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Frida Ben Rais Lasram, Tarek Hattab, Quentin Nogues, Gregory Beaugrand, Jean-Claude Dauvin, Ghassen Halouani, François Le Loc'h, Nathalie Niquil, Boris Leroy

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# 1 An open-source framework to model present and future marine species distributions at local 2 scale

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5 Frida Ben Rais Lasram<sup>1\*</sup>, Tarek Hattab<sup>1,2</sup>, Quentin Nogues<sup>3</sup>, Grégory Beaugrand<sup>1</sup>, Jean Claude  
6 Dauvin<sup>4</sup>, Ghassen Halouani<sup>3,5</sup>, François Le Loc'h<sup>6</sup>, Nathalie Niquil<sup>3</sup>, Boris Leroy<sup>7</sup>

7  
8 <sup>1</sup> Univ. Littoral Côte d'Opale, Univ. Lille, CNRS, UMR 8187, LOG, Laboratoire d'Océanologie et de  
9 Géosciences, F 62930 Wimereux, France

10 <sup>2</sup> MARBEC, Univ Montpellier, CNRS, Ifremer, IRD Sète, avenue Jean Monet, Sète, France

11 <sup>3</sup> Normandie Université UNICAEN, UMR BOREA (MNHN, UPMC, UCN, CNRS-7208, IRD-207)  
12 CS 14032, 14000 Caen, France

13 <sup>4</sup> Normandie Université UNICAEN, UMR M2C (UCN, UR, CNRS-6143), 24 rue des Tilleuls, 14000  
14 Caen Cedex, France

15 <sup>5</sup> Unité Haliutique Manche-Mer du Nord Ifremer, HMMN, F-62200 Boulogne-sur-mer, France

16 <sup>6</sup> IRD, Univ. Brest, CNRS, Ifremer, LEMAR, IUEM, 29280 Plouzané, France

17 <sup>7</sup> MNHN, UMR BOREA (MNHN, UPMC, UCN, CNRS-7208, IRD-207) 43 rue Cuvier, 75005 Paris,  
18 France

19  
20 \* Corresponding author: frida.lasram@univ-littoral.fr

## 21 22 **Highlights**

- 23 - A new habitat modelling open-source framework for non-modeller ecologists.
- 24 - An explicit consideration of the third dimension and habitat filter in the modeling procedure.
- 25 - An automated procedure for data processing.
- 26 - The proposed framework avoids higher projections of species loss.

## 27 28 **Abstract**

29 Species Distribution Models (SDMs) are useful tools to project potential future species distributions  
30 under climate change scenarios. Despite the ability to run SDMs in recent and reliable tools, there are  
31 some misuses and proxies that are widely practiced and rarely addressed together, particularly when  
32 dealing with marine species.

33 In this paper, we propose an open-source framework that includes (i) a procedure for homogenizing  
34 occurrence data to reduce the influence of sampling bias, (ii) a procedure for generating pseudo-  
35 absences, (iii) a hierarchical-filter approach, (iv) full incorporation of the third dimension by  
36 considering climatic variables at multiple depths and (v) building of maps that predict current and  
37 potential future ranges of marine species. This framework is available for non-modeller ecologists  
38 interested in investigating future species ranges with a user-friendly script. We investigated the  
39 robustness of the framework by applying it to marine species of the Eastern English Channel.  
40 Projections were built for the middle and the end of this century under RCP2.6 and RCP8.5 scenarios.

## 41 42 43 **Keywords**

44 Bioclimatic envelope models, habitat models, pseudo-absences, vertical gradient, automated  
45 modelling framework, future projections

## 46 47 48 **1. Introduction**

49 In a changing world, predicting suitable habitats and potential future species distributions is a central  
50 issue in ecology. To this end, Species Distribution Models (SDMs) (also called, depending on the  
51 study context, Ecological Niche Models (ENMs), Habitat Suitability Models (HSMs), Habitat  
52 Distribution Models (HDMs), Climate Envelope Models (CEM) and other nomenclatures) have been  
53 widely used in both terrestrial (e.g. Carboni et al. 2018) and marine realms (e.g. Cheung et al. 2009) to  
54 map and predict shifts in species ranges in response to global change, particularly climate change.

55 We refer here to all models that correlate species occurrences or abundance data with environmental  
56 spatial data layers to predict the suitability of any site for a given species. Shifts in species  
57 distributions are subsequently projected under different climate change scenarios. These SDMs are  
58 correlative and do not incorporate mechanistic information, such as species' physiological response to  
59 abiotic conditions.

60  
61 In the marine realm, there is a flourishing literature carried at global (e.g. Tittensor et al. 2010),  
62 regional (e.g. Albouy et al. 2013) and local (e.g. Hattab et al. 2014) scales that have highlighted future  
63 species range shift towards the poles (e.g. Morley et al. 2018), deepening (e.g. Pinsky et al. 2013),  
64 local extinctions (e.g. Jones & Cheung 2014), habitat fragmentation (e.g. Ben Rais Lasram et al.  
65 2010), species invasions (e.g. Byrne et al. 2016) and impacts on life-history traits (e.g. Genner et al.,  
66 2010), on abundances (e.g. Hermant et al., 2010) and on trophic networks (e.g. Doney et al. 2012) due  
67 to changing climate in the next few decades.

68  
69 SDMs have been applied at either the species (e.g. Alabia et al. 2015) or community level (Morley et  
70 al. 2018) to assess species vulnerabilities for conservation purposes (Jones et al. 2013) and fisheries  
71 management (Asch et al. 2018), and to couple with end-to-end models to simulate spatial patterns of  
72 predator-prey interactions (Grüss et al. 2018). Moreover, trophic ecologists are increasingly interested  
73 in using SDMs predictions as input for trophic models to investigate how food webs may reorganize  
74 due to individual species' responses to climate change (Woodward et al. 2010, Chaalali et al. 2016).

75  
76 Although SDMs are useful and reliable tools to predict past, present and future species ranges, they  
77 rely on strong assumptions and are subject to many uncertainties (Goberville et al. 2015). These  
78 uncertainties are well known and occur at every stage of the modelling process (e.g. data collection,  
79 choice of algorithms and parameters, model evaluation), but few studies consider them explicitly  
80 (Planque 2015, Brun et al. 2020). Moreover, despite the ability to run SDMs in recent, reliable and  
81 user-friendly packages and the availability of data in huge global databases (e.g. GBIF, OBIS and  
82 FishBase for species occurrences; Bio-ORACLE and MarSpec for environmental variables), there are  
83 some misuses and proxies (e.g. data quality, selection of environmental drivers, parametrization,  
84 model selection, spatial and temporal scales) that are widely practiced and rarely addressed in the  
85 literature (see Jarnevich et al. 2015, Yalcin & Leroux 2017, Duffy & Chown 2017 for examples of  
86 reviews and recommendations).

87  
88 Although global georeferenced data have become more available for both species  
89 occurrence/abundance data and environmental variables, less concern has been given to assessing data  
90 quality in the marine realm. For example, sampling bias due to diverse and/or non-standardized  
91 monitoring surveys may increase the risk of undersampling (e.g. due to selectivity of a sampling  
92 method) or oversampling (e.g. in neritic regions or in areas with a long history of monitoring).  
93 Consequently, occurrence data often represent a biased sample of species populations, which may  
94 significantly alter models calibration (Guillera-Aroita et al. 2015). Careful assessment and pre-  
95 processing of data are thus recommended to mitigate effects of sampling bias associated with large-  
96 scale occurrence data.

97  
98 Most studies in the marine realm have been based on two-dimensional SDMs even though species are  
99 fundamentally distributed in three dimensions. Duffy & Chown (2017) emphasized the importance of  
100 incorporating the third dimension in marine ecological models and showed that ignoring it may  
101 influence predictions greatly. Some studies (e.g. Weinmann et al. 2013, Gallardo et al. 2015, Asch et  
102 al. 2018) continue to use sea-surface temperature for both pelagic and benthic species despite the  
103 temperature gradient between the surface and the bottom.

104  
105 Moreover, species–environment relationships depend strongly on the scale at which the dependent (i.e.  
106 species occurrences) and independent (i.e. environmental data) variables are considered (Cushman &  
107 McGarigal 2004). Scale issues are thus important to consider in SDMs especially for the downscaling  
108 process (Da Re et al. 2020). It is for example important to choose the appropriate grid size and the  
109 relevant variables consistent with the scale at which the ecophysiological processes show greatest

110 variation (Austin et al. 2011). . The common view is that large-scale processes determine local species  
111 diversity, whereas small-scale processes tend to limit the number of species that currently occupy a  
112 given site (Pont et al. 2005). To address this issue, a two-stage hierarchical approach based on the  
113 concept of “hierarchical filters” is commonly (but not always) used in the terrestrial realm but more  
114 rarely in the marine realm (see Heino et al. 2009 and Hattab et al. 2014 for a review of underlying  
115 assumptions). In this filtering approach, SDMs are first built at the global scale to consider the full  
116 range of climatic conditions (temperature and salinity) species encounters (SDMs can then be termed  
117 as Bioclimatic Envelope Models (BEMs)). Then, a habitat filter considering factors at the local scale  
118 (such as seafloor type) is applied (the filter can then be termed as Habitat Models (HMs)) . This two-  
119 stage approach improves predictions of species distributions at the local scale.  
120 Finally, as policy and decision making require spatially explicit information about the state of and  
121 future trends in species ranges, it is useful to generate current and future maps, along with response  
122 curves and model performances, for each species.

123  
124 A broad set of tools exists to model species distribution (e.g. BIOMOD (Thuiller et al. 2009),  
125 MAXENT (Phillips et al. 2006), openModeller (de Souza Muñoz et al. 2011), ModEco (Guo & Liu  
126 2010), ENMTool (Warren et al. 2010), sdm (Naimi & Araújo 2016), NPPEN (Beaugrand et al. 2011)  
127 and dismo package (Hijmans et al. 2017)). These platforms include a comprehensive set of advanced  
128 algorithms that generally need to be supplemented by R scripts to pre-process data or to be coupled  
129 with GIS softwares, making them somewhat difficult for non-modeller ecologists to use.

130  
131 In this paper, we propose a framework that includes (i) a procedure for homogenizing occurrence data  
132 to eliminate the influence of sampling bias, (ii) a procedure for generating pseudo-absences, (iii) a  
133 hierarchical-filter approach (i.e. global Bioclimatic Envelope Models (BEM) combined with local  
134 Habitat Models HM), (iv) full incorporation of the third dimension by considering climatic variables at  
135 multiple depths and (v) building of maps that predict current and future ranges of marine species. This  
136 framework is available as a ready-to-use R script hosted on GitHub for non-modeller ecologists  
137 interested in investigating future species ranges with a user-friendly script.

138 We investigated the robustness of the framework by applying it to 46 species representing a large part  
139 of the biomass in the Eastern English Channel (EEC). Projections were built for the middle and the  
140 end of this century under Representative Concentration Pathway (RCP) 2.6 (i.e. rapid mitigation of  
141 anthropogenic climate change, optimistic) and RCP8.5 (i.e. business-as-usual, pessimistic) scenarios  
142 of the IPCC (Intergovernmental Panel on Climate Change).

143  
144

## 145 **2. Model framework**

146 Although designed for the ecosystem of the EEC, our script can be applied to other ecosystems by  
147 replacing the habitat data files provided with the script with similar data files for another region. To  
148 illustrate application of the script, we considered 46 species representing a large part of the biomass of  
149 the EEC (Raoux et al. 2017), with at least 300 occurrences at the global scale and 100 occurrences at a  
150 regional scale. We provide the script and environmental data online, at  
151 <https://github.com/TarekHattab/SDM>. For the sake of reproducibility, the script comes with a Docker  
152 container (Merkel et al. 2014) including everything needed to run the script. The model framework is  
153 described in Figure 2.

154

### 155 **2.1 Step 1: Setting global parameters**

156 The script is designed to manage automatically all of the framework’s processing steps, described  
157 below. Users must set four parameters: (i) species’ scientific names, (ii) species’ vertical habitats, (iii)  
158 the algorithms to be used and (iv) the value of K in K-fold cross-validation.

159

### 160 **2.2 Step 2: Data acquisition**

#### 161 **2.2.1 Species occurrence data**

162 Species occurrences used in BEMs can be downloaded from five global biogeographic databases:

- 163 ▪ Ocean Biogeographic Information System (OBIS): <http://www.iobis.org/>
- 164 ▪ Global Biodiversity Information Facility (GBIF): <http://www.gbif.org/>

- 165     ▪     iNaturalist: <http://www.inaturalist.org>
- 166     ▪     VertNet (vertebrate biodiversity networks): <http://vertnet.org/>
- 167     ▪     Ecoengine (UC Berkeley's Natural History Data): <https://ecoengine.berkeley.edu/>

168     Our script cleans the global dataset by deleting erroneous occurrences (e.g. species occurring on land)  
169     and occurrences outside a user-defined period. In this study, we deleted records before 1955 and  
170     ultimately retained 1 944 154 occurrences from the five databases for the 46 species considered.  
171     Additional scientific survey data are available at the regional scale for the EEC and the Bay of Biscay.  
172     Thus, the global dataset was supplemented by scientific survey data from IBTS (1990-2016,  
173     <http://dx.doi.org/10.18142/17>), CGFS (1988-2016, <http://dx.doi.org/10.18142/11>) and EVHOE (1997-  
174     2006, <http://dx.doi.org/10.18142/8>) available from the DATRAS database ([http://www.ices.dk/marine-  
175     data/data-portals/Pages/DATRAS.aspx](http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx)) and also from other surveys of benthic and demersal taxa,  
176     such as LANCIE (1997-2002), PECTOW(2001), BENTHOSEINE (1998-1999) and CAMANOC  
177     (<http://dx.doi.org/10.17600/14001900>) (Appendix A). Ultimately, we retained 148 096 occurrences at  
178     the regional scale.

179

### 180     **2.2.2 Current and projected climatic data**

181     To calibrate BEMs, users can consider temperature and salinity climatologies from the global database  
182     WOD 2013 V2 (<https://www.nodc.noaa.gov/OC5/woa13/>), with a spatial resolution of 0.25°. These  
183     climatologies represent mean decadal temperatures and salinities for 1955-1964, 1965-1974, 1975-  
184     1984, 1985-1994, 1995-2004 and 2005-2012 for 40 depth layers. These variables were bilinearly  
185     interpolated at a 1/12<sup>th</sup>-degree spatial resolution (5 arcmin) and aggregated vertically by calculating  
186     mean temperature and salinity for the first 50 m of depth to calibrate pelagic species models, for the  
187     first 200 m of depth for benthopelagic species models and for the last 50 m of depth for benthic and  
188     demersal species models.

189

190     For projections, the script performs climate projections for 2041-2050 and 2091-2100 under two  
191     RCP2.6 (strong mitigation) and RCP8.5 (business-as-usual) scenarios. These projections are derived  
192     from three General Circulation Models (GCMs) of the Coupled Model Intercomparison Project,  
193     Phase 5 (CMIP5) (Taylor et al. 2012): (i) ESM2G (Geophysical Fluid Dynamics Laboratory; NOAA),  
194     (ii) CM5A-MR (Institut Pierre-Simon-Laplace) and (iii) ESM-MR (Max-Planck-Institut für  
195     Meteorologie). To avoid potential bias of the GCMs compared to historical data, the script calculates  
196     anomalies between 2041-2050/2091-2100 and 1955-2012. These anomalies are then added to the  
197     observed mean temperatures and salinities for the same period in WOD 2013 data. Current and  
198     projected climatic data are provided with the script.

199

### 200     **2.2.3 Habitat data**

201     Seafloor type, bathymetry, slope and aspect of the slope (i.e. eastness and northness) are used to build  
202     HMs for benthic and demersal species. Data are available from EMODnet Bathymetry  
203     (<http://www.emodnet-bathymetry.eu/>) and EMODnet Seabed Habitats ([http://www.emodnet-  
204     seabedhabitats.eu/](http://www.emodnet-seabedhabitats.eu/)) at a spatial resolution of 250 m. In our study, we aggregated EUNIS seafloor  
205     substrate classes into six simplified categories (mud, sand, muddy sand, sandy mud, coarse sediment  
206     and gravel). Habitat data grids are provided with the script.

207

### 208     **2.3 Step 3: Data pre-processing**

209     Once occurrence data have been downloaded, the script performs a spatiotemporal match between  
210     climatologies and occurrence of each species based on geographic coordinates of occurrences and their  
211     corresponding decade (to consider climate trends over the past 58 years) and the correct vertical layer,  
212     which corresponds to the vertical habitat of the species.

213     To address the risk of oversampling, and the ensuing over-representation of environmental features  
214     (Kramer-Schadt et al. 2013), we first applied an environmental filtering procedure (Beaugrand et al.,  
215     2011, Varela et al. 2014) to species occurrences to assign the same weight to over- and under-sampled  
216     regions.

217     To do this, the script creates a grid containing all combinations of temperature and salinity at the  
218     global scale for the period 1955-2012 with a resolution of 0.3°C × 0.3 salinity (which represents 100 ×

219 100 bins). Species occurrences are then projected onto this grid, and only one occurrence is retained in  
220 each cell of the grid

221  
222 The datasets we used were obtained from online databases of occurrences including presence-only  
223 data, but the BEMs used in the script require both presence and absence data. The script therefore  
224 generates pseudo-absences to better characterize the environmental conditions experienced by a  
225 species within the environmental background (Hattab et al. 2014). Pseudo-absences were generated  
226 outside the convex hull of presences in the environmental space (Cornwell et al. 2006, Getz &  
227 Wilmers 2004). The convex hull was defined as the smallest convex area in the environmental space  
228 containing all species records. A restricted convex hull was defined as a convex hull excluding  
229 occurrence points in the 1<sup>st</sup> and 99<sup>th</sup> percentiles for each environmental parameter in order to exclude  
230 observations in the most extreme environmental conditions. Thus, pseudo-absences are randomly  
231 selected by the script outside the environmental space described by this restricted convex hull, which  
232 is a proxy of the suitable environmental conditions (Figure 1).

233  
234 In HMs (SDMs used to characterize habitat), pseudo-absences were generated similarly but were  
235 based on the “Surface Range Envelope” (Thuiller et al. 2009). In this approach, rectilinear  
236 hypervolumes describing the 1<sup>st</sup> and 99<sup>th</sup> quantiles of the cells containing presences are used instead of  
237 the convex hull. Based on the statistical theory of model-based designs (d-designs; Hengl et al. 2009),  
238 the script generates as many pseudo-absences as presences.

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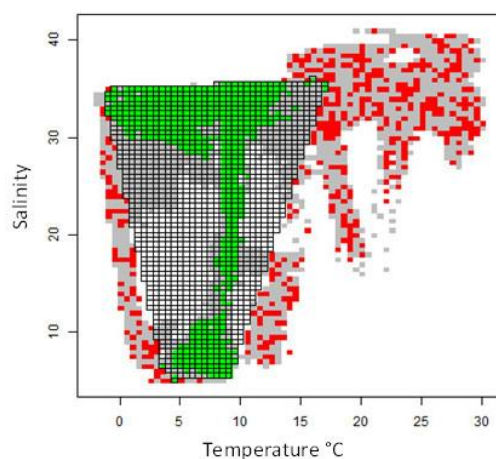
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256 Figure 1. Generation of pseudo-absences. Grey cells represent the environmental space as a  
257 combination of temperature and salinity at the global scale. Green cells represent the presence of a  
258 given species. The grid represents the restricted convex hull describing the 1<sup>st</sup> and 99<sup>th</sup> quantiles of the  
259 cells containing presences. Red cells represent pseudo-absences, which are generated randomly  
260 outside the convex hull.

261

#### 262 **2.4 Step 4: Bioclimatic envelope models BEMs**

263 Filtered presence data and the generated pseudo-absences were used to build BEMs that consisted of  
264 SDMs applied at the global scale to characterize mainly the bioclimatic envelope of each species  
265 according to its temperature and salinity preference. For each species, the script applies eight  
266 modelling techniques belonging to four model categories using the BIOMOD multi-model platform  
267 (Thuiller et al. 2009): multiple regressions (Generalized Linear Model, Generalized Additive Model,  
268 Multiple Adaptive Regression Splines), regression trees (Boosted Regression Tree, Random Forest,  
269 Classification Tree Analysis), discriminant analysis (Flexible Discriminant Analysis) and learning  
270 techniques (Artificial Neural Network). For each species, the eight models were calibrated using a  
271 random sample of the initial data (67%), while the remaining 33% were used to evaluate the model.

272 Users can perform a 3-fold cross validation procedure and assess model performance using both the  
273 True Skill Statistic (TSS; Allouche et al. 2006) and Continuous Boyce Index (CBI; Hirzel et al. 2006).  
274 Note that the script uses mean temperature and salinity from the first 50 m of depth to calibrate pelagic  
275 species models, from the first 200 m of depth for benthopelagic species models and from the last 50 m  
276 of depth for benthic and demersal species models.

277

278 For each species, 24 predictions of current climate envelopes (8 algorithms  $\times$  3 permutations) were  
279 calculated. Only models with CBI  $>$  0.5 for all three permutations were retained (i.e. models that are  
280 resilient to occurrence permutations) for projections of future potential bioclimatic envelopes for each  
281 species according to RCP2.6 and RCP8.5 scenarios. Finally, the script generates ensemble suitability  
282 maps by calculating the mean suitability of the 24 predictions weighted by the CBI to estimate model-  
283 based uncertainty (Thuiller et al. 2009). These maps could then be transformed into binary maps using  
284 a probability threshold that optimized the TSS. In addition, the script generates uncertainty maps by  
285 calculating the standard deviation of predictions.

286

### 287 **2.5 Step 5: Habitat models HMs**

288 HMs are SDMs used to characterize local habitat variability. Because habitat variables can be strongly  
289 intercorrelated, the script can remove multicollinearity by using the ordination method of Hill & Smith  
290 (1976). The resulting orthogonal and uncorrelated principal components are used as predictive  
291 variables in the HMs. The HMs, used only for benthic and demersal species, are built using the same  
292 method used to develop the BEMs.

293

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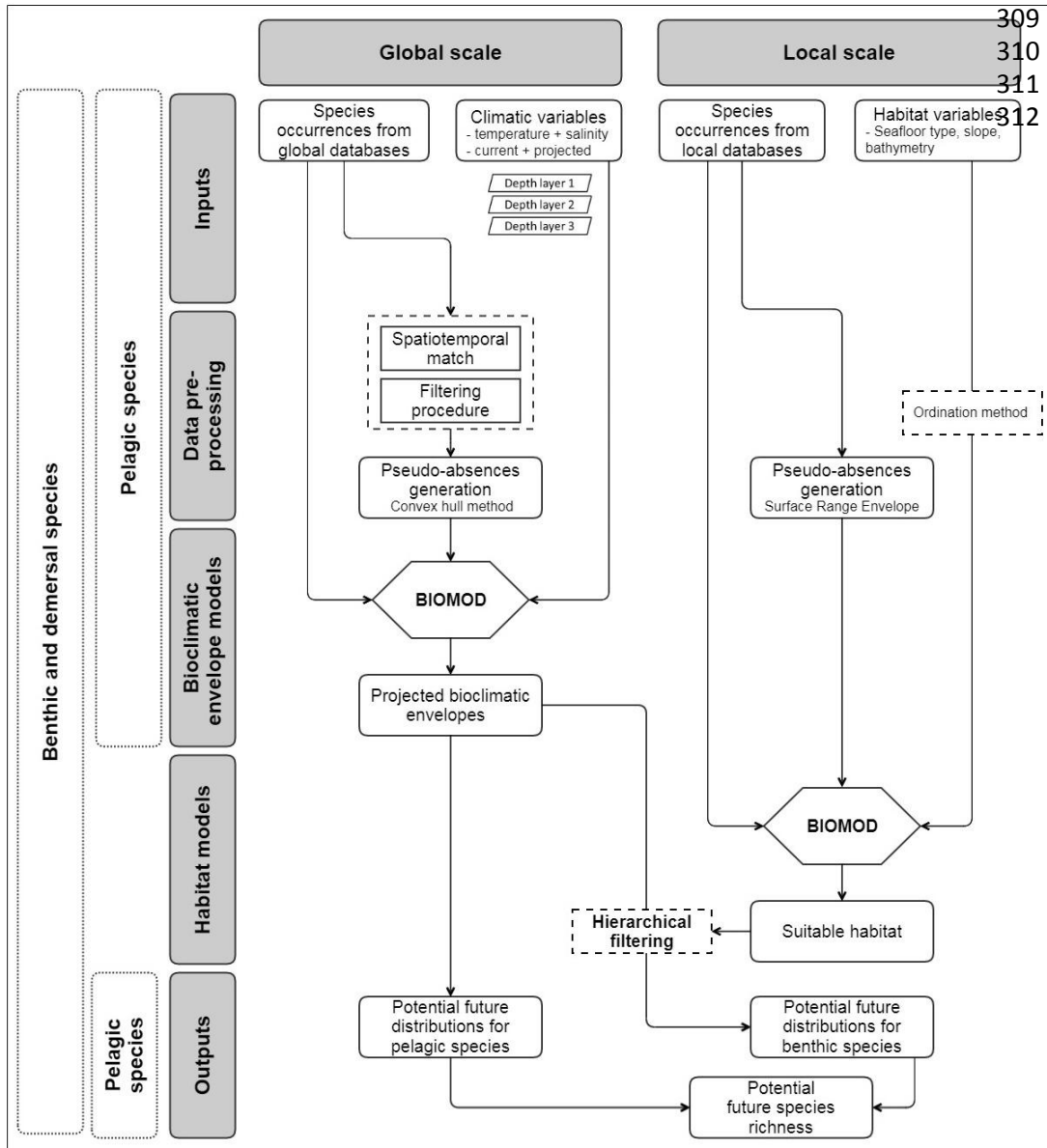
### 295 **2.6 Step 6: Combining BEMs and HMs**

296 For benthic and demersal species, users can extract the predicted bioclimatic envelope for their study  
297 area from the projected BEM maps. This represents the first hierarchical filter. Next, the habitat map is  
298 used to filter out habitats deemed unsuitable by the HM. The extracted cells can be resampled on a  
299 grid (we used one with 250 m resolution) using bilinear interpolation. Thus, an area is considered  
300 suitable for a species if both the first filter (BEM) and second filter (HM) predict it as suitable.

301

### 302 **2.7 Step 7: Visualizing predictions**

303 The final stage of the framework automatically plots current and future species ranges for both periods  
304 (2041-2050 and 2091-2100) under both scenarios (RCP2.6 and RCP8.5) using only BEM for pelagic  
305 and benthopelagic species and combined BEM and HM for benthic and demersal species. Maps are  
306 plotted in both suitability index and binary format. Response curves, model performances and number  
307 of occurrences can also be provided for each species.



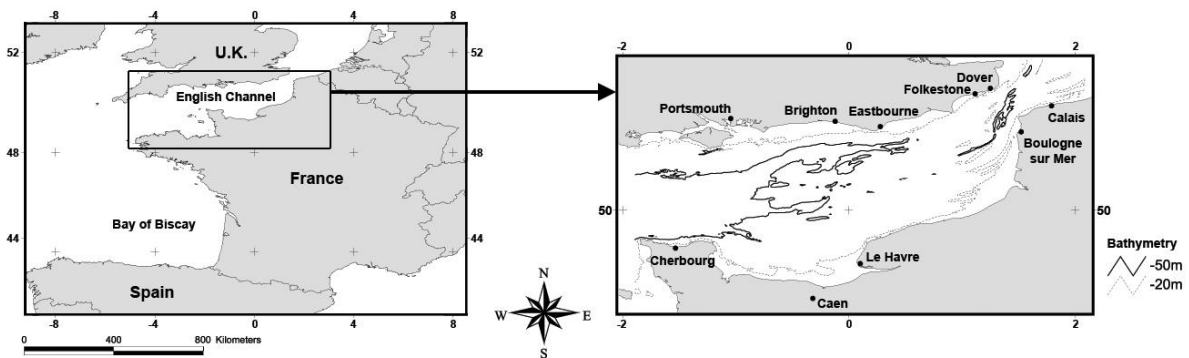
313 Figure 2. Computational framework and data processing steps  
 314  
 315

316 **3. Focus on the Eastern English Channel**

317 We applied this modelling framework to the EEC, an epicontinental sea with relatively shallow water  
318 (maximum 50 m), subject to a variety of hydrodynamic forces, characterized by a strong tidal range  
319 (up to 9 m) and under the influence of river inputs, mainly from the Seine River on the French side  
320 (Carpentier et al. 2009) (Figure 3). We considered 46 species that dominate total biomass in the EEC:  
321 15 pelagic and benthopelagic (13 bony fishes and 2 cephalopods), to which we applied BEMs, and 31  
322 benthic and demersal (12 bony fishes, 5 cartilaginous fishes, 6 molluscs, 4 echinoderms, 3 annelids  
323 and 1 cnidarian), to which we applied BEMs filtered with HMs (Appendix B).

324  
325 By the end of the century (2091-2100), the GCMs ESM2G, CM5A-MR and ESM-MR predicted  
326 increases in temperature in the EEC of 0.54, 0.79 and 0.73°C, respectively, under RCP2.6 and 1.5, 2.4  
327 and 1.7°C, respectively, under RCP8.5. For the same period, for ESM2G, CM5A-MR and ESM-MR,  
328 salinity anomalies were 0.12, -0.67 and -0.06, respectively, under RCP2.6 and -0.41, -1.45 and -1.11,  
329 respectively, under RCP8.5.

330



331  
332 Figure 3. The Eastern English Channel, study area for the application of the script

333

334

335 **3.1 Potential changing patterns of species distributions according to the proposed approach**

336 By comparing predictive maps of current species richness to those of future projections in response to  
337 changing climate, potential impact of climate change on species' assemblages can be assessed.

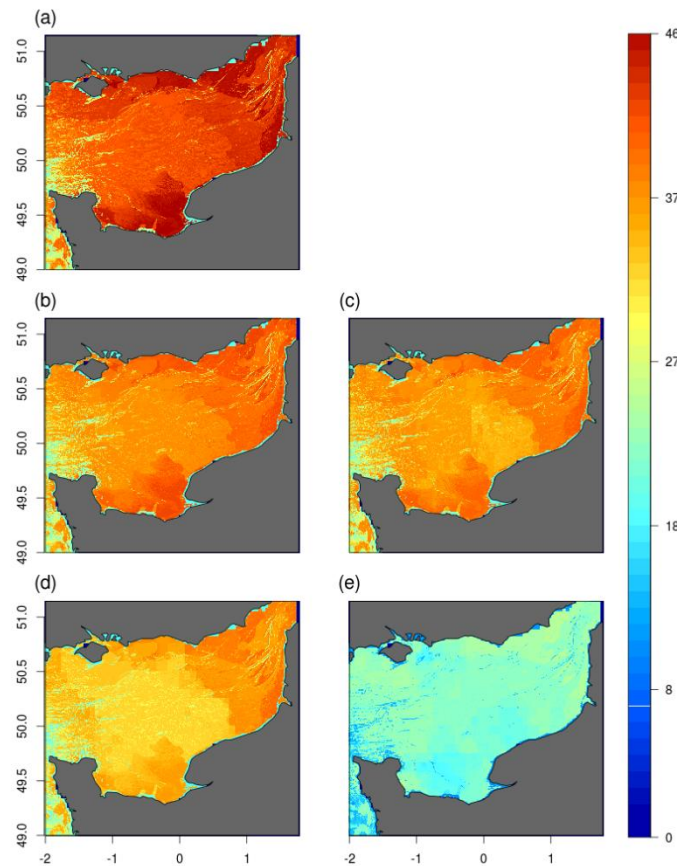
338 Species richness in the EEC currently ranges from 19-46 species. Under RCP2.6, by 2041-2050,  
339 species richness was projected to decrease by a mean of 7.8% (i.e. -3.5 species for the entire EEC) and  
340 by a maximum of 13.0% (i.e. -6.0 species). The Bay of Seine and the central EEC would lose the most  
341 species. Under RCP2.6, by 2091-2100, the decrease would be a mean of 11.5% (i.e. -5.3 species) and  
342 a maximum of 19.6% (i.e. -9.0 species). As expected, more species would be lost under RCP8.5,  
343 reaching 17.4% of the initial pool by 2041-2050 (-8.0 species) and 54.4% by 2091-2100 (-25.0  
344 species) (Figure 4).

345

346 Overall, for both scenarios and both periods, no increase in species range was projected, as none of the  
347 species considered was at its northern limit. Species range was projected to be maintained in the EEC  
348 for 42 species by 2041-2050 and 39 species by 2091-2100 under RCP2.6 and 41 species by 2041-2050  
349 and 21 species by 2091-2100 under RCP8.5.

350 Under RCP2.6, by 2041-2050, only three benthic species (the fishes *Pleuronectes platessa* and  
351 *Limanda limanda* and the gastropod *Buccinum undatum*) and one benthopelagic species (the fish  
352 *Gadus morhua*) were projected to lose 100% of their current range in the EEC (i.e. local extinction).  
353 By 2091-2100, two other benthic species (the fish *Platichthys flesus* and the sea urchin *Psammechinus*  
354 *miliaris*) and one benthopelagic species (the fish *Merlangius merlangus*) were projected to lose 50-  
355 75% of their ranges.

356 Under RCP8.5, by 2041-2050, two benthic species (the fish *P. flesus* and the sea star *Asterias rubens*),  
357 in addition to those projected to go locally extinct under RCP2.6, were projected to lose 50% and 75%  
358 of their ranges, respectively. Under RCP8.5, by 2091-2100, 19 species, both benthic/demersal and  
359 pelagic, were projected to go locally extinct.

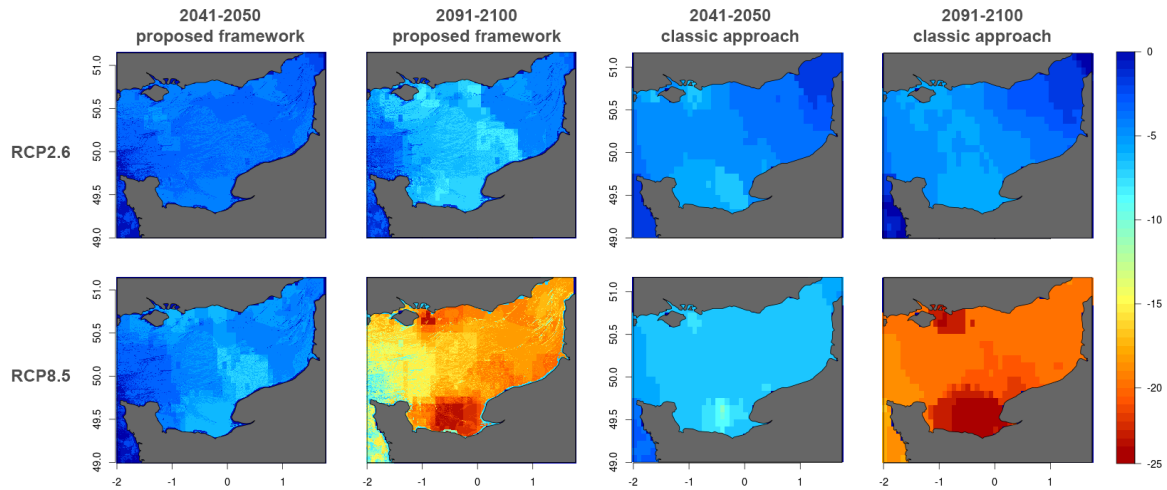


361 Figure 4. Current and projected species richness in the Eastern English Channel for a pool of the 46  
 362 most abundant species. (a) current, (b) projection under RCP2.6 by 2041-2050, (c) projection under  
 363 RCP2.6 by 2091-2100, (d) projection under RCP8.5 by 2041-2050 and (e) projection under RCP8.5 by  
 364 2091-2100.  
 365  
 366

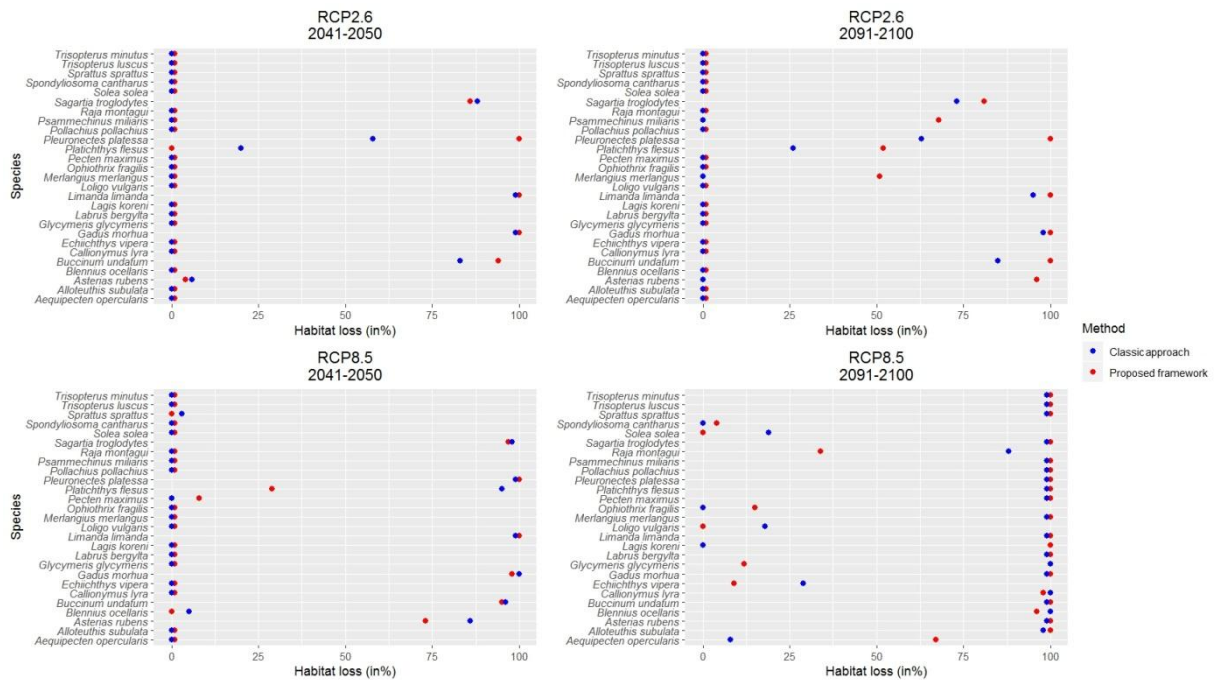
### 367 3.2 Classic approach vs. the proposed framework

368 According to the complete approach developed in our methodological framework (namely the  
 369 proposed framework), current species richness was projected to decline by a mean of 3.6% by 2041-  
 370 2050 and 5.3% by 2091-2100 under RCP2.6 and by 4.4% by 2041-2050 and 16.0% by 2091-2100  
 371 under RCP8.5. These rates could be mitigated by the arrival of species that are currently at their  
 372 northern limit in the English Channel. According to the classic approach (i.e. considering only BEMs  
 373 and sea surface temperature and salinity), species richness was projected to decline by a mean of 9.3%  
 374 by 2041-2050 and 6.5% by 2091-2100 under RCP2.6 and by 11.6% by 2041-2050 and 40.8% by  
 375 2091-2100 under RCP8.5. Thus, not considering the vertical temperature or salinity gradient or the  
 376 type of seafloor resulted in higher projections of species loss (Figure 5).  
 377

378 Moreover, considering both scenarios and both periods, the classic approach projected lower range  
 379 loss (by a mean of 32%) for eight species (mainly benthic or demersal) but projected higher range loss  
 380 (by a mean of 21%) for 11 species (also mainly benthic or demersal) (Figure 6). The proposed  
 381 framework and the classic approach yielded similar projections for eight species, mainly benthopelagic  
 382 (e.g. *Pollachius pollachius*, *Trisopterus minutus*, *Trisopterus luscus*, *Gadus morhua*).



383 Figure 5. Projected species richness anomalies between current climate conditions and projections for  
 384 both periods (2041-2050 and 2091-2100), both scenarios (RCP2.6 and RCP8.5) and both approaches  
 385 (the proposed framework with both vertical climatic conditions and habitat and the classic approach  
 386 with surface climatic conditions only)



387  
 388 Figure 6. Projected range loss for both periods (2041-2050 and 2091-2100) and both scenarios  
 389 (RCP2.6 and 8.5) according to the proposed framework (with both vertical climatic conditions and  
 390 habitat) and the classic approach (with surface climatic conditions only). Plots show species for which  
 391 a range loss was projected for at least one period, scenario or method.

392  
 393 The framework's projections of the 46 species revealed that the classic approach (i.e. considering only  
 394 BEMs without vertical climatic conditions or seafloor type) projected higher loss of species richness.  
 395 In contrast, no general trend was observed in the projected range loss for individual species.  
 396 Nevertheless, the classic approach may have projected higher range losses more often than it predicted  
 397 lower range losses, and mainly for benthic or demersal species, which depend on a specific type of  
 398 seafloor. The classic approach projected range loss of benthic and demersal species due to the loss of  
 399 suitable temperature conditions at the surface. However, since temperature fluctuates more at the

400 surface than at the bottom, temperature conditions could remain suitable at the depth range of the  
401 species modelled, thus explaining why the classic approach projected higher range losses.  
402 Our results highlight that ignoring the vertical gradient of climatic conditions, even in shallow seas,  
403 and the habitat filter leads to inconsistent results. This is even more critical in ecosystems like the EEC  
404 that are strongly structured by the seafloor substrate (Dauvin & Desroy 2005, Garcia et al. 2011).

405  
406 Similar studies exist for marine areas next to the EEC, but none used such a complete framework.  
407 Moreover, they are based on the outdated IPCC SRES scenarios and consider only a few species (e.g.  
408 only 4 benthic species in the western English Channel; (Rombouts et al. 2012)) or only benthic species  
409 (75 benthic species in the North Sea; (Weinert et al. 2016)), making comparison of results difficult.

410  
411 There are several research perspectives to refine marine species distribution models. Among them,  
412 incorporating mechanistic information such as species' physiological response to abiotic conditions  
413 (e.g., Feng et al. 2020) is a promising avenue to increase the realism of predicted responses to  
414 environmental conditions. In addition, marine species can have complex life cycles with phases that  
415 may require distinct models, and thus may be good candidates for infra-specific models (Smith et al.  
416 2018). Another important perspective to consider is the biotic interactions in the process of model  
417 building, for example by constructing joint species distribution models.

418  
419

#### 420 **4. Conclusion**

421 Our results reinforce the need to consider species' positions in the water column and their dependence  
422 on a given type of seafloor to avoid biased predictions of species distributions or even misleading  
423 results (e.g. Duffy & Chown 2017). In this paper, using the EEC as a case study, we went further and  
424 demonstrated that the simple and classic approach that considers sea surface climatic conditions as a  
425 proxy of bottom conditions and ignores habitat variables predicts higher species loss.

426 Species distribution maps are informative, and many atlases contain them. However, they remain  
427 descriptive and show only current ranges (e.g. CHARM Atlas of the English Channel; Martin et al.  
428 2009, Carpentier et al. 2009). As assessing species' future distributions is increasingly required for  
429 conservation biology and fisheries management, routinely generating maps using a relevant  
430 methodological framework would be useful.

431  
432 We developed a complete and operational framework, from data acquisition and preparation to a two-  
433 stage modelling procedure, that considers habitat type, temperature and salinity at species' depth  
434 ranges. It creates maps illustrating current and projected ranges as well as response curves for each  
435 species. Our script can be adapted for individual needs (e.g., integrating other maps of climatic  
436 variables in the same data format) and is suitable for non-modeller ecologists to easily and widely  
437 address issues related to changes in species ranges due to climate change.

438  
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443  
444

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599  
600

601 **Appendix A. Scientific surveys used in this study**

Scientific survey	Period	Organisation
IBTS	1992-2015	IFREMER <a href="http://dx.doi.org/10.18142/17">http://dx.doi.org/10.18142/17</a>
CGFS	1989-2016	IFREMER <a href="http://dx.doi.org/10.18142/11">http://dx.doi.org/10.18142/11</a>
EVHOE	1997-2006	IFREMER <a href="http://dx.doi.org/10.18142/8">http://dx.doi.org/10.18142/8</a>
CAMANOC	2014	IFREMER <a href="http://dx.doi.org/10.17600/14001900">http://dx.doi.org/10.17600/14001900</a>
LANCIE	1997	UMR6143 M2C
PECTOW	1996, 2001, 2006, 2011	UMR6143 M2C
BENTHOSEINE	1998,1999	UMR6143 M2C
BEMACE	2007	UMR6143 M2C
COLMATAGE	2008-2010	UMR6143 M2C
Saint Nicolas		UMR6143 M2C
GEDANOR	2013-2015	UMR6143 M2C
MABEMONO	2006-2007	UMR6143 M2C
ROVMACE	2009	UMR6143 M2C
VDC	2009-2011	UMR6143 M2C
Copale-Authie	1998-2000	UMR6143 M2C

602

603 **Appendix B. List of species considered in this study. BEM = bioclimatic envelope model, HM =**  
 604 **habitat model**

Species	Classification	Category in the water column	BEM only	BEM + HM
607 <i>Limanda limanda</i>	Bony fish	Benthic or demersal		x
608 <i>Platichthys flesus</i>	Bony fish	Benthic or demersal		x
609 <i>Pleuronectes platessa</i>	Bony fish	Benthic or demersal		x
610 <i>Solea solea</i>	Bony fish	Benthic or demersal		x
611 <i>Blennius ocellaris</i>	Bony fish	Benthic or demersal		x
612 <i>Callionymus lyra</i>	Bony fish	Benthic or demersal		x
613 <i>Mullus surmuletus</i>	Bony fish	Benthic or demersal		x
614 <i>Labrus bergylta</i>	Bony fish	Benthic or demersal		x
615 <i>Echiichthys vipera</i>	Bony fish	Benthic or demersal		x
616 <i>Chelidonichthys lucerna</i>	Bony fish	Benthic or demersal		x
617 <i>Trigloporus lastoviza</i>	Bony fish	Benthic or demersal		x
618 <i>Dicentrarchus labrax</i>	Bony fish	Benthic or demersal		x
619 <i>Spondyliosoma cantharus</i>	Bony fish	Benthopelagic	x	
620 <i>Zeus faber</i>	Bony fish	Benthopelagic	x	
621 <i>Pollachius pollachius</i>	Bony fish	Benthopelagic	x	
622 <i>Trisopterus minutus</i>	Bony fish	Benthopelagic	x	
623 <i>Trisopterus luscus</i>	Bony fish	Benthopelagic	x	
624 <i>Merlangius merlangus</i>	Bony fish	Benthopelagic	x	
625 <i>Gadus morhua</i>	Bony fish	Benthopelagic	x	
626 <i>Clupea harengus</i>	Bony fish	Pelagic	x	
627 <i>Engraulis encrasicolus</i>	Bony fish	Pelagic	x	
628 <i>Sprattus sprattus</i>	Bony fish	Pelagic	x	
629 <i>Sardina pilchardus</i>	Bony fish	Pelagic	x	
630 <i>Trachurus trachurus</i>	Bony fish	Pelagic	x	
631 <i>Scomber scombrus</i>	Bony fish	Pelagic	x	
632 <i>Mustelus mustelus</i>	Cartilaginous fish	Benthic or demersal		x
633 <i>Scyliorhinus canicula</i>	Cartilaginous fish	Benthic or demersal		x
634 <i>Scyliorhinus stellaris</i>	Cartilaginous fish	Benthic or demersal		x
635 <i>Raja clavata</i>	Cartilaginous fish	Benthic or demersal		x
636 <i>Raja montagui</i>	Cartilaginous fish	Benthic or demersal		x
637 <i>Lagis koreni</i>	Annelid	Benthic or demersal		x
638 <i>Lanice conchilega</i>	Annelid	Benthic or demersal		x
639 <i>Owenia fusiformis</i>	Annelid	Benthic or demersal		x
640 <i>Pecten maximus</i>	Bivalve mollusc	Benthic or demersal		x

641	<i>Glycymeris glycymeris</i>	Bivalve mollusc	Benthic or demersal		X
642	<i>Aequipecten opercularis</i>	Bivalve mollusc	Benthic or demersal		X
643	<i>Ensis directus</i>	Bivalve mollusc	Benthic or demersal		X
644	<i>Buccinum undatum</i>	Gastropod mollusc	Benthic or demersal		X
645	<i>Sepia officinalis</i>	Cephalopod mollusc	Benthic or demersal		X
646	<i>Alloteuthis subulata</i>	Cephalopod mollusc	Pelagic	X	
647	<i>Loligo vulgaris</i>	Cephalopod mollusc	Pelagic	X	
648	<i>Sagartia troglodytes</i>	Cnidarian	Benthic or demersal		X
649	<i>Ophiothrix fragilis</i>	Echinoderm	Benthic or demersal		X
650	<i>Echinocardium cordatum</i>	Echinoderm	Benthic or demersal		X
651	<i>Psammechinus miliaris</i>	Echinoderm	Benthic or demersal		X
652	<i>Asterias rubens</i>	Echinoderm	Benthic or demersal		X
653					