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

3
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24
25
26 **ABSTRACT**

27 Anthropogenic pressures have resulted in declines in diadromous fish. Many
28 diadromous fish which were commercially important are now threatened and
29 protected. Little is known about their marine life history phases, and no
30 observation-based Species Distribution Model exists for this group of species at sea.
31 Yet, fisheries dependent and independent data could provide new insights into the
32 distribution of diadromous fish at sea.

33
34 We collated a database of 168 904 hauls from fisheries observer bycatch data and
35 scientific fisheries surveys, from eastern Atlantic and Mediterranean waters. The
36 distribution of eleven rare and data-poor diadromous fish (shads, lampreys,
37 salmonids, the European eel, the thinlip mullet, smelt and the European flounder)
38 were modelled. A Bayesian site occupancy model, that incorporates imperfect
39 detection to account for repeat detections and non-detections, the non-random
40 nature of fishing gear type and spatial autocorrelation was used. From the model
41 outputs, we explored bycatch risk and the role of MPAs, required under the Marine
42 Strategy Framework Directive and Habitat Directive and assessed.

43
44 Diadromous fish were observed within relatively shallow coastal areas. Species
45 specific gear bycatch trends were observed. Core distribution areas corresponded
46 to their known water basin presence, indicating connectivity with their freshwater
47 habitats. Numerous Habitat Directive Marine Protected Areas were found to be of
48 relevance.

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 19th 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; 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) 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 ¹	EU IUCN ³	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 ²	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 ⁴	-	✓	II, V	✓	III	-	✓	-
<i>Salmo trutta</i>	Sea trout	A	Pelagic	LC	-	✓	-		-	-	-	-

171 ¹ Elliott and Dewailly, 1995; ² Almeida, 1996; ³ Freyhof and Brooks, 2011; ⁴ 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 a 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.

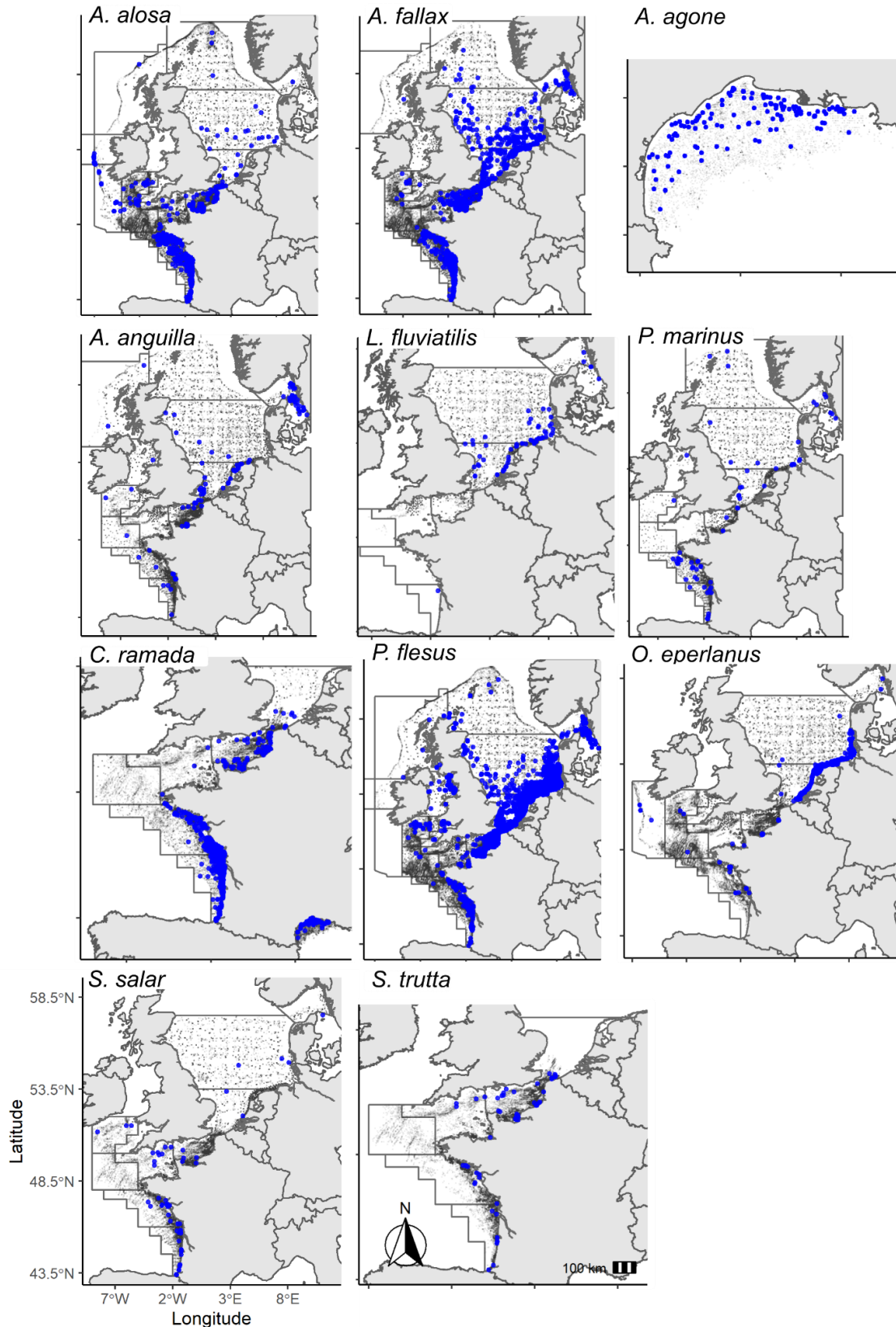
236
237 To select the model of best fit, variables that were not collinear (Pearson's
238 correlation coefficient < 0.5 or > -0.5 and a Variance Inflation Factor < 2) (Dormann
239 et al., 2013) were kept. Depth and distance from coast, and sea surface
240 temperature and net primary production were collinear. 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 (http://neo.sci.gsfc.nasa.gov) 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 (≤ 2 mm), sand (> 2 and ≤ 4 mm), coarse grain (> 4 mm and ≤ 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 ²)	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 θ_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 β 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 μ_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 θ_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 γ is the vector of the gear effects, so as $W_{j,i}\gamma$ is the gear affect associated with observation at site i .

304

305
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 θ_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).

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

2.6. Diadromous fish river basin presence

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

2.7. Habitat Directive MPAs of relevance to diadromous fish

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

3. Results

3.1. Diadromous fish hierarchical SDM

For all species the Area under the receiver operating curve and Percent Correct Classification performed very well ($\geq 75\%$; Table 3). Correct presence classification from the confusion matrices was consistently lower ($< 15\%$) than that of correct absence classification ($\geq 64\%$), and false absences were lower ($\leq 3\%$) than false presences ($\leq 22\%$) because of presence absence imbalance (Table 3; Table S1). The 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 ≤ 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

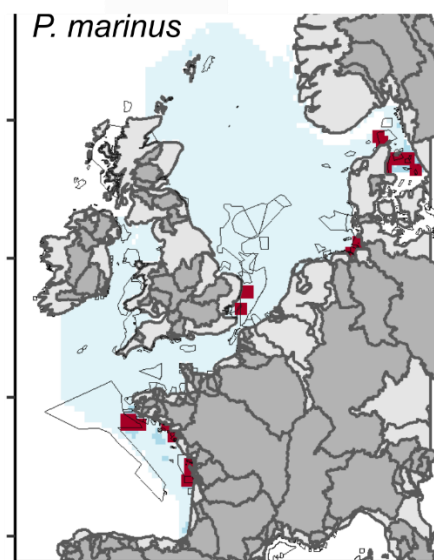
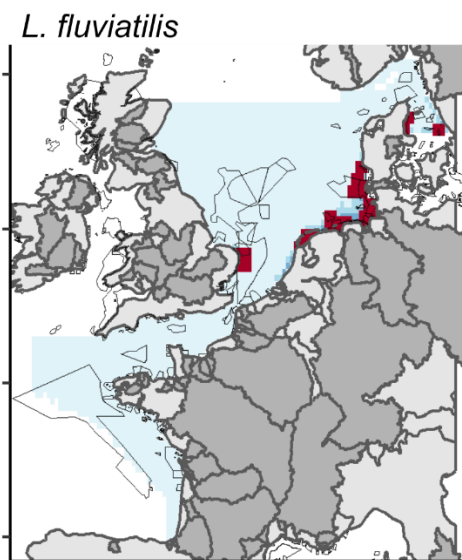
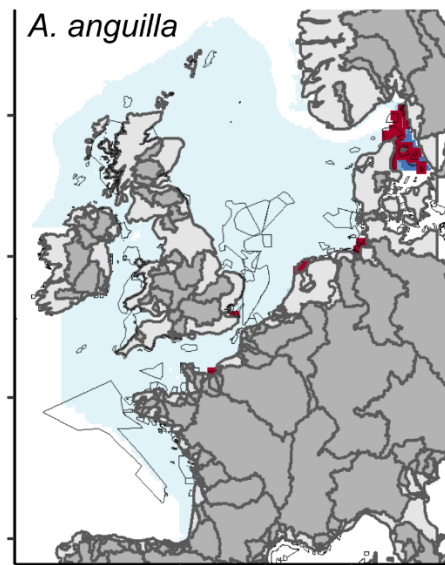
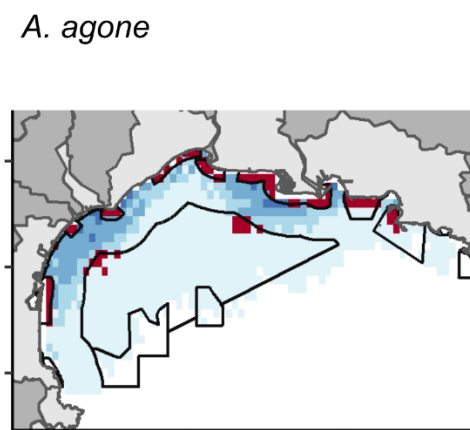
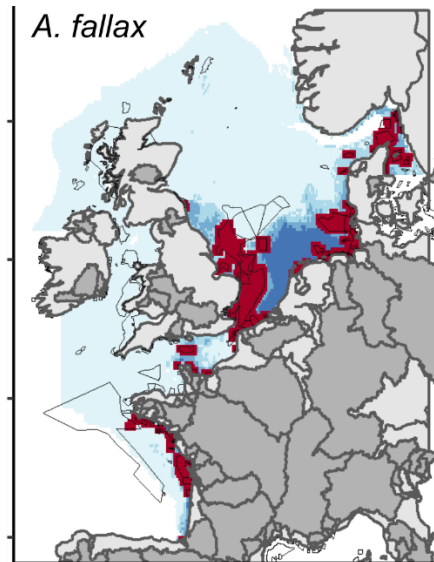
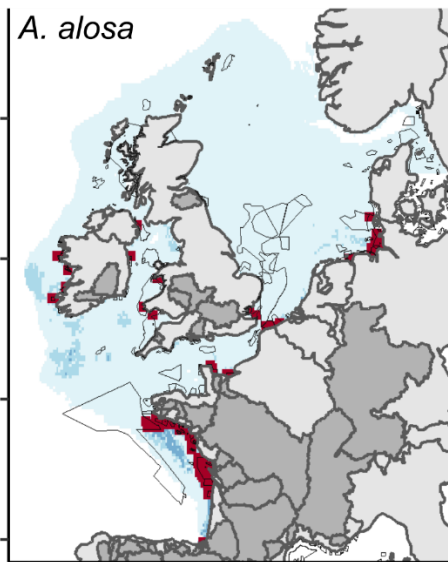
417 All species were observed to have a relatively shallow (<300m depth) coastal
418 distribution (~<300 km from the coast; Fig. 2 and 3). The main predictor variables
419 for diadromous fish habitats were depth or distance from coast and salinity (Fig. 3).
420 Since sufficient *C. ramada* were observed 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).

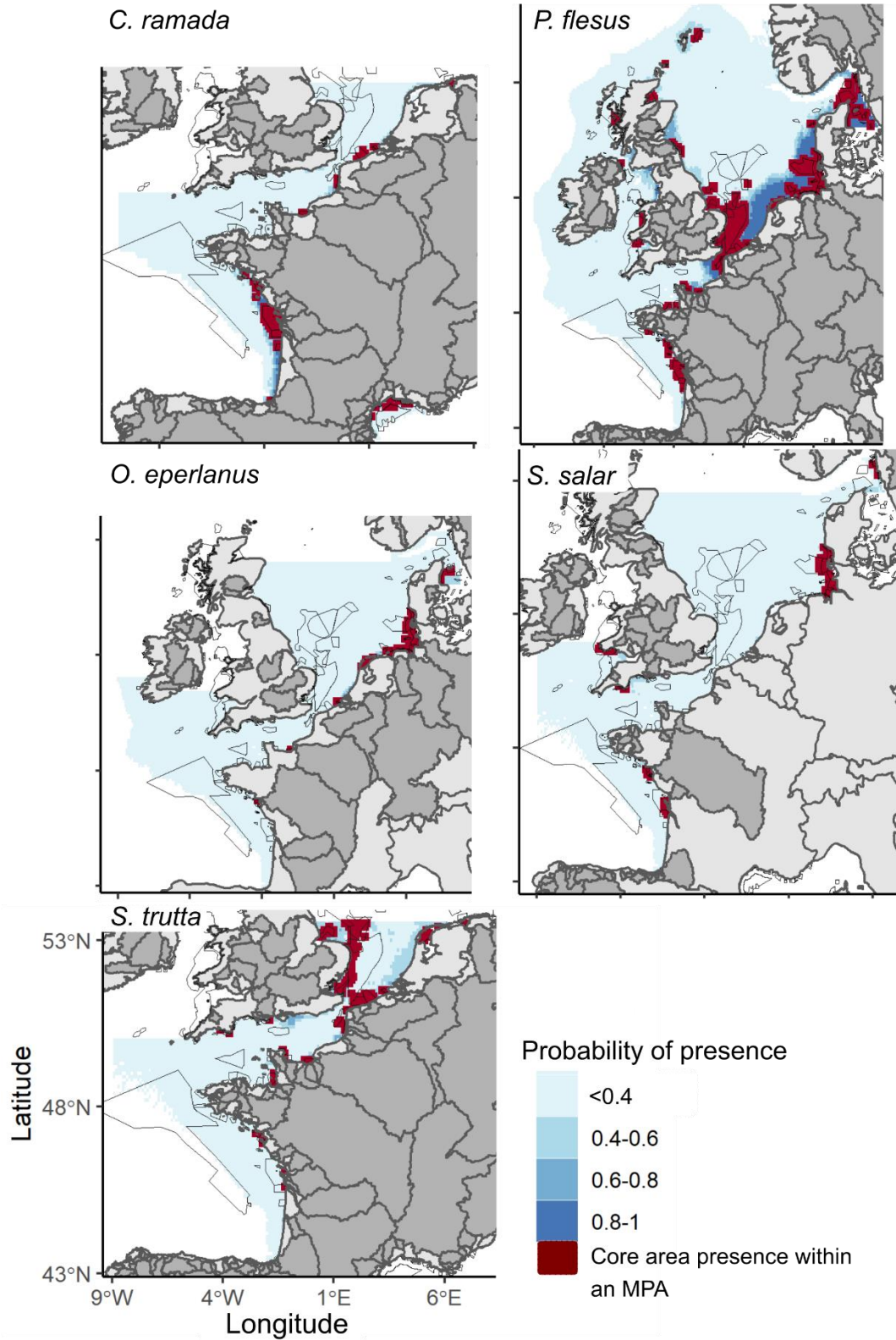
423

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

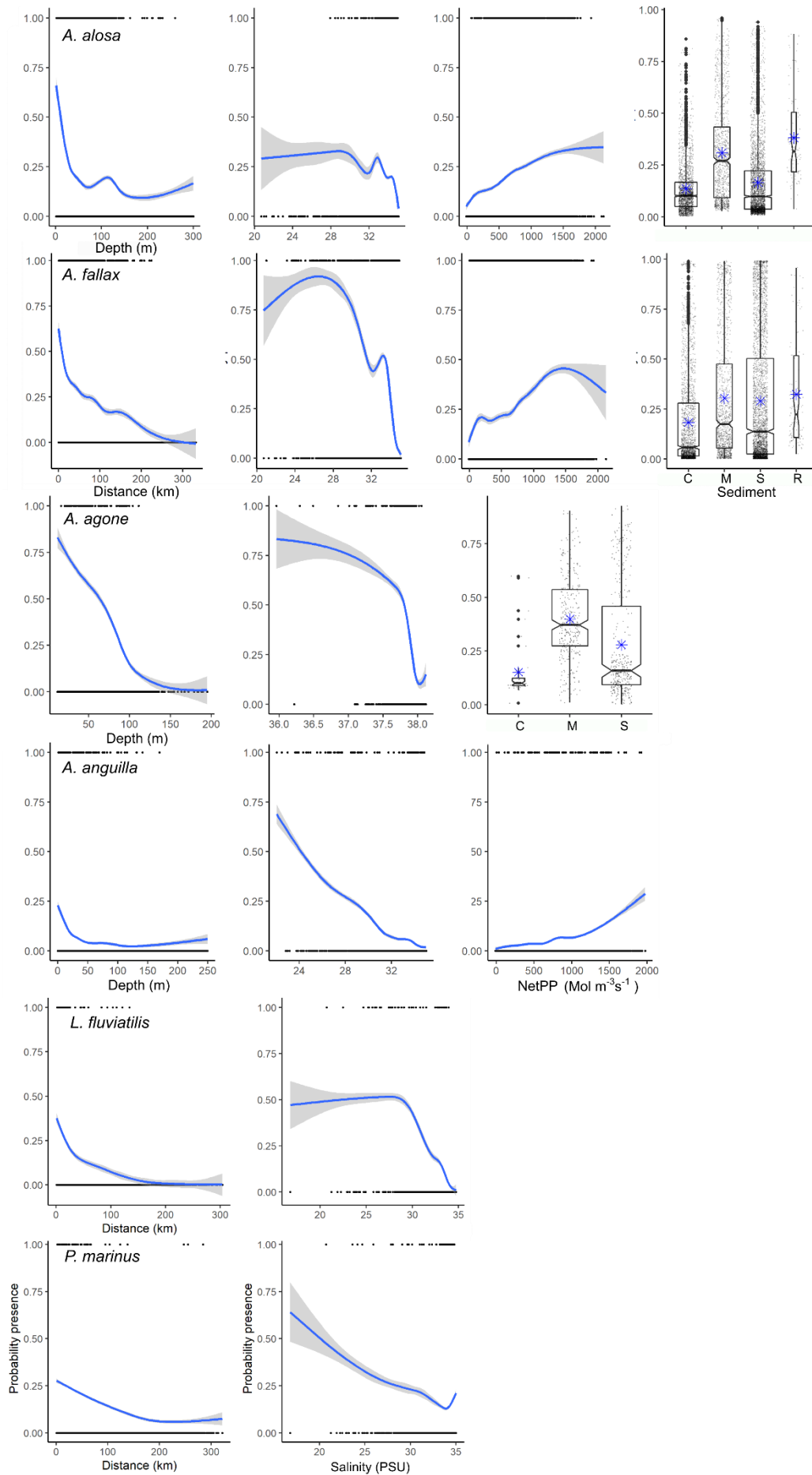
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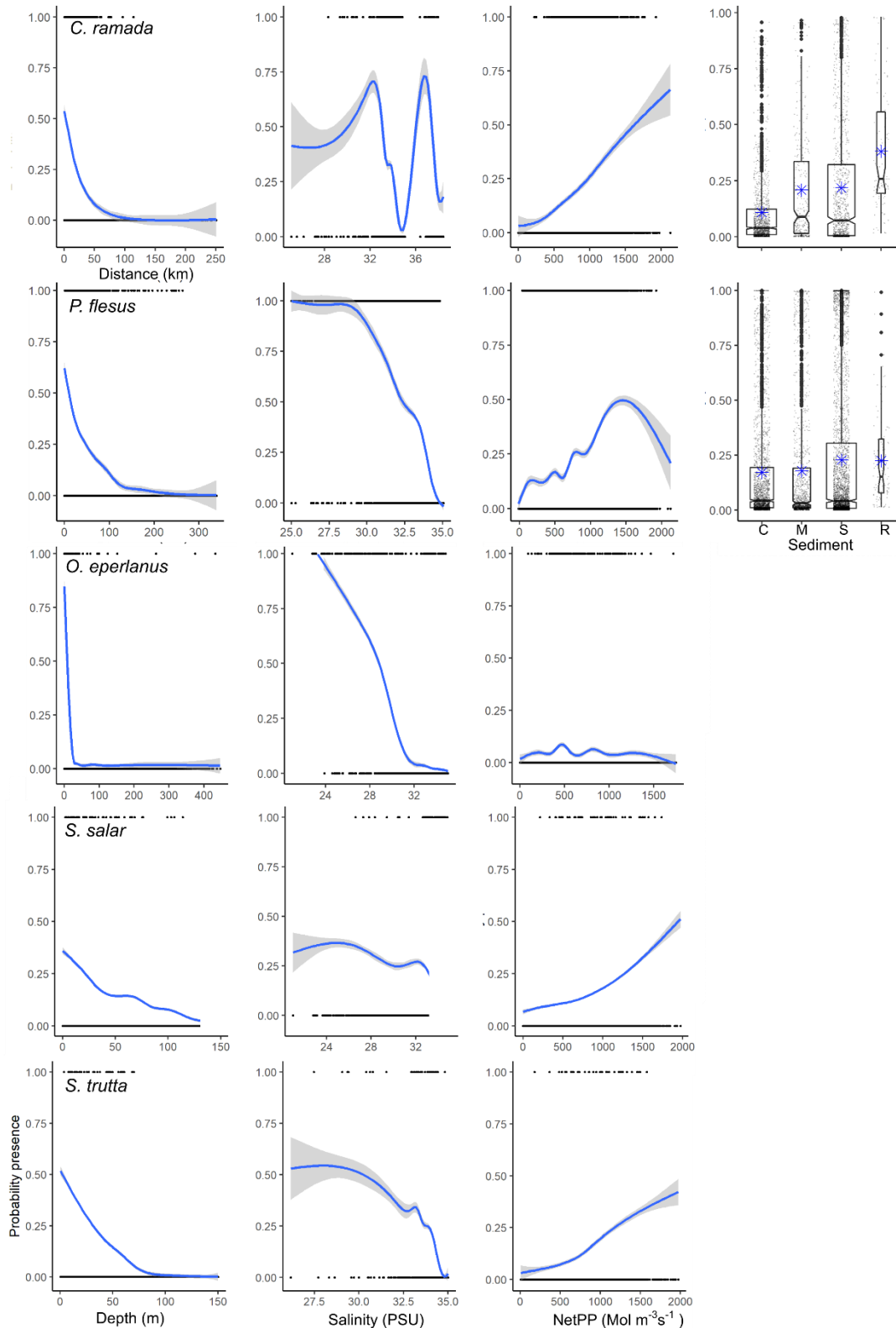




431

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*

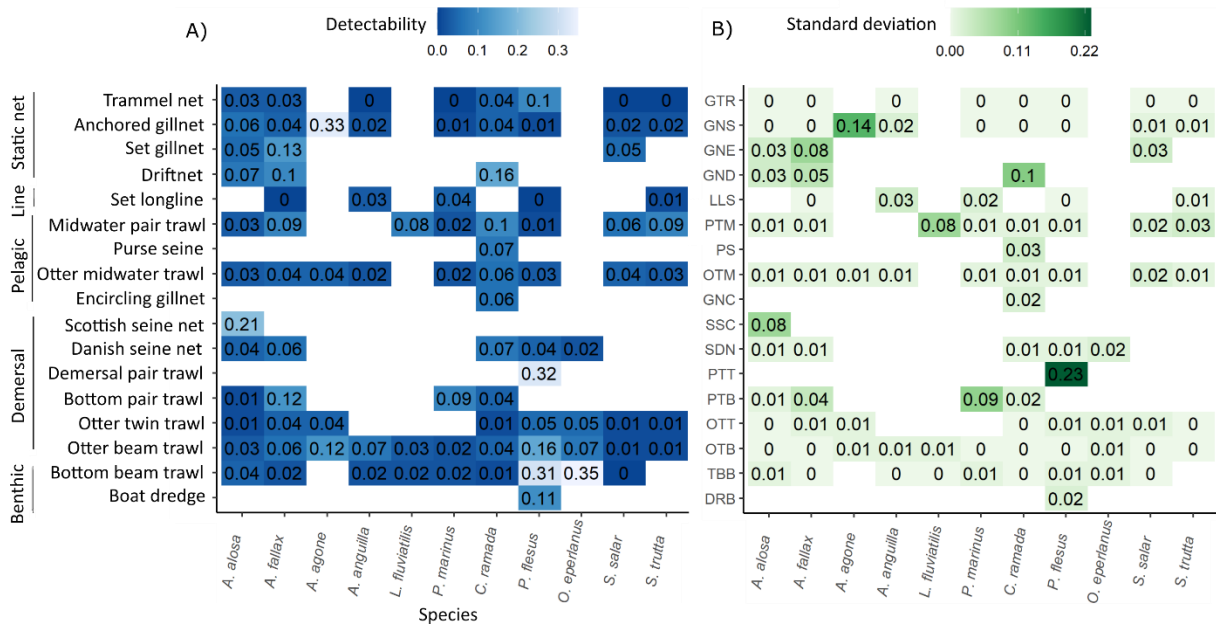
451 2717 references contained within the EuroDiad database were used to map the 11
452 diadromous fish presence within the river basin. Core distributions of diadromous
453 fish at sea largely matched with the freshwater areas of presence (Fig. 2). The
454 spatial extent of diadromous fish at sea was 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 γ ; 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).

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
<i>A. agone</i>	10	0.27
<i>A. anguilla</i>	19	0.04
<i>L. fluviatilis</i>	11	0.02
<i>P. marinus</i>	14	0.03
<i>C. ramada</i>	23	0.05
<i>P. flesus</i>	65	0.15
<i>O. eperlanus</i>	13	0.03
<i>S. salar</i>	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 All species were caught by a wide range of gear types (e.g., benthic, demersal and
642 pelagic trawls, and seine nets), despite the different gear categories being
643 deployed at different depths. The species were probably caught by a range of gear
644 categories because of their diel vertical migratory behaviour whilst at sea
645 (Kristensen et al., 2018; Lança et al., 2014; Righton et al., 2016). In addition,
646 certain gear types (e.g., trawls and static nets), can catch fish within both the
647 demersal and pelagic water zones (He et al., 2021; Borges et al., 2008). Higher
648 detectability from certain gear types were, however, observed. For example, shad
649 were mainly caught by demersal mobile gear and static gear, salmonids static and
650 pelagic mobile gear types, and *P. flesus* and *O. eperlanus* were largely captured by
651 demersal and benthic mobile gear. These results broadly match the water column
652 habitat occupancy these species are known to occupy and existing literature (ICES,
653 2005; Wilson and Veneranta, 2019). As it is thought that lampreys detach from
654 their host upon capture (Elliott et al., 2021; Halliday, 1991), bycatch is likely to be
655 minimal for these species.

656
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.

665 4.4. MPA relevance

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

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 (Arahamian 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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733 References

- 734 Admiraal, W., van der Velde, G., Smit, H., Cazemier, W.G., 1993. The rivers Rhine
735 and Meuse in The Netherlands: present state and signs of ecological recovery.
736 *Hydrobiologia* 265, 97-128. <https://doi.org/10.1007/BF00007264>
- 737 Alglave, B., Rivot, E., Etienne, M.-P., Woillez, M., Thorson, J.T., Vermard, Y.,
738 2022. Combining scientific survey and commercial catch data to map fish
739 distribution. *ICES J. Mar. Sci.* 79, 1133-1149.
740 <https://doi.org/10.1093/icesjms/fsac032>
- 741 Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species
742 distribution models: prevalence, kappa and the true skill statistic (TSS). *J.*
743 *Appl. Ecol.* 43, 1223-1232. <https://doi.org/10.1111/j.1365-2664.2006.01214.x>
- 744 Almeida, P.R., 1996. Estuarine movement patterns of adult thin-lipped grey mullet,
745 *Liza ramada* (Risso) (*Pisces, Mugilidae*), observed by ultrasonic tracking. *J.*
746 *Exp. Mar. Bio. Ecol.* 202, 137-150. [https://doi.org/10.1016/0022-](https://doi.org/10.1016/0022-0981(95)00162-X)
747 [0981\(95\)00162-X](https://doi.org/10.1016/0022-0981(95)00162-X)
- 748 Aprahamian, M., Walker, A., 2008. Status of eel fisheries, stocks and their
749 management in England and Wales. *Knowl. Manag. Aquat. Ecosyst.* 1-7.
750 <https://doi.org/10.1051/kmae/2009007>
- 751 Aprahmian, M.W., Lester, S.M., Aprahamian, S.D., 1998. Shad conservation in
752 England and Wales. R&D Technical report W110. Environment Agency:
753 [https://www.gov.uk/government/publications/shad-conservation-in-england-](https://www.gov.uk/government/publications/shad-conservation-in-england-and-wales)
754 [and-wales](https://www.gov.uk/government/publications/shad-conservation-in-england-and-wales) (last accessed 22/09/2022)
- 755 Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. *Trends*
756 *Ecol. Evol.* 22, 42-47. <https://doi.org/10.1016/j.tree.2006.09.010>
- 757 Arevalo, E., Lassalle, G., Tétard, S., Maire, A., Sauquet, E., Lambert, P., Paumier,
758 A., Villeneuve, B., Drouineau, H., 2020. An innovative bivariate approach to
759 detect joint temporal trends in environmental conditions: Application to large
760 French rivers and diadromous fish. *Sci. Total Environ.* 748, 141260.
761 <https://doi.org/10.1016/j.scitotenv.2020.141260>
- 762 Barber-O'Malley, B., Lassalle, G., Lambert, P., Quinton, E., 2022. Dataset on
763 European diadromous species distributions from 1750 to present time in
764 Europe, North Africa and the Middle East. *Data Br.* 40, 107821.
765 <https://doi.org/10.1016/j.dib.2022.107821>
- 766 Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J., Doherty, P.A., 2003.
767 Collapse and Conservation of Shark Populations in the Northwest Atlantic.
768 *Science.* 299, 389-392. <https://doi.org/10.1126/science.1079777>
- 769 Bagliniere, J.L., Elie, P., 2000. Les aloses (*Alosa alosa* et *Alosa fallax* spp.)
770 Ecobiologie et variabilité des populations. Institut National de la Recherche
771 Agronomique, Paris. ISBN 2-7380-0906-9-ISSN :0763-1707
- 772 Beaulaton, L., Taverny, C., Castelnaud, G., 2008. Fishing, abundance and life
773 history traits of the anadromous sea lamprey (*Petromyzon marinus*) in Europe.
774 *Fish. Res.* 92, 90-101. <https://doi.org/10.1016/j.fishres.2008.01.001>
- 775 Béguer, M., Beaulaton, L., Rochard, E., 2007. Distribution and richness of
776 diadromous fish assemblages in Western Europe: large-scale explanatory

- 777 factors. *Ecol. Freshw. Fish* 16, 221-237. <https://doi.org/10.1111/j.1600->
778 0633.2006.00214.x
- 779 Belmont, J., Miller, C., Scott, M., Wilkie, C., 2022. A new statistical approach for
780 identifying rare species under imperfect detection. *Divers. Distrib.* 28, 882-
781 893. <https://doi.org/10.1111/ddi.13495>
- 782 Berg, S., Krog, C., Muus, B., Nielsen, J., Fricke, R., Berghahn, R., Neudecker, T.,
783 Wolff, W.J., 1996. Red List of lampreys and marine fishes of the Wadden Sea.
784 *Helgoländer Meeresuntersuchungen* 50, 101-105.
785 <https://doi.org/10.1007/BF02366178>
- 786 Berkson, J., Thorson, J.T., 2015. The determination of data-poor catch limits in
787 the United States: is there a better way? *ICES J. Mar. Sci.* 72, 237-242.
788 <https://doi.org/10.1093/icesjms/fsu085>
- 789 Bisch, A., Elliott, S.A.M., Carpentier, A., Acou, A., 2022. Modelling the distribution
790 of vulnerable skate from fisheries dependent data using imperfect detection.
791 *Prog. Oceanogr.* 206, 102859. <https://doi.org/10.1016/j.pocean.2022.102859>
- 792 Bourdaud, P., Travers-Trolet, M., Vermard, Y., Cormon, X., Marchal, P., 2017.
793 Inferring the annual, seasonal, and spatial distributions of marine species
794 from complementary research and commercial vessels' catch rates. *ICES J.*
795 *Mar. Sci.* 74, 2415-2426. <https://doi.org/10.1093/icesjms/fsx092>
- 796 Castelnaud, G., 2000. Fishing location, fishermen and production of migratory
797 species fisheries in the French rivers. *BFPP - Bull. Fr. la Pech. la Prot. des*
798 *Milieux Aquat.* 439-458. <https://doi.org/10.1051/kmae/2001060>
- 799 Cornou, A.S., Quinio-Scavinner, M., Delaunay, D., Dimeet, J. et al., 2015.
800 Observations à bord des navires de pêche professionnelle. Bilan de
801 l'échantillonnage 2014. Ifremer, Nantes
- 802 Costa, M.J., Duarte, G., Segurado, P., Branco, P., 2021. Major threats to European
803 freshwater fish species. *Sci. Total Environ.* 797, 149105.
804 <https://doi.org/10.1016/j.scitotenv.2021.149105>
- 805 Davies, B.F.R., Holmes, L., Rees, A., Attrill, M.J., Cartwright, A.Y., Sheehan, E. V.,
806 2021. Ecosystem Approach to Fisheries Management works—How switching
807 from mobile to static fishing gear improves populations of fished and non-
808 fished species inside a marine-protected area. *J. Appl. Ecol.* 1-16.
809 <https://doi.org/10.1111/1365-2664.13986>
- 810 de Groot, R., Brander, L., van der Ploeg, S., Costanza, R., Bernard, F., Braat, L.,
811 Christie, M., Crossman, N., Ghermandi, A., Hein, L., Hussain, S., Kumar, P.,
812 McVittie, A., Portela, R., Rodriguez, L.C., ten Brink, P., van Beukering, P.,
813 2012. Global estimates of the value of ecosystems and their services in
814 monetary units. *Ecosyst. Serv.* 1, 50-61.
815 <https://doi.org/10.1016/j.ecoser.2012.07.005>
- 816 Diana, A., Matechou, E., Griffin, J.E., Buxton, A.S., Griffiths, R.A., 2021. An RShiny
817 app for modelling environmental DNA data: accounting for false positive and
818 false negative observation error. *Ecography (Cop.)*. 44, 1838-1844.
819 <https://doi.org/10.1111/ecog.05718>
- 820 Domisch, S., Friedrichs, M., Hein, T., Borgwardt, F., Wetzig, A., Jähnig, S.C.,
821 Langhans, S.D., 2018. Spatially explicit species distribution models: A missed
822 opportunity in conservation planning? *Divers. Distrib.* 25, 758-769.
823 <https://doi.org/10.1111/ddi.12891>
- 824 Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz,
825 J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean,

- 826 C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D.,
827 Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a
828 simulation study evaluating their performance. *Ecography (Cop.)*. 36, 27-46.
829 <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- 830 Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G.,
831 Davies, R.G., Hirzel, A., Jetz, W., Daniel Kissling, W., Kühn, I., Ohlemüller,
832 R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M., Wilson, R.,
833 2007. Methods to account for spatial autocorrelation in the analysis of species
834 distributional data: a review. *Ecography (Cop.)*. 30, 609-628.
835 <https://doi.org/10.1111/j.2007.0906-7590.05171.x>
- 836 Drouineau, H., Carter, C., Rambonilaza, M., Beaufaron, G., Bouleau, G., Gassiat,
837 A., Lambert, P., le Floch, S., Tétard, S., de Oliveira, E., 2018. River
838 Continuity Restoration and Diadromous Fishes: Much More than an Ecological
839 Issue. *Environ. Manage.* 61, 671-686. [https://doi.org/10.1007/s00267-017-](https://doi.org/10.1007/s00267-017-0992-3)
840 [0992-3](https://doi.org/10.1007/s00267-017-0992-3)
- 841 Dulvy, N.K., Sadovy, Y., Reynolds, J.D., 2003. Extinction vulnerability in marine
842 populations. *Fish Fish.* 4, 25-64. [https://doi.org/10.1046/j.1467-](https://doi.org/10.1046/j.1467-2979.2003.00105.x)
843 [2979.2003.00105.x](https://doi.org/10.1046/j.1467-2979.2003.00105.x)
- 844 Dureuil, M., Boerder, K., Burnett, K.A., Froese, R., Worm, B., 2018. Elevated
845 trawling inside protected areas undermines conservation outcomes in a global
846 fishing hot spot. *Science*. 362, 1403-1407.
847 <https://doi.org/10.1126/science.aau0561>
- 848 Elliott, M., Dewailly, F., 1995. The structure and components of European
849 estuarine fish assemblages. *Netherlands J. Aquat. Ecol.* 29, 397-417.
- 850 Elliott, S.A.M., Bearup, D., Carpentier, A., Larivain, A., Trancart, T., Feunteun, E.,
851 2020a. Evaluating the effectiveness of management measures on skates in a
852 changing world. *Biol. Conserv.* 248, 108684.
853 <https://doi.org/10.1016/j.biocon.2020.108684>
- 854 Elliott, S.A.M., Carpentier, A., Feunteun, E., Trancart, T., 2020b. Distribution and
855 life history trait models indicate vulnerability of skates. *Prog. Oceanogr.* 181,
856 102256. <https://doi.org/10.1016/j.pocean.2019.102256>
- 857 Elliott, S.A.M., Deleys, N., Rivot, E., Acou, A., Réveillac, E., Beaulaton, L., 2021.
858 Shedding light on the river and sea lamprey within western European marine
859 waters. *Endanger. Species Res.* 44, 409-419.
860 <https://doi.org/10.3354/esr01113>
- 861 Elliott, S.A.M., Guérin, L., Pesch, R., Schmitt, P., Meakins, B., Vina-Herbon, C.,
862 González-Irusta, J.M., de la Torre, A., Serrano, A., 2018. Integrating
863 benthic habitat indicators: Working towards an ecosystem approach. *Mar.*
864 *Policy* 90, 88-94. <https://doi.org/10.1016/j.marpol.2018.01.003>
- 865 Elliott, S.A.M., Milligan, R.J., Heath, M.R., Turrell, W.R., Bailey, D.M., 2016.
866 Disentangling habitat concepts for demersal marine fish management.
867 *Oceanogr. Mar. Biol. Annu. Rev.* 54, 173-191.
868 <https://doi.org/10.1201/9781315368597>
- 869 Engler, R., Guisan, A., Rechsteiner, L., 2004. An improved approach for predicting
870 the distribution of rare and endangered species from occurrence and pseudo-
871 absence data. *J. Appl. Ecol.* 41, 263-274. [https://doi.org/10.1111/j.0021-](https://doi.org/10.1111/j.0021-8901.2004.00881.x)
872 [8901.2004.00881.x](https://doi.org/10.1111/j.0021-8901.2004.00881.x)
- 873 ERSEM, . 2020. NEMO-ERSEM and POLCOMS-ERSEM. Licence to use Copernicus
874 Products. Reading, UK. [DOI.org/10.24381/cds.dcc9295c](https://doi.org/10.24381/cds.dcc9295c)

- 875 [https://cds.climate.copernicus.eu/cdsapp#!/dataset/10.24381/cds.dcc9295c?](https://cds.climate.copernicus.eu/cdsapp#!/dataset/10.24381/cds.dcc9295c?tab=overview)
876 [tab=overview.](https://cds.climate.copernicus.eu/cdsapp#!/dataset/10.24381/cds.dcc9295c?tab=overview)
- 877 Fauconnet, L., Trenkel, V.M., Morandeau, G., Caill-Milly, N., Rochet, M.-J., 2015.
878 Characterizing catches taken by different gears as a step towards evaluating
879 fishing pressure on fish communities. *Fish. Res.* 164, 238-248.
880 <https://doi.org/10.1016/j.fishres.2014.11.019>
- 881 Feunteun, E., 2002. Management and restoration of European eel population
882 (*Anguilla anguilla*): An impossible bargain. *Ecol. Eng.* 18, 575-591.
883 [https://doi.org/10.1016/S0925-8574\(02\)00021-6](https://doi.org/10.1016/S0925-8574(02)00021-6)
- 884 Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of
885 prediction errors in conservation presence / absence models. *Environmental*
886 *Conserv.* 24, 38-49.
- 887 Flitcroft, R.L., Arismendi, I., Santelmann, M.V., 2019. A Review of Habitat
888 Connectivity Research for Pacific Salmon in Marine, Estuary, and Freshwater
889 Environments. *JAWRA J. Am. Water Resour. Assoc.* 55, 430-441.
890 <https://doi.org/10.1111/1752-1688.12708>
- 891 Fourcade, Y., Besnard, A.G., Secondi, J., 2018. Paintings predict the distribution of
892 species, or the challenge of selecting environmental predictors and evaluation
893 statistics. *Glob. Ecol. Biogeogr.* 27, 245-256.
894 <https://doi.org/10.1111/geb.12684>
- 895 Freeman, E.A., Moisen, G., 2008a. PresenceAbsence: An R Package for Presence-
896 Absence Model Analysis. *Journal of Statistical Software*, 23(11):1-31.
897 <http://www.jstatsoft.org/v23/i11>
- 898 Freeman, E.A., Moisen, G., 2008b. PresenceAbsence: An R Package for Presence-
899 Absence Model Analysis. *Journal of Statistical Software*, 23(11):1-31.
900 <http://www.jstatsoft.org/v23/i11>
- 901 Freyhof, J., Brooks, E., 2011. European Red List of freshwater fishes. Publications
902 Office of the European Union, Luxembourg.
903 [https://ec.europa.eu/environment/nature/conservation/species/redlist/dow](https://ec.europa.eu/environment/nature/conservation/species/redlist/downloads/European_freshwater_fishes.pdf)
904 [nloads/European_freshwater_fishes.pdf](https://ec.europa.eu/environment/nature/conservation/species/redlist/downloads/European_freshwater_fishes.pdf) (last accessed 01/07/2020).
- 905 Gelman, A., 2006. Prior distributions for variance parameters in hierarchical
906 models (comment on article by Browne and Draper). *Bayesian Anal.* 515-534.
907 <https://doi.org/10.1214/06-BA117A>
- 908 Gelman, A., Jakulin, A., Pittau, M.G., Su, Y.-S., 2008. A weakly informative default
909 prior distribution for logistic and other regression models. *Ann. Appl. Stat.* 2,
910 1360-1383. <https://doi.org/10.1214/08-AOAS191>
- 911 Guillera-Arroita, G., 2017. Modelling of species distributions, range dynamics and
912 communities under imperfect detection: advances, challenges and
913 opportunities. *Ecography (Cop.)*. 40, 281-295.
914 <https://doi.org/10.1111/ecog.02445>
- 915 Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than
916 simple habitat models. *Ecol. Lett.* 8, 993-1009.
917 <https://doi.org/10.1111/j.1461-0248.2005.00792.x>
- 918 Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in
919 ecology. *Ecol. Modell.* 135, 147-186. [https://doi.org/10.1016/S0304-](https://doi.org/10.1016/S0304-3800(00)00354-9)
920 [3800\(00\)00354-9](https://doi.org/10.1016/S0304-3800(00)00354-9)
- 921 Halliday, R.G., 1991. Marine distribution of the sea lamprey (*Petromyzon marinus*)
922 in the northwest Atlantic. *Can. J. Fish. Aquat. Sci.* 48, 832-842.
923 <https://doi.org/10.1139/f91-099>

- 924 Halpern, B.S., Frazier, M., Potapenko, J., Casey, K.S., Koenig, K., Longo, C.,
925 Lowndes, J.S., Rockwood, R.C., Selig, E.R., Selkoe, K.A., Walbridge, S., 2015.
926 Spatial and temporal changes in cumulative human impacts on the world's
927 ocean. *Nat. Commun.* 6, 1-7. <https://doi.org/10.1038/ncomms8615>
- 928 He, P., Chopin, F., Suuronen, P., Ferro, R.S.T and Lansley, J. 2021. Classification
929 and illustrated definition of fishing gears. *FAO Fisheries and Aquaculture*
930 *Technical Paper No. 672*. Rome, FAO. <https://doi.org/10.4060/cb4966en> (last
931 accessed 22/09/2020).
- 932 Isaac, N.J.B., Jarzyna, M.A., Keil, P., Dambly, L.I., Boersch-Supan, P.H., Browning,
933 E., Freeman, S.N., Golding, N., Guillera-Arroita, G., Henrys, P.A., Jarvis, S.,
934 Lahoz-Monfort, J., Pagel, J., Pescott, O.L., Schmucki, R., Simmonds, E.G.,
935 O'Hara, R.B., 2020. Data Integration for Large-Scale Models of Species
936 Distributions. *Trends Ecol. Evol.* 35, 56-67.
937 <https://doi.org/10.1016/j.tree.2019.08.006>
- 938 ICES. 2005. Report of the Study Group on the Bycatch of Salmon in Pelagic Trawl
939 Fisheries (SGBYSAL), 8-11 February 2004, Bergen, Norway. *ICES CM*
940 *2005/ACFM:13*. 41 pp.
- 941 ICES. 2020. Working Group with the Aim to Develop Assessment Models and
942 Establish Biological Reference Points for Sea Trout (*Anadromous Salmo trutta*)
943 Populations (WGTRUTTA; outputs from 2019 meeting). *ICES Scientific Reports*.
944 *2:59*. 59 pp. <http://doi.org/10.17895/ices.pub.7431>
- 945 Isaac, N.J.B., Jarzyna, M.A., Keil, P., Dambly, L.I., Boersch-Supan, P.H., Browning,
946 E., Freeman, S.N., Golding, N., Guillera-Arroita, G., Henrys, P.A., Jarvis, S.,
947 Lahoz-Monfort, J., Pagel, J., Pescott, O.L., Schmucki, R., Simmonds, E.G.,
948 O'Hara, R.B., 2020. Data Integration for Large-Scale Models of Species
949 Distributions. *Trends Ecol. Evol.* 35, 56-67.
950 <https://doi.org/10.1016/j.tree.2019.08.006>
- 951 Jiménez-Valverde, A., Lobo, J.M., 2007. Threshold criteria for conversion of
952 probability of species presence to either-or presence-absence. *Acta*
953 *Oecologica* 31, 361-369. <https://doi.org/10.1016/j.actao.2007.02.001>
- 954 Kappel, C. V., 2005. Losing pieces of the puzzle: Threats to marine, estuarine, and
955 diadromous species. *Front. Ecol. Environ.* 3, 275-282.
956 [https://doi.org/10.1890/1540-9295\(2005\)003\[0275:LPOTPT\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2005)003[0275:LPOTPT]2.0.CO;2)
- 957 Keith, P., Poulet, N., Denys, G., Changeux, T., Feunteun, E., et Persat, H., 2020.
958 Les poissons d'eau douce de France. *Biotope, Publications scientifiques du*
959 *MNHN*. 703 p
- 960 Kellner, K.F., Swihart, R.K., 2014. Accounting for Imperfect Detection in Ecology: A
961 Quantitative Review. *PLoS One* 9, e111436.
962 <https://doi.org/10.1371/journal.pone.0111436>
- 963 Korpinen, S., Laamanen, L., Bergström, L., Nurmi, M., Andersen, J.H., Haapaniemi,
964 J., Harvey, E.T., Murray, C.J., Peterlin, M., Kallenbach, E., Klančnik, K.,
965 Stein, U., Tunesi, L., Vaughan, D., Reker, J., 2021. Combined effects of
966 human pressures on Europe's marine ecosystems. *Ambio* 50, 1325-1336.
967 <https://doi.org/10.1007/s13280-020-01482-x>
- 968 Kristensen, M., Righton, D., del Villar-Guerra, D., Baktoft, H., Aarestrup, K., 2018.
969 Temperature and depth preferences of adult sea trout *Salmo trutta* during
970 the marine migration phase. *Mar. Ecol. Prog. Ser.* 599, 209-224.
971 <https://doi.org/10.3354/meps12618>

- 972 Lambert, C., Authier, M., Dorémus, G., Laran, S., Panigada, S., Spitz, J., Van
973 Canneyt, O., Ridoux, V., 2020. Setting the scene for Mediterranean litterscape
974 management: The first basin-scale quantification and mapping of floating
975 marine debris. *Environ. Pollut.* 263, 114430.
976 <https://doi.org/10.1016/j.envpol.2020.114430>
- 977 Lança, M.J., Machado, M., Mateus, C.S., Lourenço, M., Ferreira, A.F., Quintella,
978 B.R., Almeida, P.R., 2014. Investigating Population Structure of Sea Lamprey
979 (*Petromyzon marinus*, L.) in Western Iberian Peninsula Using Morphological
980 Characters and Heart Fatty Acid Signature Analyses. *PLoS One* 9, e108110.
981 <https://doi.org/10.1371/journal.pone.0108110>
- 982 Lassalle, G., Béguer, M., Beaulaton, L., Rochard, E., 2008. Diadromous fish
983 conservation plans need to consider global warming issues: An approach using
984 biogeographical models. *Biol. Conserv.* 141, 1105-1118.
985 <https://doi.org/10.1016/j.biocon.2008.02.010>
- 986 Lassalle, G., 2021. EuroDiad version 4.0, <https://doi.org/10.15454/IVVAIC>, Portail
987 Data INRAE, V2, UNF:6:X15FgpfOWssoJvGSg0wyoA== [fileUNF]
- 988 Latimer, A.M., Wu, S., Gelfand, A.E., Silander Jr., J.A., 2006. Building Statistical
989 Models To Analyze Species Distributions. *Ecol. Appl.* 16, 33-50.
990 <https://doi.org/10.1890/04-0609>
- 991 Leathwick, J.R., Rowe, D., Richardson, J., Elith, J., Hastie, T., 2005. Using
992 multivariate adaptive regression splines to predict the distributions of New
993 Zealand's freshwater diadromous fish. *Freshw. Biol.* 50, 2034-2052.
994 <https://doi.org/10.1111/j.1365-2427.2005.01448.x>
- 995 Legrand, M., Briand, C., Buisson, L., Artur, G., Azam, D., Baisez, A., Barracou, D.,
996 Bourré, N., Carry, L., Caudal, A.-L., Charrier, F., Corre, J., Croguennec, E.,
997 Der Mikaélian, S., Josset, Q., Le Gurun, L., Schaeffer, F., Laffaille, P., 2020.
998 Contrasting trends between species and catchments in diadromous fish counts
999 over the last 30 years in France. *Knowl. Manag. Aquat. Ecosyst.* 2020-Janua,
1000 7. <https://doi.org/10.1051/kmae/2019046>
- 1001 Leroy, B., Delsol, R., Hugueny, B., Meynard, C.N., Barhoumi, C., Barbet-Massin, M.,
1002 Bellard, C., 2018. Without quality presence-absence data, discrimination
1003 metrics such as TSS can be misleading measures of model performance. *J.*
1004 *Biogeogr.* 45, 1994-2002. <https://doi.org/10.1111/jbi.13402>
- 1005 Limburg, K.E., Waldman, J.R., 2009. Dramatic Declines in North Atlantic
1006 Diadromous Fishes. *Bioscience* 59, 955-965.
1007 <https://doi.org/10.1525/bio.2009.59.11.7>
- 1008 Lin, H., Bush, A., Linke, S., Possingham, H.P., Brown, C.J., 2017. Climate change
1009 decouples marine and freshwater habitats of a threatened migratory fish.
1010 *Divers. Distrib.* 23, 751-760. <https://doi.org/10.1111/ddi.12570>
- 1011 Loiselle, B.A., Howell, C.A., Graham, C.H., Goerck, J.M., Brooks, T., Smith, K.G.,
1012 Williams, P.H., 2003. Avoiding Pitfalls of Using Species Distribution Models in
1013 Conservation Planning. *Conserv. Biol.* 17, 1591-1600.
1014 <https://doi.org/10.1111/j.1523-1739.2003.00233.x>
- 1015 Lomba, A., Pellissier, L., Randin, C., Vicente, J., Moreira, F., Honrado, J., Guisan,
1016 A., 2010. Overcoming the rare species modelling paradox: A novel hierarchical
1017 framework applied to an Iberian endemic plant. *Biol. Conserv.* 143, 2647-
1018 2657. <https://doi.org/10.1016/j.biocon.2010.07.007>
- 1019 Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C.,
1020 Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B.C., 2006. Depletion,

- 1021 Degradation, and Recovery Potential of Estuaries and Coastal Seas. *Science*.
1022 312, 1806-1809. <https://doi.org/10.1126/science.1128035>
- 1023 MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, A.A., Langtimm,
1024 C.A., 2002. Estimating site occupancy rates when detection probabilities are
1025 less than one. *Ecology* 83, 2248-2255. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2)
1026 [9658\(2002\)083\[2248:ESORWD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2)
- 1027 Maes, J., Stevens, M., Breine, J., 2007. Modelling the migration opportunities of
1028 diadromous fish species along a gradient of dissolved oxygen concentration in
1029 a European tidal watershed. *Estuar. Coast. Shelf Sci.* 75, 151-162.
1030 <https://doi.org/10.1016/j.ecss.2007.03.036>
- 1031 Maxwell, D., Jennings, S., 2005. Power of monitoring programmes to detect decline
1032 and recovery of rare and vulnerable fish. *J. Appl. Ecol.* 42, 25-37.
1033 <https://doi.org/10.1111/j.1365-2664.2005.01000.x>
- 1034 McDowall, R.M., 2009. Making the Best of Two Worlds : Diadromy in the Evolution,
1035 Ecology, and Conservation of Aquatic Organisms. *Am. Fish. Soc. Symp.* 69, 1-
1036 22.
- 1037 Merg, M.-L., Dézerald, O., Kreutzenberger, K., Demski, S., Reyjol, Y., Usseglio-
1038 Polatera, P., Belliard, J., 2020. Modeling diadromous fish loss from historical
1039 data: Identification of anthropogenic drivers and testing of mitigation
1040 scenarios. *PLoS One* 15, e0236575.
1041 <https://doi.org/10.1371/journal.pone.0236575>
- 1042 Meyer, C.F.J., Aguiar, L.M.S., Aguirre, L.F., Baumgarten, J., Clarke, F.M., Cosson,
1043 J.F., Villegas, S.E., Fahr, J., Faria, D., Furey, N., Henry, M., Hodgkison, R.,
1044 Jenkins, R.K.B., Jung, K.G., Kingston, T., Kunz, T.H., Cristina Macswiney
1045 Gonzalez, M., Moya, I., Patterson, B.D., Pons, J.M., Racey, P.A., Rex, K.,
1046 Sampaio, E.M., Solari, S., Stoner, K.E., Voigt, C.C., von Staden, D., Weise,
1047 C.D., Kalko, E.K.V., 2011. Accounting for detectability improves estimates of
1048 species richness in tropical bat surveys. *J. Appl. Ecol.* 48, 777-787.
1049 <https://doi.org/10.1111/j.1365-2664.2011.01976.x>
- 1050 Moland, E., Olsen, E.M., Knutsen, H., Garrigou, P., Espeland, S.H., Kleiven, A.R.,
1051 Andre, C., Knutsen, J.A., 2013. Lobster and cod benefit from small-scale
1052 northern marine protected areas: inference from an empirical before-after
1053 control-impact study. *Proc. R. Soc. B Biol. Sci.* 280, 1-10.
1054 <https://doi.org/10.1098/rspb.2012.2679>
- 1055 Moriarty, M., Sethi, S.A., Pedreschi, D., Smeltz, T.S., McGonigle, C., Harris, B.P.,
1056 Wolf, N., Greenstreet, S.P.R., 2020. Combining fisheries surveys to inform
1057 marine species distribution modelling. *ICES J. Mar. Sci.* 77, 539-552.
1058 <https://doi.org/10.1093/icesjms/fsz254>
- 1059 Nieto, A., Ralph, G.M., Comeros-Raynal, M.T., Kemp, J., Garcia Criado, M., Allen,
1060 D.J., Dulvy, N.K., Walls, R.H.L., Russell, B., Pollard, D., et al., 2015.
1061 European Red List of marine fishes. Luxembourg: Publications Office of the
1062 European Union.
1063 [https://ec.europa.eu/environment/nature/conservation/species/redlist/dow](https://ec.europa.eu/environment/nature/conservation/species/redlist/downloads/European_marine_fishes.pdf)
1064 [nloads/European_marine_fishes.pdf](https://ec.europa.eu/environment/nature/conservation/species/redlist/downloads/European_marine_fishes.pdf) (last accessed 01/07/2020)
- 1065 Mork, K.A., Gilbey, J., Hansen, L.P., Jensen, A.J., Jacobsen, J.A., Holm, M., Holst,
1066 J.C., Ó Maoiléidigh, N., Vikebø, F., McGinnity, P., Melle, W., Thomas, K.,
1067 Verspoor, E., Wennevik, V., 2012. Modelling the migration of post-smolt
1068 Atlantic salmon (*Salmo salar*) in the Northeast Atlantic. *ICES J. Mar. Sci.* 69,
1069 1616-1624. <https://doi.org/10.1093/icesjms/fss108>

- 1070 Northrup, J.M., Gerber, B.D., 2018. A comment on priors for Bayesian occupancy
1071 models. PLoS One 13, e0192819.
1072 <https://doi.org/10.1371/journal.pone.0192819>
- 1073 Pavlov, D.S., Zvezdin, A.O., Kostin, V. V., Tsimbalov, I.A., Kucheryavyy, A. V.,
1074 2017. Temporal characteristics of downstream migration of smolts of the
1075 European river lamprey *Lampetra fluviatilis* in the Chernaya River. Biol. Bull.
1076 44, 290-295. <https://doi.org/10.1134/S1062359017030062>
- 1077 Pendoley, K.L., Schofield, G., Whittock, P.A., Ierodiaconou, D., Hays, G.C., 2014.
1078 Protected species use of a coastal marine migratory corridor connecting
1079 marine protected areas. Mar. Biol. 161, 1455-1466.
1080 <https://doi.org/10.1007/s00227-014-2433-7>
- 1081 Prince, J., Hordyk, A., 2019. What to do when you have almost nothing: A simple
1082 quantitative prescription for managing extremely data-poor fisheries. Fish
1083 Fish. 20, 224-238. <https://doi.org/10.1111/faf.12335>
- 1084 Probst, W.N., Stelzenmüller, V., Rambo, H., Moriarty, M., Greenstreet, S.P.R.,
1085 2021. Identifying core areas for mobile species in space and time: A case
1086 study of the demersal fish community in the North Sea. Biol. Conserv. 254,
1087 108946. <https://doi.org/10.1016/j.biocon.2020.108946>
- 1088 Quemmerais-Amice, F., Barrere, J., La Rivière, M., Contin, G., Bailly, D., 2020. A
1089 Methodology and Tool for Mapping the Risk of Cumulative Effects on Benthic
1090 Habitats. Front. Mar. Sci. 7. <https://doi.org/10.3389/fmars.2020.569205>
- 1091 Righton, D., Westerberg, H., Feunteun, E., Økland, F., Gargan, P., Amilhat, E.,
1092 Metcalfe, J., Lobon-Cervia, J., Sjöberg, N., Simon, J., Acou, A., Vedor, M.,
1093 Walker, A., Trancart, T., Brämick, U., Aarestrup, K., 2016. Empirical
1094 observations of the spawning migration of European eels: The long and
1095 dangerous road to the Sargasso Sea. Sci. Adv. 2, e1501694.
1096 <https://doi.org/10.1126/sciadv.1501694>
- 1097 Rikardsen, A.H., Righton, D., Strøm, J.F., Thorstad, E.B., Gargan, P., Sheehan, T.,
1098 Økland, F., Chittenden, C.M., Hedger, R.D., Næsje, T.F., Renkawitz, M.,
1099 Sturlaugsson, J., Caballero, P., Baktoft, H., Davidsen, J.G., Halttunen, E.,
1100 Wright, S., Finstad, B., Aarestrup, K., 2021. Redefining the oceanic
1101 distribution of Atlantic salmon. Sci. Rep. 11, 12266.
1102 <https://doi.org/10.1038/s41598-021-91137-y>
- 1103 Royle, J.A., Link, W.A., 2006. Generalized site occupancy models allowing for false
1104 positive and false negative errors. Ecology 87, 835-841.
1105 [https://doi.org/10.1890/0012-9658\(2006\)87\[835:GSOMAF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[835:GSOMAF]2.0.CO;2)
- 1106 Simmonds, E.G., Jarvis, S.G., Henrys, P.A., Isaac, N.J.B., O'Hara, R.B., 2020. Is
1107 more data always better? A simulation study of benefits and limitations of
1108 integrated distribution models. Ecography (Cop.). 43, 1413-1422.
1109 <https://doi.org/10.1111/ecog.05146>
- 1110 Spiegelhalter, D.J., Best, N.G., Carlin, B.P., van der Linde, A., 2002. Bayesian
1111 measures of model complexity and fit. J. R. Stat. Soc. Ser. B (Statistical
1112 Methodol. 64, 583-639. <https://doi.org/10.1111/1467-9868.00353>
- 1113 Stratoudakis, Y., Correia, C., Belo, A.F., de Almeida, P.R., 2020. Improving
1114 participated management under poor fishers' organization: Anadromous
1115 fishing in the estuary of Mondego River, Portugal. Mar. Policy 119, 104049.
1116 <https://doi.org/10.1016/j.marpol.2020.104049>
- 1117 Stratoudakis, Y., Mateus, C.S., Quintella, B.R., Antunes, C., Raposo de Almeida, P.,
1118 2016. Exploited anadromous fish in Portugal: Suggested direction for

- 1119 conservation and management. *Mar. Policy* 73, 92-99.
1120 <https://doi.org/10.1016/j.marpol.2016.07.031>
- 1121 Takashina, N., Mougí, A., 2014. Effects of marine protected areas on overfished
1122 fishing stocks with multiple stable states. *J. Theor. Biol.* 341, 64-70.
1123 <https://doi.org/10.1016/j.jtbi.2013.09.027>
- 1124 Taverny, C., Elie, P., 2001. Répartition spatio-temporelle de la grande alose *Alosa*
1125 *alosa* (Linne, 1766) et de l'Alose feinte *Alosa fallax* (Lacépède, 1803) dans le
1126 Golfe de Gascogne. *Bull. Français la Pêche la Piscic.* 803-821.
1127 <https://doi.org/10.1051/kmae:2001020>
- 1128 Taverny, C., Lassalle, G., Ortusi, I., Roqueplo, C., Lepage, M., Lambert, P., 2012.
1129 From shallow to deep waters: habitats used by larval lampreys (genus
1130 *Petromyzon* and *Lampetra*) over a western European basin. *Ecol. Freshw. Fish*
1131 21, 87-99. <https://doi.org/10.1111/j.1600-0633.2011.00526.x>
- 1132 Teruzzi, A., Di Biagio, V., Feudale, L., Bolzon, G., Lazzari, P., Salon, S., Di Biagio,
1133 V., Coidessa, G., and Cossarini, G., 2021. Mediterranean Sea Biogeochemical
1134 Reanalysis (CMEMS MED-Biogeochemistry, MedBFM3 system) (Version 1) [Data
1135 set]. Copernicus Monitoring Environment Marine Service (CMEMS).
1136 https://doi.org/10.25423/CMCC/MEDSEA_MULTIYEAR_BGC_006_008_MEDBFM3
- 1137 Thiel, R., Salewski, V., 2003. Verteilung und Wanderung von Neunaugen im
1138 Elbeästuar (Deutschland). *Limnologica* 33, 214-226.
1139 [https://doi.org/10.1016/S0075-9511\(03\)80015-4](https://doi.org/10.1016/S0075-9511(03)80015-4)
- 1140 Trancart, T., Rochette, S., Acou, A., Lasne, E., Feunteun, E., 2014. Modeling
1141 marine shad distribution using data from French bycatch fishery surveys. *Mar.*
1142 *Ecol. Prog. Ser.* 511, 181-192. <https://doi.org/10.3354/meps10907>
- 1143 Verhelst, P., Reubens, J., Buysse, D., Goethals, P., Van Wichelen, J., Moens, T.,
1144 2021. Toward a roadmap for diadromous fish conservation: the Big Five
1145 considerations. *Front. Ecol. Environ.* fee.2361.
1146 <https://doi.org/10.1002/fee.2361>
- 1147 Vieilledent, G., Merow, C., Guelat, J., Latimer, A.M., Kery, M., Gelfand, A.E.,
1148 Wilson, A.M., Mortier, F., Silander Jr., J.A., 2014. hSDM: Hierarchical
1149 Bayesian Species Distribution Models. R package version 1.4. [https://CRAN.R-](https://CRAN.R-project.org/package=hSDM)
1150 [project.org/ package=hSDM](https://CRAN.R-project.org/package=hSDM)
- 1151 Waldman, J.R., Quinn, T.P., 2022. North American diadromous fishes: Drivers of
1152 decline and potential for recovery in the Anthropocene. *Sci. Adv.* 8.
1153 <https://doi.org/10.1126/sciadv.abl5486>
- 1154 Wauchope, H.S., Jones, J.P.G., Geldmann, J., Simmons, B.I., Amano, T., Blanco,
1155 D.E., Fuller, R.A., Johnston, A., Langendoen, T., Mundkur, T., Nagy, S.,
1156 Sutherland, W.J., 2022. Protected areas have a mixed impact on waterbirds,
1157 but management helps. *Nature* 605, 103-107.
1158 <https://doi.org/10.1038/s41586-022-04617-0>
- 1159 Wilson, K., and Veneranta, L. (Eds). 2019. Data-limited diadromous species -
1160 review of European status. ICES Cooperative Research Report No. 348. 273 pp.
1161 <http://doi.org/10.17895/ices.pub.5253>
- 1162 Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S.,
1163 Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A.,
1164 Stachowicz, J.J., Watson, R., 2006. Impacts of Biodiversity Loss on Ocean
1165 Ecosystem Services. *Science* (80-.). 314, 787-790.
1166 <https://doi.org/10.1126/science.1132294>

- 1167 Worm, B., Davis, B., Ketteimer, L., Ward-Paige, C.A., Chapman, D., Heithaus, M.R.,
1168 Kessel, S.T., Gruber, S.H., 2013. Global catches, exploitation rates, and
1169 rebuilding options for sharks. *Mar. Policy* 40, 194-204.
1170 <https://doi.org/10.1016/j.marpol.2012.12.034>
- 1171 Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty,
1172 M.J., Fulton, E.A., Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K.,
1173 Mace, P.M., McClanahan, T.R., Minto, C., Palumbi, S.R., Parma, A.M., Ricard,
1174 D., Rosenberg, A.A., Watson, R., Zeller, D., 2009. Rebuilding global fisheries.
1175 *Science*. 325, 578-85. <https://doi.org/10.1126/science.1173146>
- 1176 Worm, B., Sandow, M., Oschlies, A., Lotze, H., Myers, R., 2005. Global patterns of
1177 predator diversity in the open oceans. *Science*. 309, 1365-9.
1178 <https://doi.org/10.1126/science.1113399>

