

# Spatial separation of catches in highly mixed fisheries

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- 1 Mixed fisheries capture a mix of species at the same time and are the dominant type of  
2 fishery worldwide. Overexploitation in mixed fisheries occurs when catches continue for  
3 available quota species while low quota species are discarded<sup>1</sup>. As EU fisheries manage-  
4 ment moves to count all fish caught against quota (the ‘landings obligation’), the challenge  
5 is to catch available quota within new constraints, else lose productivity. A mechanism for  
6 decoupling exploitation of species caught together is spatial targeting, but this remains  
7 challenging due to complex fishery and population dynamics in space and time<sup>2,3</sup>. How  
8 far spatial targeting can go to practically separate species is often unknown and anec-  
9 dotal. Here we develop a dimension-reduction framework based on joint species distri-  
10 bution modelling (spatial dynamic factor analysis) to understand how spatial community  
11 and fishery dynamics interact to determine species and size composition. In the example  
12 application to the highly mixed fisheries of the Celtic Sea, clear common spatial patterns  
13 emerge for three distinct species-groups. While distribution varies inter-annually, the same  
14 species-groups are consistently found in higher densities together, with more subtle dif-

15 **ferences within species-groups, where spatial separation may not be practically possible.**  
16 **We highlight the importance of dimension reduction techniques to focus management dis-**  
17 **cussion on axes of maximal separation in space and time. We propose that spatiotemporal**  
18 **modelling of available data is a scientific necessity to address the pervasive and nuanced**  
19 **challenges of managing mixed fisheries.**

20

21 **Mixed fisheries and the EU landings obligation** Efforts to reduce exploitation rates in commer-  
22 cial fisheries have begun the process of rebuilding depleted fish populations<sup>4</sup>. Improved fisheries  
23 management can increase population sizes and allow increased sustainable catches, yet fisheries  
24 catch globally remains static<sup>5</sup>. With future increased demand for fish protein there is an impor-  
25 tant role for well managed fisheries in supporting future food security<sup>6</sup> necessitating fisheries are  
26 managed efficiently to maximise productivity.

27 A challenge in realising increased catches from rebuilt populations is maximising yields from mixed  
28 fisheries<sup>2,7,8</sup>. In mixed fisheries managed by individual quotas, if catches do not match available  
29 stock quotas, either a vessel must stop fishing when the first quota is reached (the 'choke' species)  
30 or overexploitation of the weaker species occurs while fishers catch more healthy species and  
31 throw back ('discard') the fish for which they have no quota<sup>1</sup>. There is a pressing need for scientific  
32 tools that simplify the complexities of mixed fisheries to help avoid discarding.

33 Sustainability of European fisheries has been hampered by this 'mixed fishery problem' for decades  
34 with large-scale discarding<sup>9</sup>. Under the EU Common Fisheries Policy (CFP) reform of 2012, by  
35 2019 all fish that are caught are due to be counted against the respective stock quota. Unless

36 fishers can avoid catch of unwanted species they will have to stop fishing when reaching their  
37 first restrictive quota, introducing a significant cost to under-utilised quota<sup>8</sup> and strong incentive to  
38 mitigate such losses<sup>10</sup>.

39 The ability to align catch with available quota depends on being able to exploit target species while  
40 avoiding unwanted catch, either by switching fishing method, changing technical gear character-  
41 istics, or the timing and location of fishing activity<sup>11</sup>. Spatiotemporal measures have been applied  
42 to reduce unwanted catch with varying degrees of success<sup>3,12</sup>, partly because they have been  
43 targeted at individual species without considering associations among several species. Highly  
44 mixed fisheries are complex with spatial, technological and community interactions; our goal is  
45 to develop a framework for understanding these complexities. We do so by 1) implementing a  
46 spatiotemporal dimension reduction method, 2) using results to draw inference on the fishery-  
47 community dynamics, 3) creating a framework to identify trends common among species, and 4)  
48 describing the potential for and limitations of spatial measures to mitigate unwanted catches in  
49 highly mixed fisheries.

50 **Framework for analysing spatio-temporal mixed fisheries interactions** We characterise the  
51 spatiotemporal dynamics of key components of a fish community by implementing a factor analysis  
52 decomposition to describe trends in spatiotemporal dynamics of the different species as a function  
53 of latent variables<sup>13</sup> representing spatial variation (9 factors; 'average' spatial variation) and spatio-  
54 temporal variation (9 factors) for encounter probability and positive catch rates ('positive density')  
55 separately<sup>14</sup>. This allows us to take account of how the factors contribute to affect catches of  
56 the species in mixed fisheries. Gaussian Markov Random Fields (GMRFs) capture spatial and  
57 temporal dependence within and among species groups for both encounter probability and positive  
58 density<sup>15</sup>. Fixed effects account for systematic differences driving encounter and catches such as

59 differences in sampling efficiency (a.k.a. catchability), while random effects capture the spatio-  
60 temporal dynamics of the fish community.

61 **Dynamics of Celtic Sea fisheries** The Celtic Sea is a temperate sea where fisheries are spatially  
62 and temporally complex<sup>16,17</sup>. Close to 150 species have been identified in the commercial catches  
63 of the Celtic Sea, with approximately 30 species dominating the catch<sup>18</sup>. We parameterise our  
64 model using catch data from seven fisheries-independent surveys undertaken over the period  
65 1990 - 2015 (Extended Data Table 1) and include nine of the main commercial species (see  
66 Extended Data Table 2, Fig. 2) which make up >60 % of landings by towed fishing gears for the  
67 area (average 2011 - 2015<sup>19</sup>). Each species was separated into juvenile and adult size classes  
68 based on their legal minimum conservation reference size (Extended Data Table 2).

69 **Common average spatial patterns driving species associations** A spatial dynamic factor anal-  
70 ysis decomposes the dominant spatial patterns driving differences in encounter probability and  
71 positive density. The first three factors account for 83.7% of the between species variance in av-  
72 erage encounter probability and 69% of the between species variance in average positive density.  
73 A clear spatial pattern can be seen both for encounter probability and positive density, with a  
74 positive value associated with the first factor in the inshore north easterly part of the Celtic Sea  
75 into the Bristol Channel and Western English Channel, moving to a negative value offshore in the  
76 south-westerly waters (Fig. 1). The species loadings coefficients show plaice, sole and whiting  
77 to be positively associated with the first factor for encounter probability while the other species  
78 are negatively associated. For average positive density, positive associations are also found for  
79 haddock and juvenile cod.

80 On the second spatial factor for encounter probability a north / south split can be seen at approxi-

81 mately 49° N while positive density is more driven by a positive value in the deeper westerly waters  
82 as well as some inshore areas. Species values for the second factor indicate there are positive  
83 associations for juvenile monkfish (*L. piscatorius*), juvenile hake, juvenile megrim, plaice and ju-  
84 venile whiting with average positive density, which may reflect two different spatial distributions in  
85 the more offshore and in the inshore areas (Fig. 1).

86 On the third factor, there is a positive association with the easterly waters for encounter probability  
87 and negative with the westerly waters. This splits the roundfish species cod, haddock and whiting  
88 which have a positive association with the third factor for average encounter probability from the  
89 rest of the species. Positive density is driven by a north / south split (Fig. 1), with positive values  
90 in the northerly areas. Juvenile monkfish (*L. budgessa* and *L. piscatorius*), cod, juvenile haddock,  
91 hake, adult plaice and whiting are also positively associated with the third factor in the north while  
92 adult monkfish (*L. budgessa* and *L. piscatorius*), adult haddock, megrims, juvenile plaice and sole  
93 are negatively associated (Fig. 1).

94 **Time-varying species distributions, but stability within species groups** Inter-annual differ-  
95 ences in factor coefficients show less structure (Extended Data Figs. 5, 6). These inter-annual  
96 differences are important as they reflect the ability of fishers to predict where they can target  
97 species from one year to the next. Common patterns in spatiotemporal factor coefficients among  
98 species drive spatiotemporal distributions of megrim, anglerfish species and hake (the deeper  
99 water species, species-group negatively associated with the second axes of Fig. 2a) and the  
100 roundfish and flatfish (species-group more positively associated with the second axes of Fig. 2a).  
101 For spatio-temporal positive density (Fig. 2b) cod, haddock and whiting (the roundfish species)  
102 are separated from plaice, sole (the flatfish) and deeper water species.

103 **Three clusters of species show similar spatial patterns** To gain greater insight into the com-  
104 munity dynamics we considered how species covary in space and time through among species  
105 correlations. Pearson correlation coefficients for the modelled average spatial encounter probabili-  
106 ty (Fig. 3a) show clear strong associations between adult and juvenile size classes for all species  
107 ( $>0.75$  for all species except hake, 0.56). Hierarchical clustering identified the same three com-  
108 mon groups with roundfish (cod, haddock, whiting), flatfish (plaice and sole) and species found in  
109 the deeper waters (hake, megrim and both anglerfish species) showing strong intra-group correla-  
110 tions indicating similar spatial distributions. Correlation coefficients for the average positive density  
111 also have strong associations among roundfish (Fig. 3b).

112 **Subtle differences in distributions may be important to separate catches within groups** If  
113 production from mixed fisheries is to be maximised, decoupling catches of species between and  
114 within the groups will be key. For example, asking where the maximal separation in the densities of  
115 two coupled species is likely to occur? We map the difference in spatial distribution for each pair of  
116 species within a species-group for a single year (2015; Fig. 4) to facilitate discussion on maximal  
117 separation, for example, between difficult to separate species such as haddock and whiting (Fig.  
118 4c).

119 Predicted catch distribution from a “typical” otter trawl gear and beam trawl fishing at three dif-  
120 ferent locations highlights the differences fishing gear and location makes on catches (Fig. 4h).  
121 In the inshore area (location ‘A’) plaice and sole are the two main species caught reflecting their  
122 distribution and abundance, though the otter trawl gear catches a greater proportion of plaice to  
123 sole than the beam trawl. The area between Britain and Ireland (location ‘B’) has a greater contri-  
124 bution of whiting, haddock, cod, hake and anglerfishes in the catch with the otter trawl catching a  
125 greater proportion of the roundfish, haddock, whiting and cod while the beam trawl catches more

126 anglerfishes and megrims. The offshore area has a higher contribution of megrim, anglerfishes  
127 and hake with the otter trawl catching a greater share of hake and the beam trawl a greater pro-  
128 portion of megrim. Megrim dominates the catch for both gears in location 'C', reflecting its relative  
129 abundance in the area.

130 **Addressing the scientific challenges of the landing obligation in mixed fisheries** We have  
131 identified spatial separation of three distinct species-groups (roundfish, flatfish and deeper water  
132 species) while showing that only subtle differences exist in distributions within species-groups.  
133 The differences in catch compositions between gears at the same location (Fig. 4h) show that  
134 changing fishing methods can go some way to affecting catch, yet that differences in catches  
135 between locations are likely to be more important. This highlights that changes in spatial fishing  
136 patterns are likely to play an important role in supporting implementation of the landings obligation.

137 More challenging is within-group spatial separation due to overlaps in spatial distributions for the  
138 species, driven by common environmental factors. Subtle changes in location fished may yield  
139 some benefit in changing catch composition, yet the outcome is likely to be much more difficult  
140 to predict. Subtle differences in the distribution of cod, haddock and whiting can be seen in Figs.  
141 4a-c, showing spatial separation of catches is likely to need to be supported by other measures  
142 such as changes to the selectivity characteristics of gear<sup>20</sup>.

143 A role that science can play in supporting effectiveness of spatiotemporal avoidance is in providing  
144 probabilistic advice on hotspots for species which can inform fishing decisions. Previous modelling  
145 studies have shown how spatiotemporal models could improve predictions of high ratios of bycatch  
146 species to target species<sup>21–23</sup>, and geostatistical models are well suited as they incorporate spatial  
147 dependency while providing for probabilities to be drawn from posterior distributions of parameter

148 estimates. We posit such advice could be enhanced by integrating data obtained directly from  
149 commercial fishing vessels at a higher temporal resolution, providing real-time forecasts to inform  
150 fishing choices that also captures seasonal differences in distributions. Such advice could inform  
151 optimal policies for time-area closures, move-on rules or even as informal information utilised by  
152 fishers directly.

153 An important question for the implementation of the EU's landing obligation is how far spatial  
154 avoidance can go to achieve catch balancing in fisheries. Our model captures differences between  
155 location fished for two gear types and broad scale effect on catch composition. Empirical studies<sup>2,7</sup>  
156 suggest limits to the effectiveness of spatial avoidance, with differences in ability to change catch  
157 composition observed for different fleets<sup>24</sup>. This analysis likely reflects a lower bound on avoidance  
158 as fine-scale behavioural decisions such as time-of-day, gear configuration and location choices  
159 can also be used to affect catch<sup>25,26</sup>.

160 Complex environmental, fishery and community drivers of distribution for species highlights the  
161 scale of the challenge in separating catches using spatial management measures. This has im-  
162 portant implications for management of the mixed fisheries under the EU landings obligation. Our  
163 analysis identifies where it may be easier to separate catches of species (among groups) and  
164 where it is more challenging (within groups). We propose that the framework presented in Figs.  
165 1-4 provides a viable route to reducing the complexity of highly mixed systems. This can allow  
166 informed management discussion over more traditional anecdotal knowledge of single-species  
167 distribution in space and time.

168 **Methods**

169 **Model structure:** We use a geostatistical Vector Autoregressive Spatiotemporal model (VAST)<sup>1</sup>  
170 to implement a delta-generalised linear mixed modelling (GLMM) framework that takes account  
171 of spatio-temporal correlations among species through implementation of a spatial dynamic factor  
172 analysis (SDFA). Spatial variation is captured through a Gaussian Markov Random Field, while we  
173 model random variation among species and years. Covariates affecting catchability (to account for  
174 differences between fishing surveys) and density (to account for environmental preferences) can  
175 be incorporated for predictions of presence and positive density. The following briefly summarises  
176 the key methods implemented in the VAST framework. For full details of the model the reader is  
177 invited directed to Thorson *et al* 2017<sup>27</sup>.

178 **SDFA:** A spatial dynamic factor analysis incorporates advances in joint dynamic species models<sup>27</sup>  
179 to take account of associations among species by modelling response variables as a multivariate  
180 process. This is achieved through implementing a factor analysis decomposition where common  
181 latent trends are estimated so that the number of common trends is less than the number of  
182 species modelled. The factor coefficients are then associated through a function for each factor  
183 that returns a positive or negative association of one or more species with any location. Log-  
184 density of any species is then be described as a linear combination of factors and loadings:

$$\theta_c(s, t) = \sum_{j=1}^{n_j} L_{c,j} \psi_j(s, t) + \sum_{k=1}^{n_k} \gamma_{k,c} \chi_k(s, t) \quad (1)$$

185 Where  $\theta_c(s, t)$  represents log-density for species  $c$  at site  $s$  at time  $t$ ,  $\psi_j$  is the coefficient for factor

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<sup>1</sup>Software in the R statistical programming language can be found here: [www.github.com/james-thorson/  
VAST](https://www.github.com/james-thorson/VAST)

<sup>186</sup>  $j$ ,  $L_{c,j}$  the loading matrix representing association of species  $c$  with factor  $j$  and  $\gamma_{k,c}\chi_k(s,t)$  the  
<sup>187</sup> linear effect of covariates at each site and time<sup>28</sup>.

<sup>188</sup> The factor analysis can identify community dynamics and where species have similar spatio-  
<sup>189</sup> temporal patterns, allowing inference of species distributions and abundance of poorly sampled  
<sup>190</sup> species through association with other species and allows for computation of spatio-temporal cor-  
<sup>191</sup> relations among species<sup>28</sup>.

<sup>192</sup> We use the resultant factor analysis to identify community dynamics and drivers common among  
<sup>193</sup> 18 species and results presented through transformation of the loading matrices using PCA rota-  
<sup>194</sup> tion.

<sup>195</sup> **Estimation of abundances:** Spatio-temporal encounter probability and positive catch rates are  
<sup>196</sup> modelled separately with spatio-temporal encounter probability modelled using a logit-link linear  
<sup>197</sup> predictor;

$$\text{logit}[p(s_i, c_i, t_i)] = \beta_p(c_i, t_i) + \sum_{f=1}^{n_\omega} L_\omega(c_i, f)\omega_p(s_i, f) + \sum_{f=1}^{n_\varepsilon} L_\varepsilon(c_i, f)\varepsilon_p(s_i, f, t_i) + \sum_{v=1}^{n_v} \delta_p(v)Q_p(c_i, v_i) \quad (2)$$

<sup>198</sup> and positive catch rates modelling using a gamma-distribution<sup>14</sup>.

$$\text{log}[r(s_i, c_i, t_i)] = \beta_r(c_i, t_i) + \sum_{f=1}^{n_\omega} L_\omega(c_i, f)\omega_r(s_i, f) + \sum_{f=1}^{n_\varepsilon} L_\varepsilon(c_i, f)\varepsilon_r(s_i, f, t_i) + \sum_{v=1}^{n_v} \delta_r(v)Q_r(c_i, v_i) \quad (3)$$

199 where  $p(s_i, c_i, t_i)$  is the predictor for encounter probability for observation  $i$ , at location  $s$  for species  
 200  $c$  and time  $t$  and  $r(s_i, c_i, t_i)$  is similarly the predictor for the positive density.  $\beta_*(c_i, t_i)$  is the inter-  
 201 cept,  $\omega_*(s_i, c_i)$  the spatial variation at location  $s$  for factor  $f$ , with  $L_\omega(c_i, f)$  the loading matrix for  
 202 spatial covariation among species.  $\varepsilon_*(s_i, c_i, t_i)$  is the linear predictor for spatio-temporal variation,  
 203 with  $L_\varepsilon(c_i, f)$  the loading matrix for spatio-temporal covariance among species and  $\delta_*(c_i, v_i)$  the  
 204 contribution of catchability covariates for the linear predictor with  $Q_{c_i, v_i}$  the catchability covariates  
 205 for species  $c$  and vessel  $v$ ; \* can be either  $p$  for probability of encounter or  $r$  for positive density.

206 The Delta-Gamma formulation is then:

$$\begin{aligned}
 Pr(C = 0) &= 1 - p \\
 Pr(C = c | c > 0) &= p \cdot \frac{\lambda^k c^{k-1} \cdot \exp(-\lambda c)}{\Gamma_k}
 \end{aligned} \tag{4}$$

207 for the probability  $p$  of a non-zero catch  $C$  given a gamma distribution for the positive catch with  
 208 a rate parameter  $\lambda$  and shape parameter  $k$ .

209 **Spatio-temporal variation:** The spatiotemporal variation is modelled using Gaussian Markov  
 210 Random Fields (GMRF) where observations are correlated in space through a Matérn covariance  
 211 function with the parameters estimated within the model. Here, the correlation decays smoothly  
 212 over space the further from the location and includes geometric anisotropy to reflect the fact that  
 213 correlations may decline in one direction faster than another (e.g. moving offshore)<sup>15</sup>. The best fit  
 214 estimated an anisotropic covariance where the correlations were stronger in a north-east - south-  
 215 west direction, extending approximately 97 km and 140 km before correlations for encounter prob-  
 216 ability and positive density reduced to <10 %, respectively (Extended Data Fig. 9). Incorporating

217 the spatiotemporal correlations among and within species provides more efficient use of the data  
218 as inference can be made about poorly sampled locations from the covariance structure.

219 A probability distribution for spatio-temporal variation in both encounter probability and positive  
220 catch rate was specified,  $\varepsilon_*(s, p, t)$ , with a three-dimensional multivariate normal distribution so  
221 that:

$$vec[\mathbf{E}_*(t)] \sim MVN(0, \mathbf{R}_* \otimes \mathbf{V}_{\varepsilon*}) \quad (5)$$

222 Here,  $vec[\mathbf{E}_*(t)]$  is the stacked columns of the matrices describing  $\varepsilon_*(s, p, t)$  at every location,  
223 species and time,  $\mathbf{R}_*$  is a correlation matrix for encounter probability or positive catch rates  
224 among locations and  $\mathbf{V}_*$  a covariance matrix for encounter probability or positive catch rate among  
225 species (modelled within the factor analysis).  $\otimes$  represents the Kronecker product so that the cor-  
226 relation among any location and species can be computed<sup>27</sup>.

227 **Incorporating covariates** Survey catchability (the relative efficiency of a gear catching a species)  
228 was estimated as a fixed effect in the model,  $\delta_s(v)$ , to account for differences in spatial fishing  
229 patterns and gear characteristics which affect encounter and capture probability of the sampling  
230 gear<sup>29</sup>. Parameter estimates (Extended Data Fig. 10) showed clear differential effects of surveys  
231 using otter trawl gears (more effective for round fish species) and beam trawl gears (more effective  
232 for flatfish species).

233 No fixed covariates for habitat quality or other predictors of encounter probability or positive density  
234 were included. While incorporation may improve the spatial predictive performance<sup>27</sup>, it was not  
235 found to be the case here based on model selection with Akaike Information Criterion (AIC) and

236 Bayesian Information Criterion (BIC).

237 **Parameter estimation** Parameter estimation was undertaken through Laplace approximation of  
238 the marginal likelihood for fixed effects while integrating the joint likelihood (which includes the  
239 probability of the random effects) with respect to random effects. This was implemented using  
240 Template Model Builder (TMB;<sup>30</sup>) with computation through support by the Irish Centre for High  
241 End Computing (ICHEC; <https://www.ichec.ie>) facility.

242 **Data** The model integrates data from seven fisheries independent surveys taking account of cor-  
243 relations among species spatio-temporal distributions and abundances to predict spatial density  
244 estimates consistent with the resolution of the data.

245 The model was been fit to nine species separated into adult and juvenile size classes (Extended  
246 Data Table 2) to seven survey series (Extended Data Table 1) in the Celtic Sea bound by 48° N  
247 to 52 ° N latitude and 12 ° W to 2° W longitude (Extended Data Fig. 8) for the years 1990 - 2015  
248 inclusive.

249 The following steps were undertaken for data processing: i) data for survey stations and catches  
250 were downloaded from ICES Datras ([www.ices.dk/marine-data/data-portals/Pages/  
251 DATRAS.aspx](http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx)) or obtained directly from the Cefas Fishing Survey System (FSS); ii) data were  
252 checked and any tows with missing or erroneously recorded station information (e.g. tow duration  
253 or distance infeasible) removed; iii) swept area for each of the survey tows was estimated based  
254 on fitting a GAM to gear variables so that  $\text{Doorspread} = s(\text{Depth}) + \text{DoorWt} + \text{WarpLength} +$   
255  $\text{WarpDiameter} + \text{SweepLength}$  and a gear specific correction factor taken from the literature<sup>31</sup>; iii)  
256 fish lengths were converted to biomass (Kg) through estimating a von bertalanffy length weight

257 relationship,  $Wt = a \cdot L^b$ , fit to sampled length and weight of fish obtained in the EVHOE survey  
258 and aggregated within size classes (adult and juvenile).

259 The final dataset comprised of estimates of catches (including zeros) for each station and species  
260 and estimated swept area for the tow.

261 **Model setup** The spatial domain was setup to include 250 knots representing the Gaussian Ran-  
262 dom Fields. The model was configured to estimate nine factors each to describe the spatial and  
263 spatiotemporal encounter probability and positive density parameters, with a logit-link for the linear  
264 predictor for encounter probability and log-link for the linear predictor for positive density, with an  
265 assumed gamma distribution.

266 Three candidate models were identified, i) a base model where the vessel interaction was a ran-  
267 dom effect, ii) the base but where the vessel x species effect was estimated as a fixed covariate, iii)  
268 with vessel x species effect estimated, but with the addition of estimating fixed density covariates  
269 for both predominant habitat type at a knot and depth. AIC and BIC model selection favoured the  
270 second model (Extended Data Table 3). The final model included estimating 1,674 fixed parame-  
271 ters and predicting 129,276 random effect values.

272 **Model validation** Q-Q plots show good fit between the derived estimates and the data for positive  
273 catch rates and between the predicted and observed encounter probability (Extended Data Figs.  
274 11,12). Further, model outputs are consistent with stock-level trends abundances over time from  
275 international assessments (Extended Data Fig. 13), yet also provide detailed insight into species  
276 co-occurrence and the strength of associations in space and time.

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**Author contributions** P.J.D., C.M and J.T.T. designed the study. P.J.D. conducted the analysis. All authors contributed to writing the manuscript.

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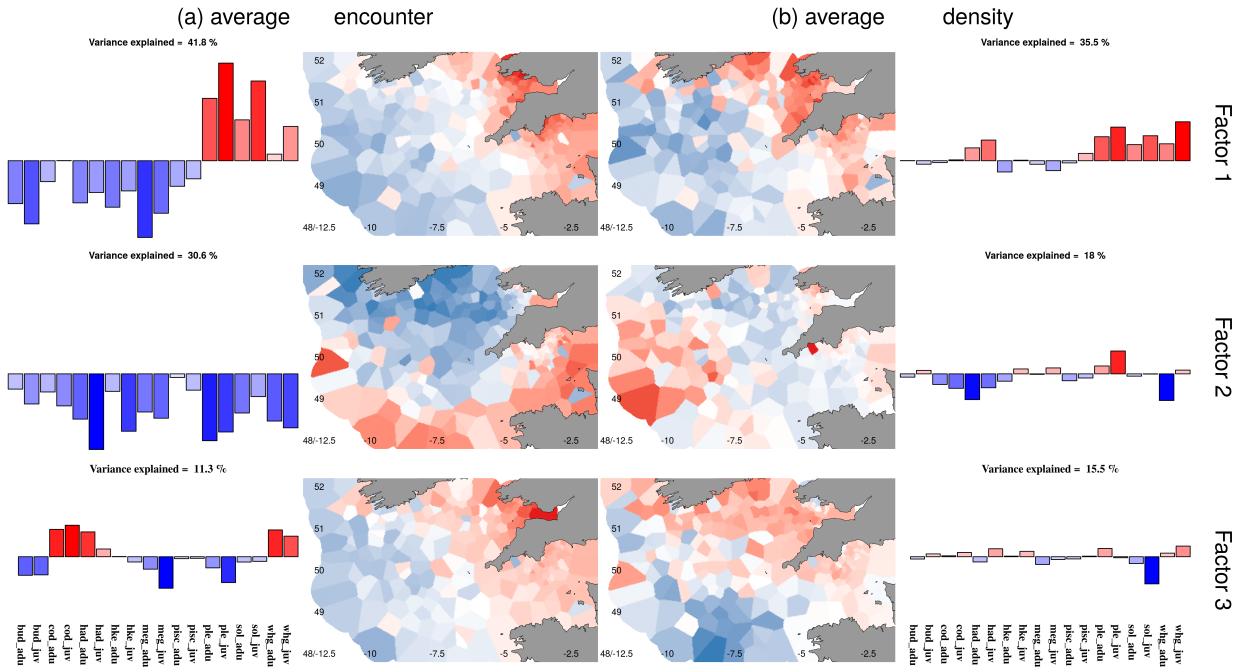


Figure 1: Factor values for the first three factors for (a) Average encounter probability and (b) Average positive density for the species (outer figures) and spatially (inner figures). Red: positive association to the factor, Blue: negative association.

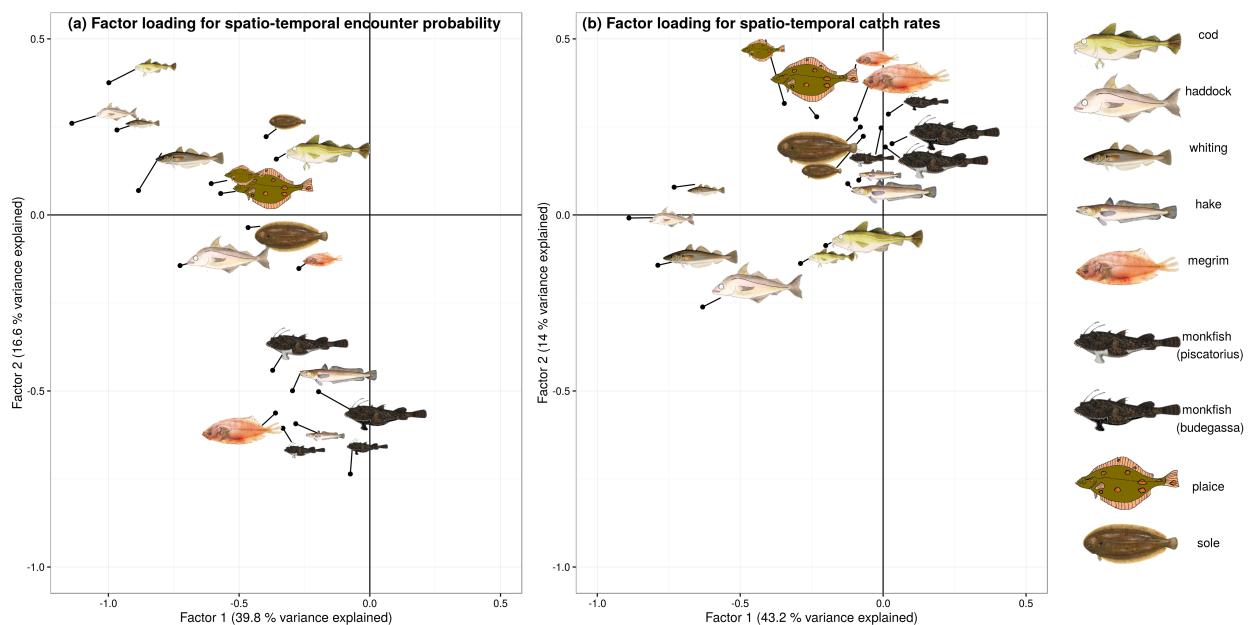


Figure 2: Position of each species on the first two axes from the factor analysis for (a) spatio-temporal encounter probability and (b) spatio-temporal positive density.

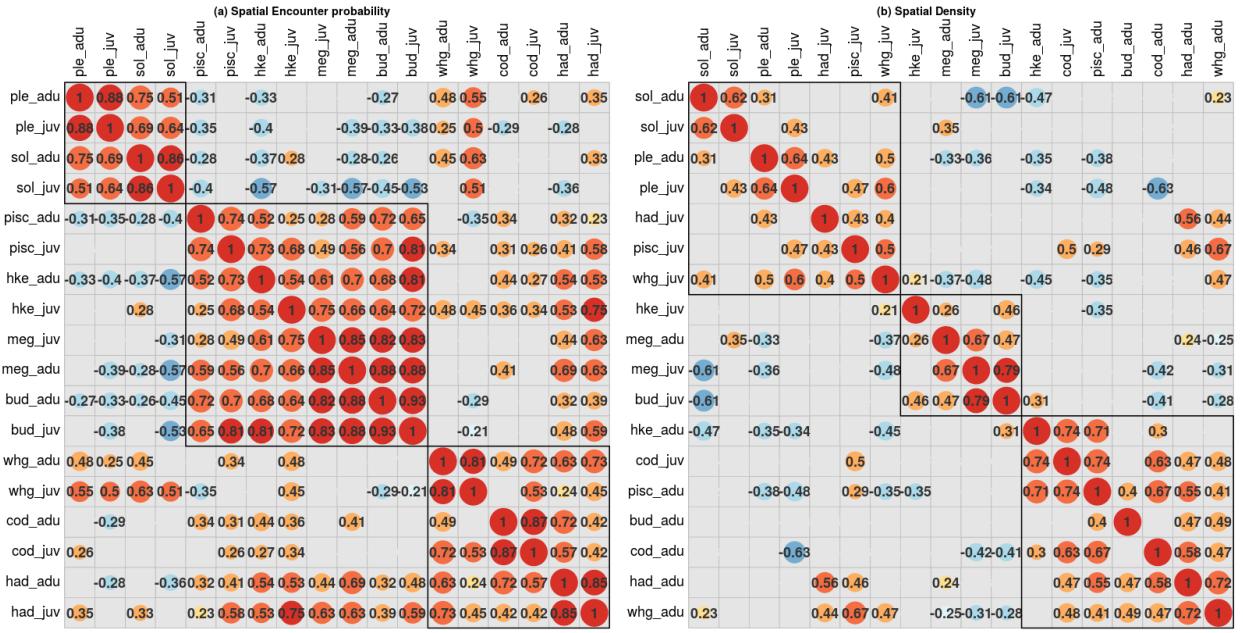


Figure 3: Inter-species correlations for (a) spatial encounter probability over all years and (b) spatial positive density. Species are clustered into three groups based on a hierarchical clustering method with non-significant correlations (the Confidence Interval  $[+/- 1.96 * \text{SEs}]$  spanned zero) left blank.

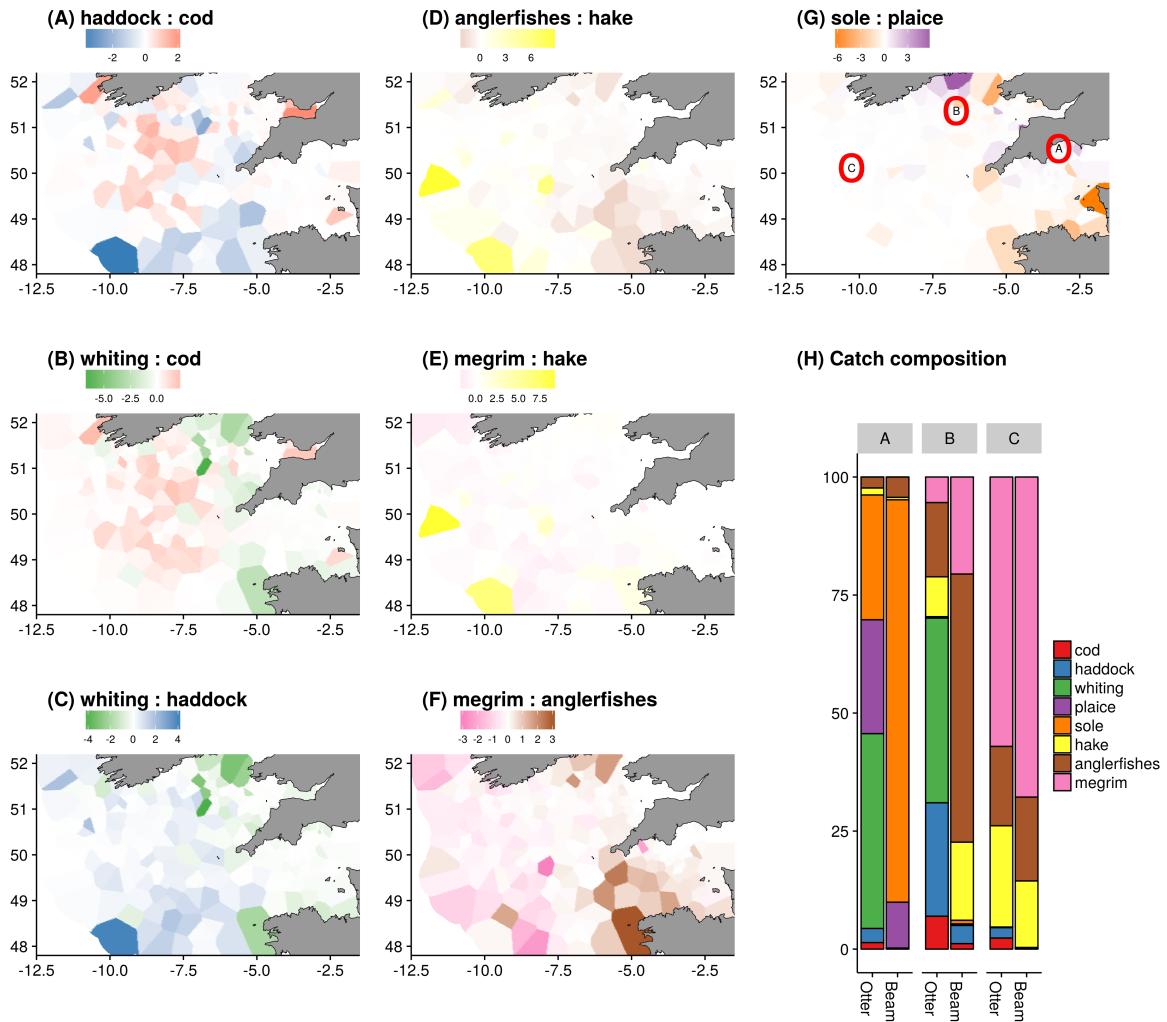


Figure 4: Differences in the standardised spatial density for pairs of species and expected catch rates for two different gears at three different locations in 2015.