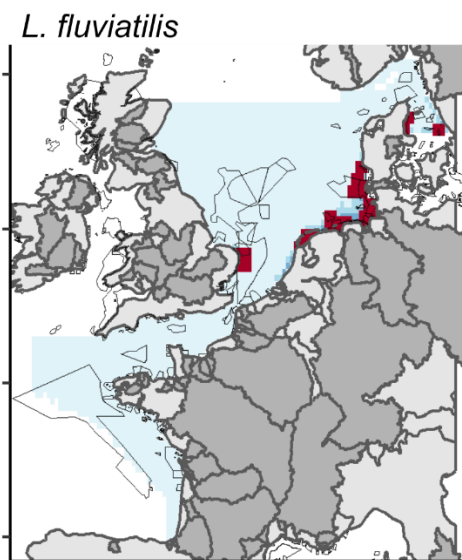
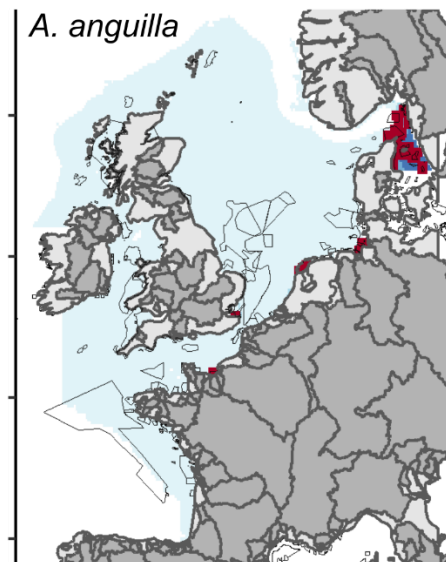
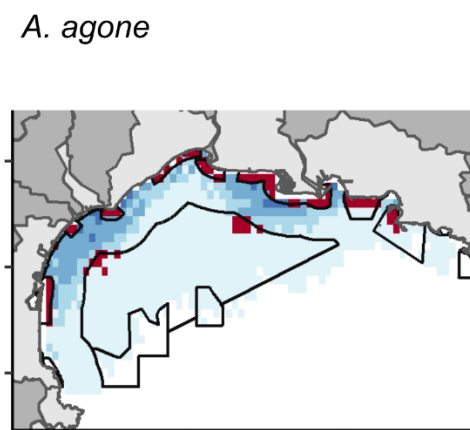
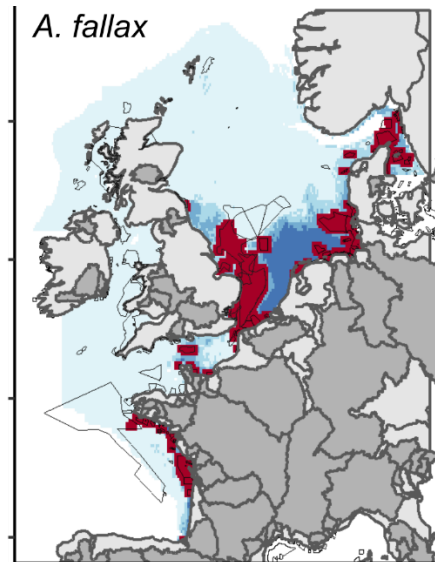
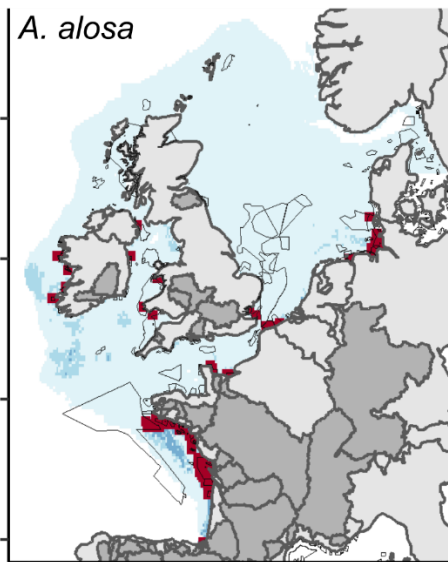
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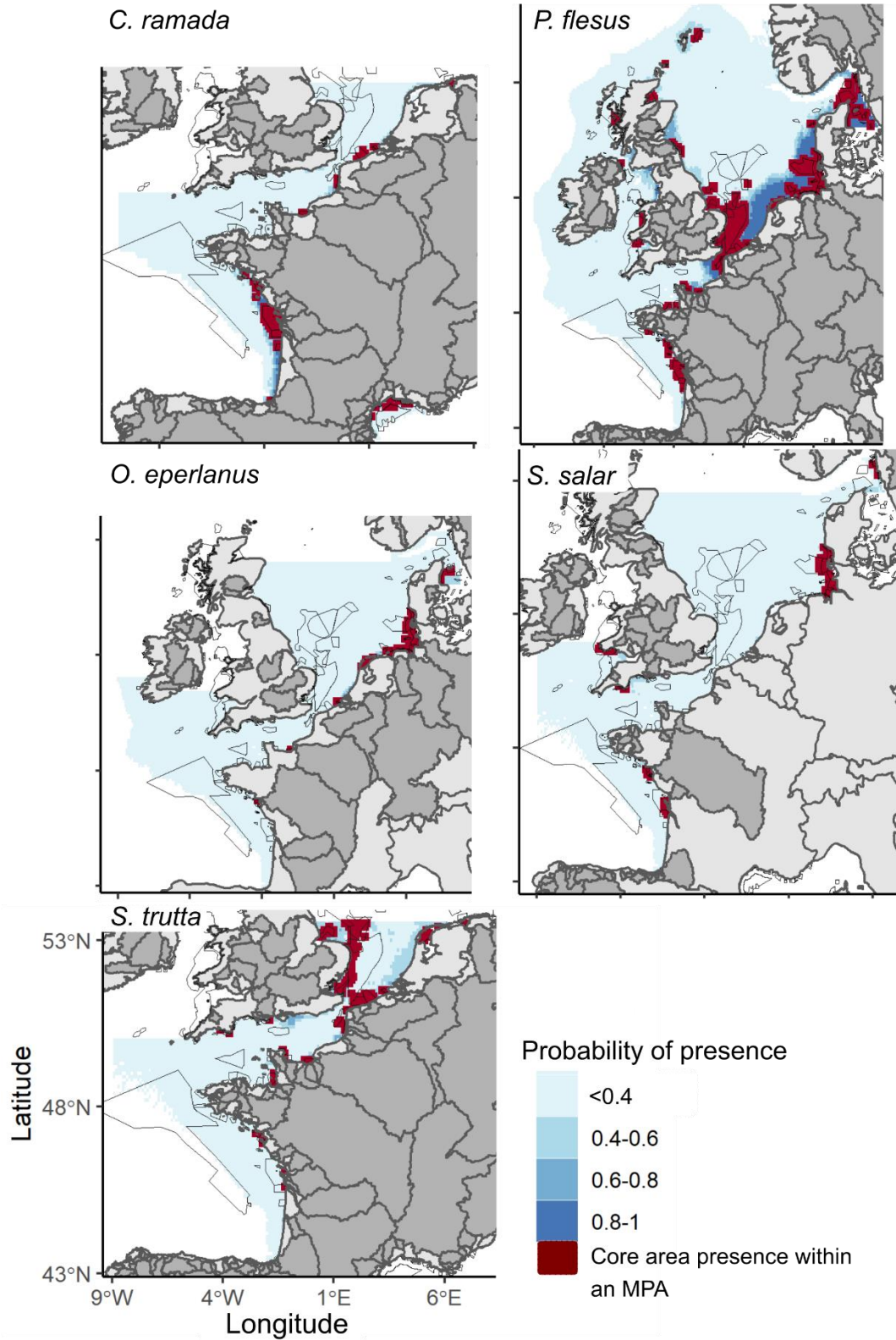


424 **Table 3.** Hierarchical species distribution model outputs. All models contained gear as part of the observation process. AUC =  
 425 Area Under the receiver operating Curve score, PCC = Percent Correct Classification, NetPP = Net Primary Production. Max depth  
 426 is the maximum depth at which the dataset was cut. Note most environmental variables (all except distance and depth) were  
 427 not available within very coastal areas (e.g., within estuaries and inlets). Numerous presences and absences were therefore lost  
 428 when extracting the environmental variables for modelling.

Species	Model selected	Hauls	Presence	Absence (%)	Max depth (m)	Sensitivity	Specificity	AUC	PCC	Cell size (decimal degrees)
<i>A. alosa</i>	Depth + Salinity + NetPP + Sediment	86 292	802	99	300	0.79	0.92	0.95	0.95	0.1x0.1
<i>A. fallax</i>	Distance + Salinity + NetPP + Sediment	91 135	1385	98	300	0.88	0.81	0.90	0.82	0.1x0.1
<i>A. agone</i>	Depth + Salinity + Sediment	5086	176	97	200	0.81	0.74	0.86	0.75	0.04x0.04
<i>A. anguilla</i>	Depth + Salinity + NetPP	54 124	176	99	250	0.53	0.99	0.98	0.98	0.1x0.1
<i>L. fluviatilis</i>	Distance + Salinity	16 536	68	99	150	0.71	0.95	0.96	0.94	0.2x0.2
<i>P. marinus</i>	Distance + Salinity	28 582	74	99	300	0.60	0.98	0.94	0.97	0.2x0.2
<i>C. ramada</i>	Distance + Salinity + Netpp + Sediment	53 083	925	98	300	0.84	0.93	0.96	0.92	0.1x0.1
<i>P. flesus</i>	Distance + Salinity + NetPP + Sediment	92 400	5394	94	300	0.90	0.93	0.97	0.93	0.1x0.1
<i>O. eperlanus</i>	Depth + Salinity + NetPP	48 877	1035	98	450	0.81	0.99	0.99	0.99	0.1x0.1
<i>S. salar</i>	Depth + Salinity + NetPP	36 008	68	99	150	0.66	0.98	0.95	0.98	0.1x0.1
<i>S. trutta</i>	Depth + Salinity + NetPP	31 754	63	99	150	0.71	0.94	0.93	0.93	0.1x0.1

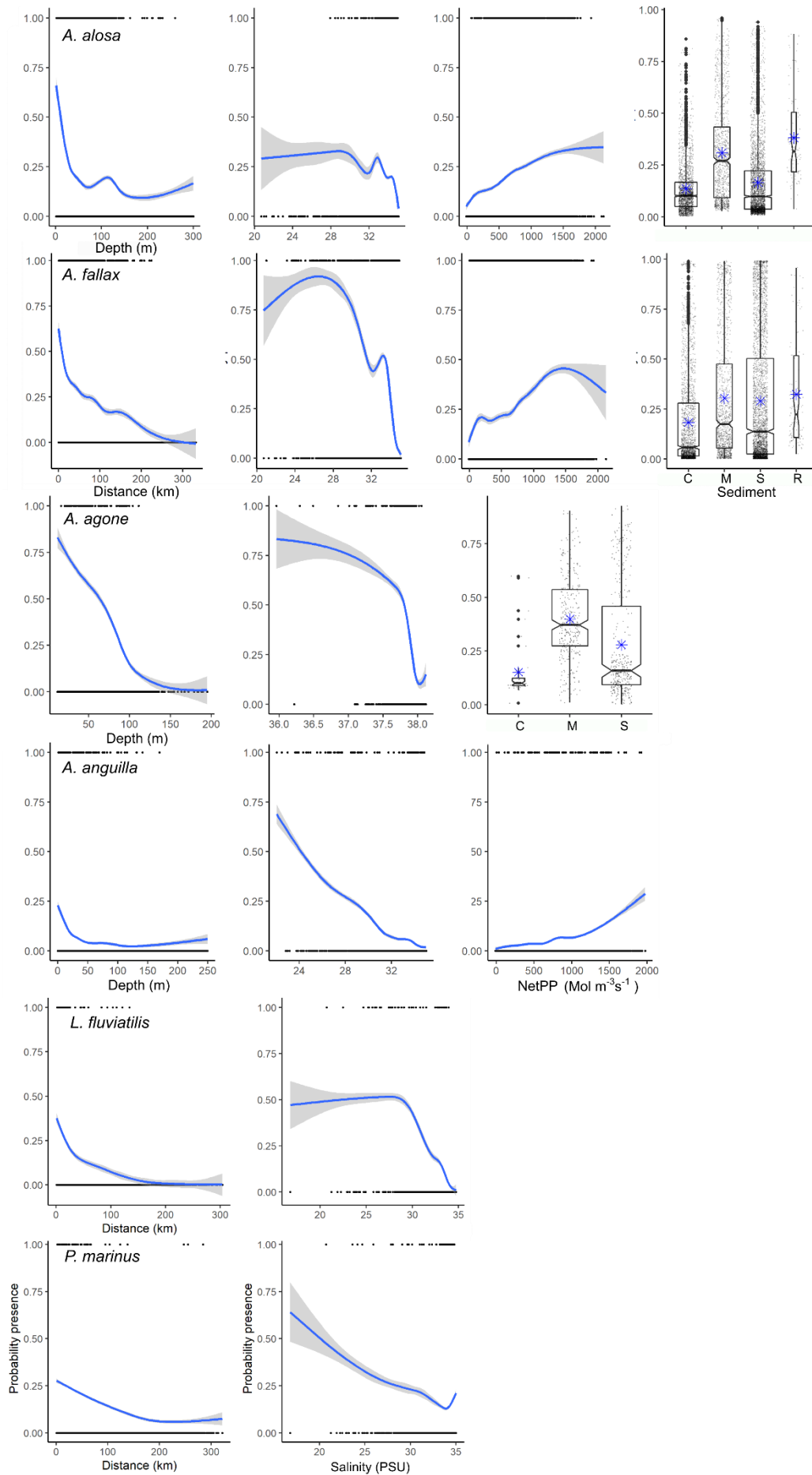
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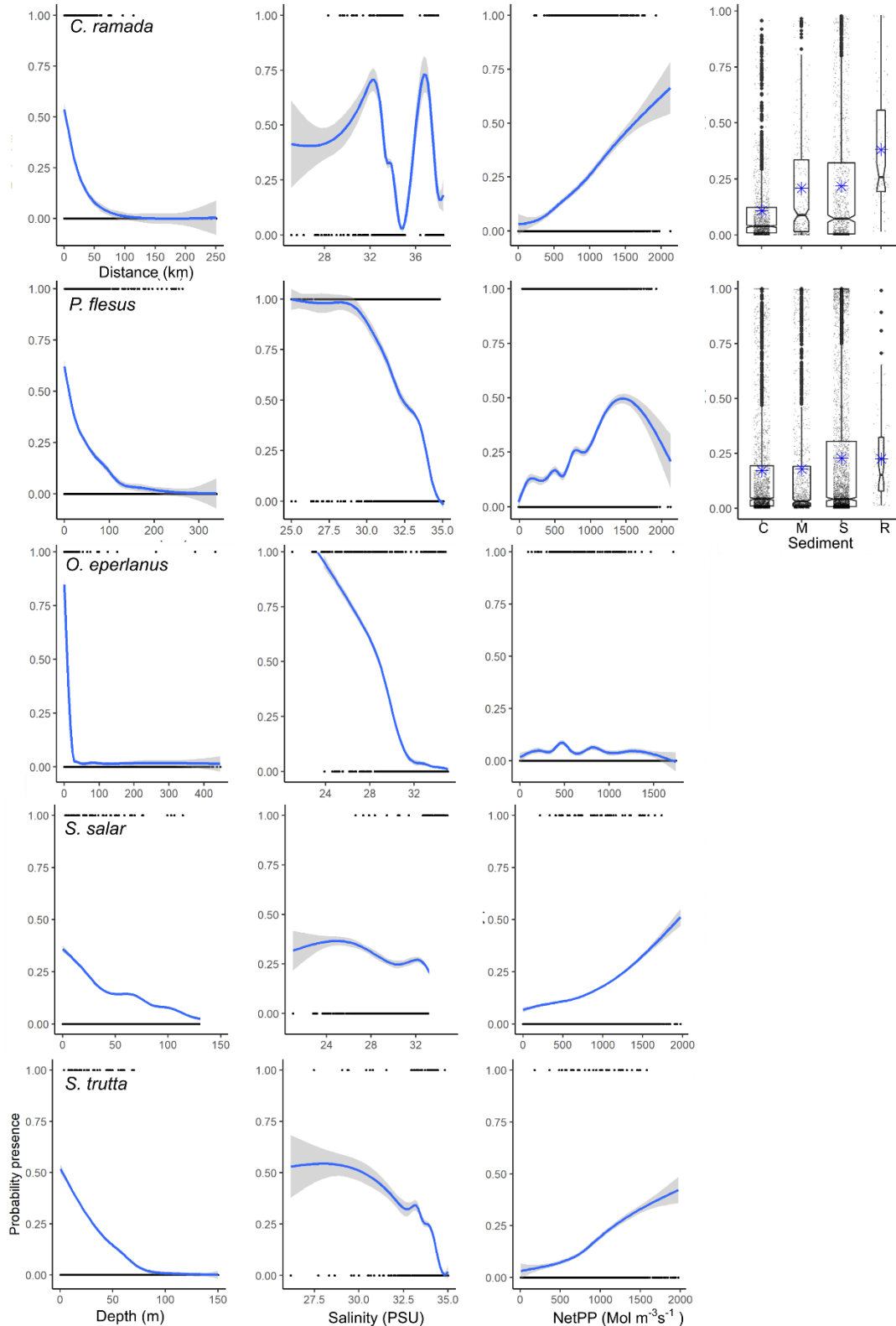




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433 **Fig. 2.** Diadromous fish hierarchical species distribution model probability of  
434 presence. Darker blue shades = SDM probability of presence > 0.4, light blue shade  
435 = SDM probability of presence  $\leq$  0.4. Habitat Directive Marine protected Areas  
436 (MPAs) outlined in black. MPAs of relevance to core (probability of presence > 0.4)  
437 diadromous fish distribution, highlighted in dark red. Dark red cells are larger than  
438 the gridded cells to ensure smaller core areas within MPAs are visible. Darker grey  
439 terrestrial areas represent river basins which the diadromous fish migratory  
440 populations have been observed (EuroDiad V.4). Note, no data were available  
441 within the EuroDiad database from Dutch river basins.





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**Fig. 3.** Diadromous fish hierarchical species distribution model environmental predictor effects. NetPP = Net Primary Production, C = Course grain, M = Mud, S = Sand, R = Rock. The solid line represents the smooth function estimate; the shaded region represents the approximate 95% credibility interval. Boxplot blue stars represent means and small black dots the predictions.

450       3.2. *Diadromous fish river basin connectivity*

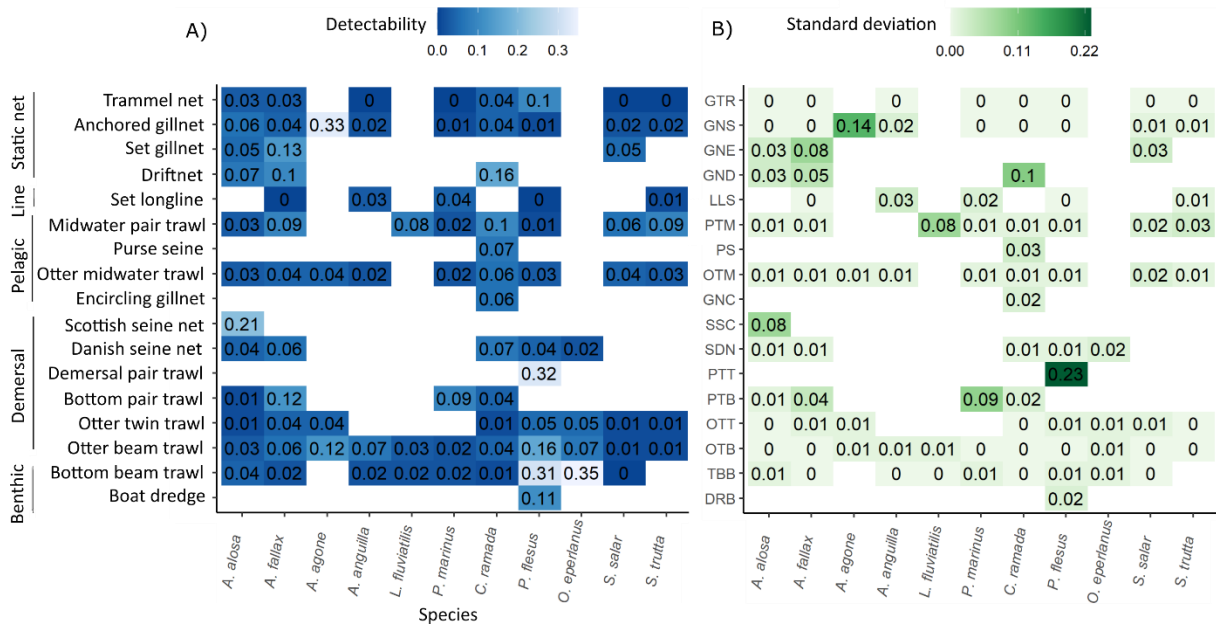
451 2717 references contained within the EuroDiad database were used to map the 11  
452 diadromous fish presence within the river basin. Core distributions of diadromous  
453 fish at sea largely matched with the freshwater areas of presence (Fig. 2). The  
454 spatial extent of diadromous fish at sea was often less than that observed within  
455 river basins (e.g., lampreys, *C. ramada*, *O. eperlanus* and *S. trutta*; Fig. 2). It  
456 should be noted that there are gaps in the EuroDiad database (refer to Barber-  
457 O'Malley et al., (2022)). For example, no diadromous fish presence data were  
458 available within Dutch freshwater habitats, and salmon populations are known to  
459 exist within Danish waters (de Groot et al., 2012; Maes et al., 2007; Rikardsen et  
460 al., 2021). Presences of *A. alosa* and *A. fallax* within the Mediterranean from the  
461 EuroDiad database will have been due to historic classification (Bagliniere and Elie,  
462 2000; Keith et al., 2020).

463

464       3.3. *Gear type detectability*

465 All species were caught by a range of gear categories ranging from benthic,  
466 demersal and pelagic mobile trawls, seine nets, line gear types (Fig. 4; Table S2).  
467 Some general patterns were, however, evident. Line gear types caught the least  
468 diadromous fish (2% (weighted), 17 presences over ~2887 hauls), whereas demersal  
469 mobile trawl gear types (otter beam trawl and otter twin trawl) caught the most  
470 (67%, 7409 presences over ~82 531 hauls; Fig. 4; Table S2). Shad had a higher  
471 detectability with static and demersal mobile gears. *A. anguilla* were detected by a  
472 wide range of gear types. Lamprey were mainly detected by mobile trawl gears. *P.*  
473 *flesus* and *O. eperlanus* had a higher detectability with demersal and benthic  
474 mobile gear, and salmonid had a higher detectability with static nets and pelagic  
475 gears. Rarer species and species that were caught by a wider range of gear types  
476 had lower detectability than more abundance species caught by fewer gear types  
477 (Fig. 4). On average static nets (e.g., trammel net and set gillnets) and pelagic  
478 mobile gears (e.g., Otter midwater trawls) caught larger diadromous fish than  
479 mobile demersal and benthic gear types (Fig. S1). Although the modelled species  
480 were not target species of the fisheries within the observer database, some species  
481 were landed (Table 4).

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**Fig. 4.** Matrix of the posterior mean (marginal posterior distribution) for gear A) detectability (inverse logit of  $\gamma$ ; the probability to detect the presence of fish when they are present) and B) its standard deviation. Lighter blue shades represent higher detectability (A) and darker green shades higher detectability standard deviation (B).

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**Table 4.** Landed and discarded diadromous fish from the ObsMer data. Excluding targeted catches. Proportion landed = total landed / landed + discards.

Species	Landed	Discard	Hauls	Proportion landed
<i>A. alosa</i>	182	515	70 378	0.26
<i>A. fallax</i>	152	608	64 300	0.20
<i>A. agone</i>	28	69	7373	0.29
<i>A. anguilla</i>	10	8	28 194	0.56
<i>L. fluviatilis</i>	0	2	828	0.00
<i>P. marinus</i>	2	18	10 030	0.10
<i>C. ramada</i>	643	101	45 699	0.86
<i>P. flesus</i>	856	648	66 196	0.57
<i>O. eperlanus</i>	6	45	31 311	0.12
<i>S. salar</i>	29	27	26 009	0.52
<i>S. trutta</i>	43	18	31 666	0.70

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### 3.4. Habitat Directive MPAs relevance

A total of 482 Habitat Directive MPAs have been designated within the area in which the species were modelled (Fig. 2). Despite the small area of core habitats relative to the model prediction area, for most Habitat Directive listed species, numerous MPAs overlap with species core habitats, indicating their potential for the protection of diadromous fish at sea (Table 5; Fig. 2).



500 **Table 5.** Habitat Directive Marine Protected Areas of relevance to core diadromous  
501 fish distribution (probability of presence >0.4). Diadromous fish listed under the  
502 Habitat Directive in bold.  
503

Species	Number MPAs of relevance	Proportion of MPAs of relevance
<i>A. alosa</i>	35	0.08
<i>A. fallax</i>	60	0.13
<b><i>A. agone</i></b>	10	0.27
<i>A. anguilla</i>	19	0.04
<i>L. fluviatilis</i>	11	0.02
<b><i>P. marinus</i></b>	14	0.03
<i>C. ramada</i>	23	0.05
<i>P. flesus</i>	65	0.15
<i>O. eperlanus</i>	13	0.03
<b><i>S. salar</i></b>	17	0.04
<i>S. trutta</i>	28	0.06

504

#### 505 4. Discussion

506 To our knowledge this is the first comprehensive study to model the distribution of  
507 diadromous fish at sea across eastern Atlantic and French Mediterranean waters.  
508 Using a hierarchical model allowed us to integrate an extensive database that we  
509 collated, containing both fisheries dependent and independent data to model the  
510 distribution of eleven rare diadromous fish over a wide spatial area. The model also  
511 enabled us to evaluate the probability to detect the presence of fish by the  
512 different gear types, and thus provide key information to evaluate the risk of  
513 bycatch of diadromous fish by commercial fisheries at sea.

514

515 Diadromous fish are bound to coastal areas because of their migratory behaviour.  
516 They are known to be fragile species because of the physiological and  
517 osmoregulatory changes required to undertake migrations between fresh water and  
518 marine environments (McDowall, 2009). Yet, coastal ecosystems, particularly  
519 within eastern Atlantic and Mediterranean waters, are subject to some of the  
520 highest anthropogenic impacts (Halpern et al., 2015; Korpinen et al., 2021; Lotze  
521 et al., 2006). Even though more data were collected within coastal areas, and the  
522 species are known to migrate from freshwater habitats, our study confirms that the  
523 investigated species were found to mainly concentrate in coastal and relatively  
524 shallow waters. The strong dependency of diadromous fish species to coastal areas,  
525 as evidenced in this study, reinforces the importance of investigating the  
526 vulnerability of diadromous fish to coastal anthropogenic pressures (Halpern et al.,  
527 2015; Limburg and Waldman, 2009; Lotze et al., 2006; Worm et al., 2006).

528

##### 529 4.1. Hierarchical Bayesian SDM

530 On average, the eleven SDMs performed well. All the models had lower sensitivity  
531 and positive prediction values scores, because of low presence. Areas of both high  
532 probability and very low probability of presence had lower uncertainty, giving a

533 more accurate picture of confidence in the distributions (e.g., higher certainty that  
534 most species are absent within waters further from the coast). In addition to  
535 problems with very low occurrence, the areas of higher uncertainty for certain  
536 species (e.g., *S. salar* and *S. trutta*, *A. alosa* and *A. fallax*), may be partially  
537 because of misidentification between these groups of diadromous fish. The core  
538 areas of probability of presence, in combination with the confidence maps provide  
539 a better understanding of confidence of these predictions. To improve problems of  
540 false presence predictions which might occur with species that are difficult to  
541 identify, Bayesian models incorporating false positive errors could be undertaken  
542 (e.g. Diana et al., 2021; Guillera-Arroita, 2017; Royle and Link, 2006).

543  
544 Separating out the spatial random field of presence absence from the observations  
545 enabled us to explicitly consider the imperfect detection of the observation  
546 process. Since our database contained non-diadromous fish specific survey and  
547 catch data which sampled the same grid cell numerous times, the use of the site  
548 occupancy model enabled imperfect detection parameters to be estimated.  
549 Disregarding false absences would have led to biased inferences and over-stated  
550 parameter precision (Guillera-Arroita, 2017). The spatial random field of the  
551 probability of presence explicitly integrates spatial autocorrelation in the  
552 probability of presence, which limits the bias in inferences due to the non-random  
553 spatial repartition of observations.

554  
555 Since there were few presences for most species, our results were sensitive to the  
556 choice of prior on the variance of the spatial random effect. We tested both the  
557 inverse-gamma or a uniform distribution (the two prior forms that are available  
558 using the hSDM package; Vieilledent et al., 2014) and found that the uniform  
559 distribution provided better result. Some alternative prior choice such as the half-  
560 Cauchy are advocated in the literature (Gelman, 2006), and future work should  
561 explore if other prior choice could provide more accurate inferences. Equally, for  
562 increased confidence in predictions of rare species, several different distribution  
563 models could be compared or an ensemble model (that uses the means of several  
564 models) implemented to stabilise inferences (Araújo and New, 2007; Latimer et al.,  
565 2006; Loiselle et al., 2003).

566  
567 For conservation purposes low thresholds are advised for low occurring species such  
568 as diadromous fish (Freeman and Moisen, 2008a;b; Jiménez-Valverde and Lobo,  
569 2007). However, when lowering the threshold an increase in false positives can  
570 occur (Freeman and Moisen, 2008b). Our objective for the distribution models was  
571 to minimise false presence and absences where possible, to provide more accurate  
572 predictions whilst trying to meet conservations needs and minimise potential  
573 impacts on sea-users any spatial protection measure that might be implemented  
574 (Domisch et al., 2018; Loiselle et al., 2003; Maxwell and Jennings, 2005). Lack of  
575 understanding in species distribution can lead to inefficient spatial protection  
576 measures (Wauchope et al., 2022) and resource conflict (Probst et al., 2021).

#### 577 578 *4.2. Diadromous fish river basin connectivity*

579 The EuroDiad database is a large database that incorporates information on  
580 diadromous fish presence and abundance during their freshwater stage (Barber-  
581 O'Malley et al., 2022; Béguer et al., 2007). Using the Eurodiad database to provide

582 large scale understanding of river basin presence of diadromous fish, we provide a  
583 first attempt at qualitatively linking diadromous fish freshwater and marine  
584 distributions within north-eastern Atlantic waters. Although the probabilities of  
585 presence for most species were low, and gaps within the EuroDiad database  
586 evident (e.g., gaps in diadromous fish presence from Denmark and Netherlands),  
587 connectivity with their freshwater habitats appears to be visible, indicating  
588 migration pathways.

589  
590 It is thought *A. alosa* no longer exists within the Greater North Sea (Baglinière et  
591 al., 2003; Wilson and Veneranta, 2019). Presences observed may have been from  
592 misidentified *A. fallax*. The high probability of presence of *A. fallax* along the east  
593 coast of the UK may be because of suitable conditions for this species as few  
594 spawning rivers have been recorded along the east coast (Aprahamian et al., 1998).  
595 For *A. agone* probabilities of presence clearly match that of their watersheds.  
596 Predicted *A. anguilla* presences closely match tagged river presences from Righton  
597 et al., (2016) despite the gaps found in the EuroDiad database. Predicted presence  
598 of *L. fluviatilis* was higher along the north-west coast of Germany and Holland.  
599 Presences have been observed here, albeit in low numbers (Admiraal et al., 1993;  
600 Pavlov et al., 2017; Thiel and Salewski, 2003). *P. marinus* predicted presence was  
601 slightly more scattered which fits with its wide distribution including into deeper  
602 waters (Elliott et al., 2021; Lança et al., 2014). The very low occurrences of *A.*  
603 *anguilla*, and the lamprey species is also likely to be due to inadequate sampling  
604 methods used to study these species.

605  
606 Probabilities of presence of *C. ramada*, *P. flesus* and *O. eperlanus* matched  
607 relatively well their known presence from the EuroDiad database. From the  
608 EuroDiad database, there are few *S. salar* river basin presences within the North  
609 Sea. However, *S. salar* are known to occur within the North Sea and migrate  
610 Northwards to their feeding grounds (Mork et al., 2012; Rikardsen et al., 2021).  
611 Occurrences observed were most likely 1 sea winter and 2 sea winters individuals  
612 returning to their natal rivers given their size ranges. From the rivers that are  
613 monitored, *S. trutta* distribution matched well their freshwater river occupancy  
614 (ICES, 2020). The few salmonids observed may be as a result of the relatively few  
615 pelagic trawls, in addition to misreporting (ICES, 2005).

616  
617 Given the coastal habitat occupancy for most of these diadromous fish and declines  
618 observed (Limburg and Waldman, 2009; Merg et al., 2020), detailed analysis of the  
619 connectivity between both habitats is essential (Flitcroft et al., 2019; Lin et al.,  
620 2017; McDowall, 2009). Unfortunately, such a model was not possible here,  
621 because it would require more detailed knowledge on their freshwater habitat  
622 occupancy (i.e., numerous outlets diadromous fish were observed within proximity  
623 to, were not contained within the EuroDiad database) and their river fidelity.  
624 Furthermore, seasonal and stage specific SDMs, which would provide more  
625 information on their ontogenetic migration movements, were not possible because  
626 of the low prevalence of the data and dispersion. Developing future research to  
627 model the connectivity between both habitats is key to improving our  
628 understanding of the pressures faced during their migrations (Flitcroft et al., 2019;  
629 Lin et al., 2017; McDowall, 2009).

630

#### 631 4.3. Gear type detectability

632 Even though little bycatch was observed, given a number of the diadromous fish  
633 studied here are threatened, even a small amount of bycatch may impact their  
634 populations (Dulvy et al., 2003). Furthermore, misreporting and illegal fishing is  
635 likely to remain (Elliott et al., 2020a; ICES, 2005; Stratoudakis et al., 2020; Worm  
636 et al., 2013). Bycatch detectability results from our models could help provide  
637 management advice so that gear types and areas with higher bycatch rate be  
638 avoided. Such advice can provide direct information for the MSFD and the Habitat  
639 Directive that requires the identification of gear types which may threaten  
640 protected species (1992/43/EEC; 2008/56/EC).

641  
642 All species were caught by a wide range of gear types (e.g., benthic, demersal and  
643 pelagic trawls, and seine nets), despite the different gear categories being  
644 deployed at different depths. The species were probably caught by a range of gear  
645 categories because of their diel vertical migratory behaviour whilst at sea  
646 (Kristensen et al., 2018; Lança et al., 2014; Righton et al., 2016). In addition,  
647 certain gear types (e.g., trawls and static nets), can catch fish within both the  
648 demersal and pelagic water zones (He et al., 2021; Borges et al., 2008). Higher  
649 detectability from certain gear types were, however, observed. For example, shad  
650 were mainly caught by demersal mobile gear and static gear, salmonids static and  
651 pelagic mobile gear types, and *P. flesus* and *O. eperlanus* were largely captured by  
652 demersal and benthic mobile gear. These results broadly match the water column  
653 habitat occupancy these species are known to occupy and existing literature (ICES,  
654 2005; Wilson and Veneranta, 2019). As it is thought that lampreys detach from  
655 their host upon capture (Elliott et al., 2021; Halliday, 1991), bycatch is likely to be  
656 minimal for these species.

657  
658 To improve understanding of bycatch risk on a spatial level, fishing intensity by  
659 gear type should be mapped, ideally using Vessel Monitoring System data and  
660 overlaying it with the predicted distributions (Elliott et al., 2018; Quemmerais-  
661 Amice et al., 2020). Unfortunately, this information was not available to us.  
662 Additionally, since the fisheries observer data we had access to is only a small  
663 sample of the existing French fishing activity (Cornou et al., 2015), and it does not  
664 include other countries fishing effort, results would be biased.

#### 666 4.4. MPA relevance

667 To improve protection of diadromous fish at sea, numerous mechanisms could be  
668 implemented. For example, identifying areas of high bycatch risk with measures to  
669 limit bycatch within these areas, improving diadromous fish migratory pathways,  
670 and spatial protection measures (Verhelst et al., 2021; Wilson and Veneranta,  
671 2019). Few MPAs within European waters protect marine fish and instead focus on  
672 protecting seabed features with a few exceptions (e.g., protected seabirds and  
673 marine mammals). Therefore the only protection measure that exist for vulnerable  
674 marine fish is through the removal of targeted fishing (Dureuil et al., 2018; Probst  
675 et al., 2021; Stratoudakis et al., 2016). There is, however, increasing evidence that  
676 MPAs may have positive impacts on fish populations if appropriate management  
677 measures are implemented (Davies et al., 2021; Moland et al., 2013; Probst et al.,  
678 2021; Worm et al., 2006). The value of protected areas for highly migratory species

679 has been questioned, but there is evidence that MPAs may have positive impacts on  
680 migratory species (Pendoley et al., 2014; Takashina and Mougi, 2014).

681  
682 Our results show relatively high core area presence of protected diadromous fish  
683 within Habitat Directive MPAs. Most marine Sites of Community Importance have  
684 not been designated to protect Habitat Directive listed diadromous fish.

685 Nonetheless, our results highlight the value of these MPAs for diadromous fish  
686 protection. Specific management measures limiting threats (e.g., limiting access to  
687 gear types with higher probability of capture) to diadromous fish within these  
688 areas, would be of benefit to their protection (Domisch et al., 2019; Stratoudakis  
689 et al., 2016). Detailed analysis of Sites of Community Importance and other  
690 categories of designated MPAs should be undertaken to evaluate their potential to  
691 protect diadromous fish.

#### 692 693 *4.5. Conclusion*

694 Understanding the spatial distribution of species and their habitats is essential for  
695 effective management and conservation (Halpern et al., 2015; Worm et al., 2009,  
696 2005). Much research has been carried out on the conservation of freshwater  
697 diadromous fish (Drouineau et al., 2018; Merg et al., 2020; Verhelst et al., 2021).  
698 Very little research has been dedicated to the value of marine and estuary habitats  
699 for the conservation of these species and their risk of bycatch (Feunteun, 2002;  
700 Flitcroft et al., 2019; Lin et al., 2017). Here we provide an insight into the  
701 distribution and bycatch of diadromous fish at sea.

702  
703 Despite diadromous fish vulnerability, targeted fishing within estuaries for  
704 numerous species remains (Aprahamian and Walker, 2008; Castelnaud, 2000;  
705 Feunteun, 2002; Kappel, 2005; Stratoudakis et al., 2020). Given the very coastal  
706 distribution of these species, more detailed analysis into such catch data (small  
707 fishing vessels targeting diadromous fish) is required. Smaller vessels and artisanal  
708 fisheries are still largely overlooked, regardless of their potential threat to  
709 diadromous fish (Beaulaton et al., 2008; Castelnaud, 2000; Stratoudakis et al.,  
710 2016). Having a better understanding of fishing pressure, combined with the  
711 outputs of the distributions and gear capture from these models, could help  
712 improve understanding of fishing impacts on diadromous fish.

713  
714 Finally, it has been well acknowledged that although a large impetus for the  
715 designation of MPAs has been undertaken in the last two decades (Probst et al.,  
716 2021; Worm et al., 2006). The implementation of management measures has been  
717 slow to put in place (Dureuil et al., 2018; Probst et al., 2021; Stratoudakis et al.,  
718 2016). Furthermore, little has been undertaken to protect diadromous fish within  
719 marine ecosystems (Dureuil et al., 2018; Probst et al., 2021; Stratoudakis et al.,  
720 2016). We highlight the value of Habitat Directive MPAs that have the jurisdiction  
721 to protect diadromous fish. Limiting access of fisheries with a higher probability of  
722 capture to such areas could provide additional protection for diadromous fish and  
723 their habitats.

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