

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

15 species-groups - where spatial separation may not be practically possible. **The results**  
16 ~~highlight both opportunities for and limitations of the ability to spatiotemporally separate~~  
17 ~~catches.~~ We highlight the importance of dimension reduction techniques to focus man-  
18 agement discussion on axes of maximal separation in space and time. We propose that  
19 spatiotemporal modelling of available data is a scientific necessity to address the perva-  
20 sive and nuanced challenges of managing mixed fisheries.

21

22 **Mixed fisheries and the EU landings obligation** Recent Efforts to reduce exploitation rates in  
23 commercial fisheries have begun the process of rebuilding depleted fish populations <sup>1</sup>. Improved  
24 fisheries management ~~has the potential to~~ can increase population sizes and allow increased sus-  
25 tainable catches, yet fisheries catch globally remains stagnant <sup>2</sup>. In light of projected increased  
26 demand for fish protein <sup>3</sup> there is an important role for well managed fisheries in supporting fu-  
27 ture food security <sup>4</sup> and <sup>coolin</sup> there necessitating that remains a need to ensure <sup>coolin</sup> fisheries are  
28 managed efficiently to maximise productivity.

29 A particular challenge in realising increased catches from rebuilt populations is maximising yields  
30 from mixed fisheries <sup>5–7</sup>. In mixed fisheries, ~~the predominant type of fishery worldwide~~, several  
31 fish species are caught together in the same net or fishing operation (~~known as a ‘technical~~  
32 ~~interaction’~~). If managed by individual quotas, and catches do not match available stock quotas, ei-  
33 ther a vessel must stop fishing when the first quota is reached (the ‘choke’ species) or overexploita-  
34 tion of the weaker species occurs while fishers continue to catch more healthy species and throw  
35 back ('discard') the fish for which they have no quota <sup>8</sup>. There is, ~~therefore~~, a pressing need for  
36 scientific tools which simplify the complexities of mixed fisheries to help ~~avoid discarding managers~~

37 and fishers maximise catches<sup>coolin</sup>.

38 Sustainability of European fisheries has been hampered by this 'mixed fishery problem' for decades  
39 with large-scale discarding resulting <sup>9</sup>. A paradigm shift is being introduced Under the EU Com-  
40 mon Fisheries Policy (CFP) reform of 2012 through two significant management changes. First,  
41 by 2019 all fish that are caught are due to be counted against the respective stock quota; second,  
42 by 2020 all fish stocks must be fished so as to be able to produce their Maximum Sustainable Yield  
43 (MSY)<sup>10</sup>. The changes are, expected to contribute to attainment of the goal of Good Environmental  
44 Status (GES) under the European Marine Strategy Framework Directive (MSFD;<sup>11</sup>) and move  
45 Europe towards an ecosystem based approach to fisheries management<sup>12coolin</sup>.

46 Societal objectives for fisheries to achieve MSY across ecosystem components are paralleled by  
47 Individual fishers goals are to<sup>coolin</sup> maximise utility; whether that be profit, income or the continu-  
48 ance of traditional practices. Under the new policy; Unless fishers can avoid catch of unwanted  
49 species they will have to stop fishing when reaching their first restrictive quota. This introduces  
50 a potential significant cost to fishers of under-utilised quota<sup>7</sup> and provides a strong incentive to  
51 mitigate such losses <sup>13</sup>. The ability of fishers to align their catch with available quota depends  
52 on being able to exploit target species while avoiding unwanted catch, Methods by which fishers  
53 can alter their fishing patterns include either by switching fishing method (e.g. trawling to netting),  
54 changing technical gear characteristics (e.g. introducing escapement panels in nets), or the timing  
55 and location of fishing activity <sup>14</sup>. For example, otter trawl gears are known to have higher catch  
56 rates of roundfish due to the higher headline and wider sweeps which herd demersal fish into the  
57 net while beam trawls employ chain mesh to lift<sup>'dig'</sup><sup>coolin</sup> benthic flatfish species from the seabed<sup>15</sup>.  
58 Spatiotemporal management measures (such as time-limited fishery closures) have been applied

59 to reduce unwanted catch with varying degrees of success (e.g. <sup>16,17</sup>). However, such measures  
60 have generally been targeted at individual species without considering associations and inter-  
61 actions among several species. Highly mixed fisheries are complex with spatial, technological  
62 and community interactions combining. ~~The design of spatio-temporal management measures~~  
63 ~~which aim to allow exploitation of high quota stocks while protecting low quota stocks requires~~  
64 ~~understanding of these interactions at a scale meaningful to managers and fishers. Here,~~ Our  
65 goal is to develop a framework for understanding these complexities. We do so by implementing a  
66 spatio-temporal dimension reduction method and use the results to draw inference on the fishery-  
67 community dynamics, creating a framework to identify trends common among species-groups. We  
68 use this to describe the potential for and limitations of ~~where~~<sup>coolin</sup> spatial measures ~~for~~ ~~an~~ contribute  
69 ~~to~~<sup>coolin</sup> mitigating unwanted catches in highly mixed fisheries.

70 **Framework for analysing spatio-temporal mixed fisheries interactions** We present a framework  
71 for analysing how far spatio-temporal avoidance can contribute towards mitigating imbalances  
72 in quota in mixed fisheries. We use fisheries-independent survey data to characterise the spa-  
73 tiotemporal dynamics of key components of a fish community by employing a geostatistical Vector  
74 Autoregressive Spatiotemporal model (VAST). We implement a factor analysis decomposition to  
75 describe trends in spatiotemporal dynamics of the different species as a function of latent vari-  
76 ables <sup>18</sup> representing spatial variation (9 factors; ~~which we call~~ 'average' spatial variation) and  
77 spatio-temporal variation (9 factors) for encounter probability and positive catch rates (~~which we~~  
78 ~~call~~ 'positive density') separately <sup>19</sup>. ~~We use~~ The resultant factor analysis is used to identify com-  
79 munity dynamics and drivers common among 18 species-groups and results presented through  
80 transformation of the loading matrices using PCA rotation. By describing the species-groups dy-  
81 namics through underlying contributory spatiotemporal factors we can take account of how the

82 factors contribute to affect catches of the species-groups in mixed fisheries. We use Gaussian  
83 Markov Random Fields (GMRFs) to capture spatial and temporal dependence within and among  
84 species groups for both encounter probability and positive density<sup>20</sup>. VAST is set in a mixed  
85 modelling framework to allow estimation of Fixed effects to account for systematic differences  
86 driving encounter and catches, such as differences in sampling efficiency (a.k.a. catchability),  
87 while random effects capture the spatio-temporal dynamics of the fish community.

88 **Dynamics of Celtic Sea fisheries** We use the highly mixed demersal fisheries of the Celtic Sea  
89 as a case study. The Celtic Sea is a temperate sea where fisheries are spatially and temporally  
90 complex; mixed fisheries are undertaken by several nations using different gear types<sup>21,22</sup>. Close  
91 to 150 species have been identified in the commercial catches of the Celtic Sea, with approxi-  
92 mately 30 species dominating the catch<sup>23</sup>.

93 We parametrise our spatiotemporal model using catch data from seven fisheries-independent sur-  
94 veys undertaken in the Celtic Sea over the period 1990 - 2015 (Table S1) and include nine of  
95 the main commercial species (see Table S2, Figure 2) : Atlantic cod (*Gadus morhua*), Atlantic  
96 haddock (*Melanogrammus aeglefinus*), Atlantic whiting (*Merlangius merlangus*), European Hake  
97 (*Merluccius merluccius*), white-bellied anglerfish (*Lophius piscatorius*), black-bellied anglerfish (*Lophius budegassa*),  
98 megrim (*Lepidorhombus whiffiagonis*), European Plaice (*Pleuronectes platessa*) and Common  
99 Sole (*Solea solea*). These species which make up >60 % of landings by towed fishing gears  
100 for the area (average 2011 - 2015;<sup>24</sup>). Each species was separated into juvenile and adult size  
101 classes based on their legal minimum conservation reference size (Table S2).

102 We analyse the data to understand how the different associations among emergent species-groups  
103 (combination of species and size class) and their potential drivers affect catch compositions in

104 ~~mixed fisheries. We consider how these have changed over time, and the implications for mixed~~  
105 ~~fisheries in managing catches of quota species under the EU landing obligation.~~<sup>coolin</sup>

106 **Common average spatial patterns driving species associations** A spatial dynamic factor anal-  
107 ysis decomposes the dominant spatial patterns driving differences in encounter probability and  
108 positive density. The first three factors [\(after PCA rotation\)](#) account for 83.7% of the between  
109 species-group variance in average encounter probability and 69% of the between species-group  
110 variance in average positive density. A clear spatial pattern can been seen both for encounter  
111 probability and positive density, with a positive value associated with the first factor in the inshore  
112 north easterly part of the Celtic Sea into the Bristol Channel and Western English Channel, moving  
113 to a negative value offshore in the south-westerly waters (Figure 1). The species-group loadings  
114 coefficients show plaice, sole and whiting to be positively associated with the first factor for en-  
115 counter probability while the other species-groups are negatively associated. For average positive  
116 density, positive associations are also found for haddock and juvenile cod. [This is indicative of a](#)  
117 [more inshore distribution for these species-groups.](#)

118 On the second spatial factor for encounter probability a north / south split can be seen at approxi-  
119 mately 49° N while positive density is more driven by a positive value in the deeper westerly waters  
120 as well as some inshore areas. Species-group values for the second factor indicate there are pos-  
121 itive associations for juvenile monkfish (*L. piscatorius*), juvenile hake, juvenile megrim, plaice and  
122 juvenile whiting with average positive density, which may reflect two different spatial distributions  
123 in the more offshore and in the inshore areas (Figure 1).

124 On the third factor, there is a positive association with the easterly waters for encounter probability  
125 and negative with the westerly waters. This [manifests in the species associations as splitting](#) the

126 roundfish species cod, haddock and whiting which all have a positive association with the third  
127 factor for average encounter probability from the rest of the species-groups ~~which have a negative~~  
128 ~~association~~. Positive density is driven by a north / south split (Figure 1), with positive values in the  
129 northerly areas. Juvenile monkfish (*L. budgeessa* and *L. piscatorius*), cod, juvenile haddock, hake,  
130 adult plaice and whiting are also positively associated with the third factor towards the north while  
131 adult monkfish (*L. budgeessa* and *L. piscatorius*), adult haddock, megrims, juvenile plaice and sole  
132 are negatively associated ~~reflecting their more southerly distribution~~ (Figure 1).

133 ~~While this exploratory factor analysis is modelling unobserved drivers of distribution~~, We consid-  
134 ered what might be driving the differences seen in the spatial factor loadings. The first factor was  
135 highly correlated with log(depth) for both encounter probability (-0.85, CI = -0.88 to -0.81; Figure  
136 S1) and positive density (-0.71, CI = -0.77 to -0.65; Figure S2), ~~A random forest classification tree~~  
137 ~~assigned~~ with 80 % of the variance in the first factor for encounter probability to depth and predom-  
138 inant substrate type, with the majority (86 %) of the variance explained by depth (random forest  
139 classification tree). ~~The variance explained by these variables dropped to 25 % on the second~~  
140 ~~factor with a more even split between depth and substrate, while explaining 60 % of the variance~~  
141 ~~on the third factor. For positive density, the variables explained less of the variance with 62 %, 35~~  
142 ~~%, and 31 % for each of the factors, respectively.~~

143 It is clear that depth and to a lesser extent substrate are important predictors for the main driver of  
144 similarities and differences in distributions and abundances for the different species-groups. ~~The~~  
145 ~~first factor correlates strongly with these variables, despite them not explicitly being incorporated~~  
146 ~~in the model. While depth was incorporated as a covariate in an alternative model formulation~~  
147 ~~(see Methods), it was found not to improve predictions. The utility of these variables as predictors~~  
148 ~~of species distributions has been~~, as identified in other marine species distribution models <sup>25</sup>; the

149 advantage to the approach taken here is that, where such data is unavailable at appropriate spatial  
150 resolution, the spatial factor analysis can adequately characterise these influences on species  
151 spatial dynamics.

152 **Changes in spatial patterns over time, but stability in species dynamics** While there are clear  
153 spatial patterns in the factor coefficients describing differences in average (over time) encounter  
154 probability and positive density (Figure 1). The inter-annual differences in factor coefficients show  
155 less structure (Figures S5, S6). These inter-annual differences are important as they reflect the  
156 ability of fishers to predict where they can target species from one year to the next, without which  
157 it may be difficult to avoid unwanted catch in close to real-time<sup>coolin</sup>. There were, however, While  
158 spatio-temporal factor coefficients did not show consistent trends from year to year across all  
159 species; common patterns in spatiotemporal factor coefficients among species-groups there were  
160 clear relationships (Figure 2). The same factors appear to drive spatiotemporal distributions of  
161 megrim, anglerfish species and hake (the deeper water species, species-grouping negatively as-  
162 sociated with the second axes of Figure 2a) and the roundfish and flatfish (species-grouping more  
163 positively associated with the second axes of Figure 2a). For spatio-temporal positive density  
164 (Figure 2b) cod, haddock and whiting (the roundfish species) are separated from plaice, sole (the  
165 flatfish) and deeper water species. As such, From this it can be predicted that higher catches of a  
166 species within a group (e.g. cod in roundfish) would be expected when catching another species  
167 within that group (e.g. whiting in roundfish), . This suggesting that one or more common environ-  
168 mental drivers are influencing the distributions of the species groups, and that driver differentially  
169 affects the species groups, but this could not be explained by temperature is often included as a  
170 covariate in species distribution models, but was found not to contribute to the variance in the first  
171 factor values (Figure S6, no correlations found for either encounter probability or positive density).

172 **Three clusters of species show similar spatial patterns** To gain greater insight  
173 into the community dynamics we considered how species-groups covary in space and time through  
174 among species-group correlations. Pearson correlation coefficients for the modelled average spa-  
175 tial encounter probability (Figure 3a) show clear strong associations between adult and juvenile  
176 size classes for all species ( $>0.75$  for all species except hake, 0.56). Among species-groups, hi-  
177 erarchical clustering identified the same three common groups as our visual inspection of factor  
178 loadings above, with roundfish (cod, haddock, whiting) closely grouped in their association, with  
179 correlations for adult cod with adult haddock and adult whiting of 0.73 and 0.5 respectively, while  
180 adult haddock with adult whiting was 0.63 (Figure 3a), flatfish (plaice and sole) are also strongly  
181 correlated with adult plaice and sole having a coefficient of 0.75. The final group are principally  
182 the and species found in the deeper waters (hake, megrim and both anglerfish species) with the  
183 megrim strongly associated with the budegassa anglerfish species (0.88). Negative relationships  
184 were found between plaice, sole and the monkfish species (-0.27, -0.26 for the adult size class  
185 with budegassa adults respectively) and hake (-0.33, -0.37) (Figure 3a) showing strong intra-  
186 group correlations indicating spatial separation in distributions. This confirms the associations  
187 among species seen in the factor loadings, with three distinct species-group assemblages be-  
188 ing present. This is also evident in correlation coefficients for the average positive density, with  
189 strong associations among the roundfish (Figure 3b) show fewer significant positive or negative  
190 relationships among species-groups than for encounter probability, but still evident are the strong  
191 association among the roundfish with higher catches of cod are associated with higher catches of  
192 haddock (0.58) and whiting (0.47), as well as the two anglerfish species (0.71 for piscatorius and  
193 0.44 for budegassa) and hake (0.73). Similarly, plaice and sole are closely associated (0.31) and  
194 higher catches of one would expect to see higher catches of the other, but also higher catches of  
195 some juvenile size classes of roundfish (whiting and haddock) and anglerfish species. Negative

196 association of juvenile megrim, anglerfish (budegassa) and hake with adult sole (-0.61, -0.61 and  
197 -0.47 respectively), plaice (-0.36 and -0.35 for megrim and hake only) indicate high catches of one  
198 can predict low catches of the other successfully.

199 In addition to the average spatial correlations, we also estimate spatiotemporal correlations. Spatial  
200 population correlations (representing the average correlations between pairs for species-group x  
201 and species group y across all years) are linearly associated with the spatiotemporal population  
202 correlations (representing how correlations between species-group x and species-group y change  
203 from year to year), indicating generally predictable relationships between species-groups from one  
204 year to the next. This suggests that a positive or negative association between two species-groups  
205 is likely to persist from one year to the next, and that species-groups are consistently associated  
206 with each other in the catch. The correlation coefficients were 0.59 (0.52–0.66) and 0.47 (0.38  
207 –0.55) for encounter probability and positive density respectively. However, a linear regression  
208 between the spatial correlations and the spatio-temporal correlations shows high variance ( $R^2$   
209 = 0.36 and 0.22 respectively), indicating that the scale of these relationships does change from  
210 one-year to the next. This would have implications for the predictability of the relationship between  
211 catches of one species-group and another when trying to balance catch with quotas in mixed  
212 fisheries. It can also be seen in the spatial factor maps that there are subtle differences in spatial  
213 patterns in factor loading values from one year to the next (Figures S4 and S5) indicating changes  
214 may be driven by temporally changing environmental factors and species behaviour.

215 Subtle differences in distributions may be important to separate catches within groups  
216 under the landing obligation<sup>coillín</sup>: The analysis shows the interdependence within species-groups  
217 of roundfish, flatfish and deeper water species, where catching one species within the group  
218 indicates a high probability of catching the other species, which has important implications for how

219 spatial avoidance can be used to support implementation of the EU's landings obligation.<sup>coolin</sup> If  
220 production from mixed fisheries is to be maximised, decoupling catches of species between and  
221 within the groups will be key. For example, asking where the maximal separation in the densities of  
222 two coupled species is likely to occur? To address this requirement, we map the difference in spa-  
223 tial distribution within a group for each pair of species within a species-groupings for a single year  
224 (2015; Figure 4). **MAYBE PICK HADDOCK AND WHITING AS A QUICK REALLY IMPORTANT**  
225 **EXAMPLE?**<sup>coolin</sup>

226 ~~Cod had a more north-westerly distribution than haddock, while cod was more westerly distributed~~  
227 ~~than whiting roughly delineated by the 7° W line (Figure 4a).~~ Whiting appeared particularly  
228 ~~concentrated in an area between 51 and 52 ° N and 5 and 7 ° W, which can be seen by comparing~~  
229 ~~the whiting distribution with both cod (Figure 4b) and haddock (Figure 4c).~~ For the deeper water  
230 ~~species (Figures 4d and 4e), hake are more densely distributed in two areas compared to anglerfishes~~  
231 ~~megrim (though megrim has a stable density across the modelled area as indicated by the large~~  
232 ~~amount of white space).~~ For anglerfishes and megrim (Figure 4f), anglerfishes have a more  
233 ~~easterly distribution than megrim.~~ For the flatfish species plaice and sole (Figure 4g), plaice appear  
234 ~~to be more densely distributed along the coastal areas of Ireland and Britain, while sole are more~~  
235 ~~densely distributed in the Southern part of the English Channel along the coast of France.~~

236 Predicted catch distribution from a “typical” otter trawl gear and beam trawl fishing at three different  
237 locations highlights the differences fishing gear and location makes on catches (Figure 4h). **As**  
238 ~~can be seen, both the gear selectivity and area fished play important contributions to the catch~~  
239 ~~compositions;~~ In the inshore area (location ‘A’) plaice and sole are the two main species in catch  
240 reflecting their distribution and abundance, though the otter trawl gear catches a greater proportion  
241 of plaice to sole than the beam trawl. The area between Britain and Ireland (location ‘B’) has a

242 greater contribution of whiting, haddock, cod, hake and anglerfishes in the catch with the otter  
243 trawl catching a greater proportion of the roundfish, haddock, whiting and cod while the beam  
244 trawl catches more anglerfishes and megrims. The offshore area has a higher contribution of  
245 megrim, anglerfishes and hake with the otter trawl catching a greater share of hake and the beam  
246 trawl a greater proportion of megrim. Megrim dominates the catch for both gears in location 'C',  
247 reflecting its relative abundance in the area.

248 **Addressing the scientific challenges of the landing obligation in mixed fisheries In-application**

249 **to-the-Celtic-Sea** We have identified spatial separation of three distinct species-groupings (round-  
250 fish, flatfish and deeper water species) while showing that only subtle differences exist in distri-  
251 butions within species-groups. The differences in catch compositions between gears at the same  
252 location (Figure 4h) show that changing fishing methods can go some way to affecting catch, yet  
253 that differences in catches between locations are likely to be more important. For example, beam  
254 trawls fishing at the inshore locations (e.g. location 'A' in Figure 4) are likely to predominately  
255 catch plaice and sole, yet switching to the offshore locations (e.g. location 'C') would likely yield  
256 greater catches of megrim and anglerfishes. Such changes in spatial fishing patterns are likely to  
257 play an important role in supporting implementation of the landings obligation.

258 More challenging is within-group spatial separation due to significant overlap in spatial distributions  
259 for the species, driven by common environmental factors. Subtle changes may yield some benefit  
260 in changing catch composition, yet the outcome is likely to be much more difficult to predict. **For**  
261 **example**, Subtle differences in the distribution of cod, haddock and whiting can be seen in Figures  
262 4a-c, showing spatial separation of catches is much more challenging and likely to need to be  
263 supported by other measures such as changes to the selectivity characteristics of gear (e.g. <sup>26</sup>).

264 A role that science can play in supporting effectiveness of spatiotemporal avoidance could be to  
265 provide probabilistic advice on likely hotspots for species occurrence and high species density  
266 which can inform fishing decisions. Previous modelling studies have shown how spatiotemporal  
267 models could improve predictions of high ratios of bycatch species to target species<sup>27-29</sup>, and  
268 geostatistical models are well suited to this as they incorporate spatial dependency while providing  
269 for probabilities to be drawn from posterior distributions of the parameter estimates. We posit  
270 that such advice could be enhanced by integrating data obtained directly from commercial fishing  
271 vessels at a higher temporal resolution, providing real-time forecasts to inform fishing choices that  
272 also captures seasonal differences in distributions,[akin to weather forecasting](#). Advice informed  
273 by [a model including](#) a seasonal or real-time component could inform optimal policies for time-area  
274 closures, move-on rules or even as informal information to be utilised by fishers directly without  
275 being reliant on costly continuous data collection on environmental parameters,[but by using the](#)  
276 [vessels-as-laboratories approach](#).

277 An important question for the implementation of the EU's landing obligation is how far spatial avoid-  
278 ance can go to achieving catch balancing in fisheries. Our model captures differences between  
279 location fished for two gear types and their broad scale effect on catch composition,[information](#)  
280 [crucial for managers in implementing the landing obligation](#). It is likely,[however, that](#) this analysis  
281 reflects a lower bound on [the utility of spatial](#)<sup>collin</sup> avoidance as fine-scale behavioural decisions  
282 such as time-of-day, gear configuration and location choices can also be used to affect catch<sup>30,31</sup>.  
283 Results of empirical studies undertaken elsewhere<sup>5,6</sup> suggest limits to the effectiveness of spatial  
284 avoidance. Differences in ability to change catch composition have also been observed for differ-  
285 ent fleets; in the North Sea targeting ability was found to differ between otter and beam trawlers  
286 as well as between vessels of different sizes<sup>32</sup>.

287 Our framework allows for a quantitative understanding of the broad scale global production set  
288 available to fishers<sup>33</sup> and thus the extent to which they can alter catch compositions while operating  
289 in a mixed fishery. Simulations of spatial effort allocation scenarios based on the production  
290 sets derived from the model estimates could be used as inputs to fisher behavioural models to  
291 allow for identification of the lower bounds of optimum spatial harvest strategies. This would  
292 provide managers with information useful for examining trade-offs in quota setting by integrating  
293 potential for spatial targeting in changing catch composition, thus provide a scientific contribution  
294 to meeting the goal of maximising catches in mixed fisheries within single stock quota constraints<sup>7</sup>.  
295 Further, the correlations among species could provide information on fisheries at risk of capturing  
296 protected, endangered or threatened species such as elasmobranches, and allow identification of  
297 areas where there are high ratios of protected to target species.

298 Complex environmental, fishery and community drivers of distribution for groups of species high-  
299 lights the scale of the challenge in separating catches within the species-groups using spatial  
300 management measures. This has important implications for management of the mixed fisheries  
301 under the EU landings obligation. Our analysis identifies where it may be easier to separate  
302 catches of species (among groups) and where it is more challenging (within groups). We propose  
303 that the framework presented in Figures 1-4 provides a viable route to reducing the complexity  
304 of highly mixed systems. This can allow informed management discussion over more traditional  
305 anecdotal knowledge of single-species distribution in space and time.

306 **Methods**

307 **Model structure:** VAST<sup>1</sup> implements a delta-generalised linear mixed modelling (GLMM) frame-  
308 work that takes account of spatio-temporal correlations among species-groups through implemen-  
309 tation of a spatial dynamic factor analysis (SDFA). Spatial variation is captured through a Gaus-  
310 sian Markov Random Field, while we model random variation among species-groups and years.  
311 Covariates affecting catchability (to account for differences between fishing surveys) and density  
312 (to account for environmental preferences) can be incorporated for predictions of presence and  
313 positive density. The following briefly summarises the key methods implemented in the VAST  
314 framework. For full details of the model the reader is invited directed to Thorson *et al* 2017<sup>34</sup>.

**SDFA:** A spatial dynamic factor analysis incorporates advances in joint dynamic species models

<sup>34</sup> to take account of associations among species-groups by modelling response variables as a multivariate process. This is achieved through implementing a factor analysis decomposition where common latent trends are estimated so that the number of common trends is less than the number of species-groups modelled. The factor coefficients are then associated through a function for each factor that returns a positive or negative association of one or more species with any location. Log-density of any species is then described as a linear combination of factors and loadings:

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

315 Where  $\theta_c(s, t)$  represents log-density for species  $c$  at site  $s$  at time  $t$ ,  $\psi_j$  is the coefficient for factor  
316  $j$ ,  $L_{c,j}$  the loading matrix representing association of species  $c$  with factor  $j$  and  $\gamma_{k,c} \chi_k(s, t)$  the  
317 linear effect of covariates at each site and time<sup>35</sup>.

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

318 The factor analysis can identify community dynamics and where species have similar spatio-  
 319 temporal patterns, allowing inference of species distributions and abundance of poorly sampled  
 320 species through association with other species and allows for computation of spatio-temporal cor-  
 321 relations among species-groups <sup>35</sup>.

**Estimation of abundances:** Spatio-temporal encounter probability and positive catch rates are modelled separately with spatio-temporal encounter probability modelled using a logit-link linear predictor;

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

and positive catch rates modelling using a gamma-distribution <sup>19</sup>.

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

322 where  $p(s_i, c_i, t_i)$  is the predictor for encounter probability for observation  $i$ , at location  $s$  for  
 323 species-group  $c$  and time  $t$  and  $r(s_i, c_i, t_i)$  is similarly the predictor for the positive density.  $\beta_*(c_i, t_i)$   
 324 is the intercept,  $\omega_*(s_i, c_i)$  the spatial variation at location  $s$  for factor  $f$ , with  $L_\omega(c_i, f)$  the load-  
 325 ing matrix for spatial covariation among species-groups.  $\varepsilon_*(s_i, c_i, t_i)$  is the linear predictor for  
 326 spatio-temporal variation, with  $L_\varepsilon(c_i, f)$  the loading matrix for spatio-temporal covariance among  
 327 species-groups and  $\delta_*(c_i, v_i)$  the contribution of catchability covariates for the linear predictor with  
 328  $Q_{c_i, v_i}$  the catchability covariates for species-group  $c$  and vessel  $v$ ; \* can be either  $p$  for probability  
 329 of encounter or  $r$  for positive density.

The Delta-Gamma formulation is then:

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

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

332 **Spatio-temporal variation:** The spatiotemporal variation is modelled using Gaussian Markov  
 333 Random Fields (GMRF) where data is associated to nearby locations through a Matérn covariance  
 334 function with the parameters estimated within the model. Here, the correlation decays smoothly  
 335 over space the further from the location and includes geometric anisotropy to reflect the fact that  
 336 correlations may decline in one direction faster than another (e.g. moving offshore)<sup>20</sup>. The best  
 337 fit estimated an anisotropic covariance where the correlations were stronger in a north-east -  
 338 south-west direction, extending approximately 97 km and 140 km before correlations for encounter  
 339 probability and positive density reduced to <10 %, respectively (Figure S9). Incorporating the  
 340 spatiotemporal correlations among and within species-groups provides more efficient use of the  
 341 data as inference can be made about poorly sampled locations from the covariance structure.

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

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

- 342 Here,  $vec[\mathbf{E}_*(t)]$  is the stacked columns of the matrices describing  $\varepsilon_*(s, p, t)$  at every location,  
 343 species-group and time,  $\mathbf{R}_*$  is a correlation matrix for encounter probability or positive catch rates

344 among locations and  $\mathbf{V}_*$  a covariance matrix for encounter probability or positive catch rate among  
345 species-groups (modelled within the factor analysis).  $\otimes$  represents the Kronecker product so that  
346 the correlation among any location and species-group can be computed<sup>34</sup>.

347 **Incorporating covariates** Survey catchability (the relative efficiency of a gear catching a species-  
348 group) was estimated as a fixed effect in the model,  $\delta_s(v)$ , to account for differences in spatial  
349 fishing patterns and gear characteristics which affect encounter and capture probability of the  
350 sampling gear<sup>36</sup>. Parameter estimates (Figure S10) showed clear differential effects of surveys  
351 using otter trawl gears (more effective for round fish species) and beam trawl gears (more effective  
352 for flatfish species).

353 No fixed covariates for habitat quality or other predictors of encounter probability or positive density  
354 were included. While incorporation may improve the spatial predictive performance<sup>34</sup>, it was not  
355 found to be the case here based on model selection with Akaike Information Criterion (AIC) and  
356 Bayesian Information Criterion (BIC).

357 **Parameter estimation** Parameter estimation was undertaken through Laplace approximation of  
358 the marginal likelihood for fixed effects while integrating the joint likelihood (which includes the  
359 probability of the random effects) with respect to random effects. This was implemented using  
360 Template Model Builder (TMB;<sup>37</sup>) with computation through support by the Irish Centre for High  
361 End Computing (ICHEC; <https://www.ichec.ie>) facility.

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

365 The model was been fit to nine species separated into adult and juvenile size classes (Table S2)  
366 to seven survey series (Table S1) in the Celtic Sea bound by 48° N to 52 ° N latitude and 12 ° W  
367 to 2° W longitude (Figure S8) for the years 1990 - 2015 inclusive.

368 The following steps were undertaken for data processing: i) data for survey stations and catches  
369 were downloaded from ICES Datras ([www.ices.dk/marine-data/data-portals/Pages/  
370 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  
371 checked and any tows with missing or erroneously recorded station information (e.g. tow duration  
372 or distance infeasible) removed; iii) swept area for each of the survey tows was estimated based  
373 on fitting a GAM to gear variables so that  $\text{Doorspread} = s(\text{Depth}) + \text{DoorWt} + \text{WarpLength} +$   
374  $\text{WarpDiameter} + \text{SweepLength}$  and a gear specific correction factor taken from the literature<sup>38</sup>;  
375 iii) fish lengths were converted to biomass (Kg) through estimating a von bertalanffy length weight  
376 relationship,  $Wt = a \cdot L^b$ , fit to sampled length and weight of fish obtained in the EVHOE survey  
377 and aggregated within size classes (adult and juvenile).

378 The final dataset comprised of estimates of catches (including zeros) for each station and species-  
379 group and estimated swept area for the tow.

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

385 Three candidate models were identified, i) a base model where the vessel interaction was a ran-

386 dom effect, ii) the base but where the vessel x species effect was estimated as a fixed covariate, iii)  
387 with vessel x species effect estimated, but with the addition of estimating fixed density covariates  
388 for both predominant habitat type at a knot and depth. AIC and BIC model selection favoured the  
389 second model (Table S3). The final model included estimating 130,950 coefficients (1,674 fixed  
390 parameters and 129,276 random effect values).

391 **Model validation** Q-Q plots show good fit between the derived estimates and the data for positive  
392 catch rates and between the predicted and observed encounter probability (S11, S12). Further,  
393 model outputs are consistent with stock-level trends abundances over time from international as-  
394 sessments (S13), yet also provide detailed insight into species co-occurrence and the strength of  
395 associations in space and time.

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**Author contributions** XXXX

**Competing Interests** The authors declare that they have no competing financial interests.

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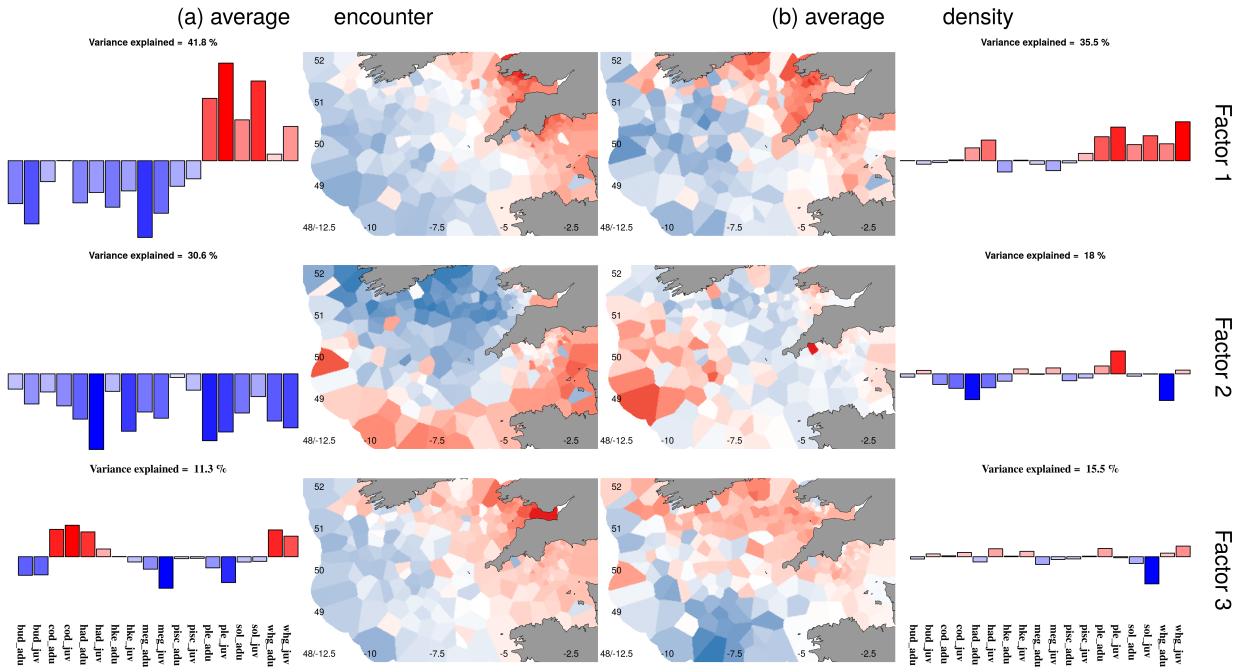


Figure 1: Factor values for the first three factors for (a) Average encounter probability and (b) Average positive density for the species-groups (outer figures) and spatially (inner figures). Red: positive association to the factor, Blue: negative association

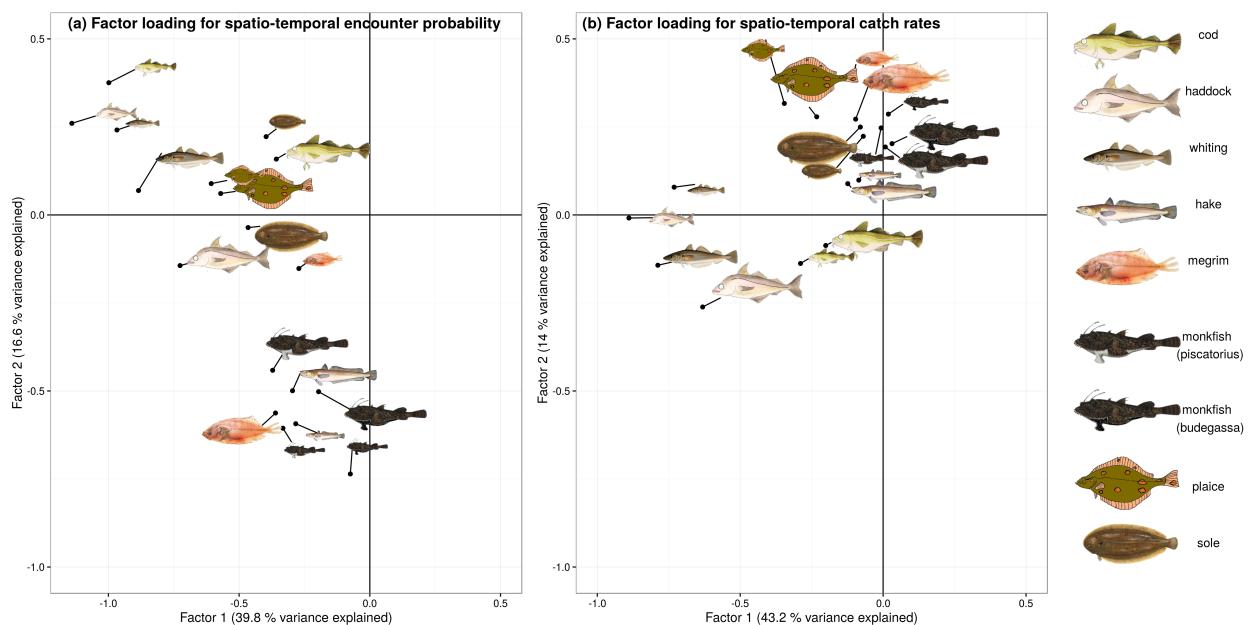


Figure 2: Position of each species-group on the first two axes from the factor analysis for (a) spatio-temporal encounter probability and (b) spatio-temporal positive density.

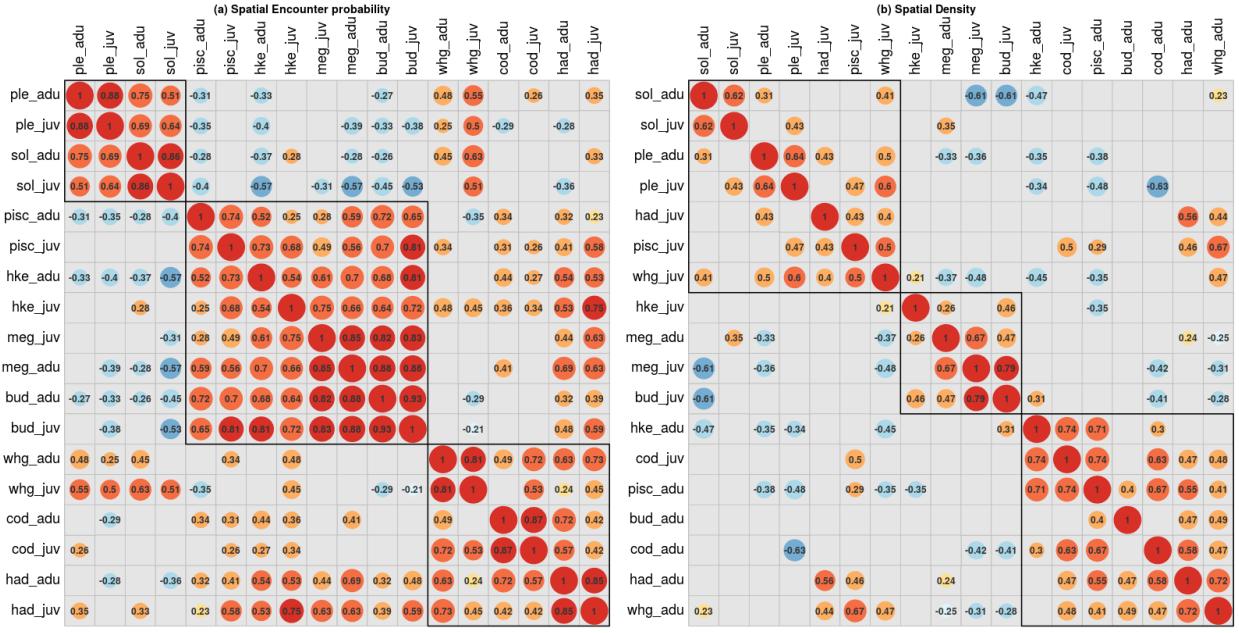


Figure 3: Inter-species correlations for (a) spatial encounter probability over all years and (b) spatial positive density. Species-groups are clustered into three groups based on a hierarchical clustering method with non-significant correlations (the Confidence Interval [ $\pm 1.96 \times \text{SEs}$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

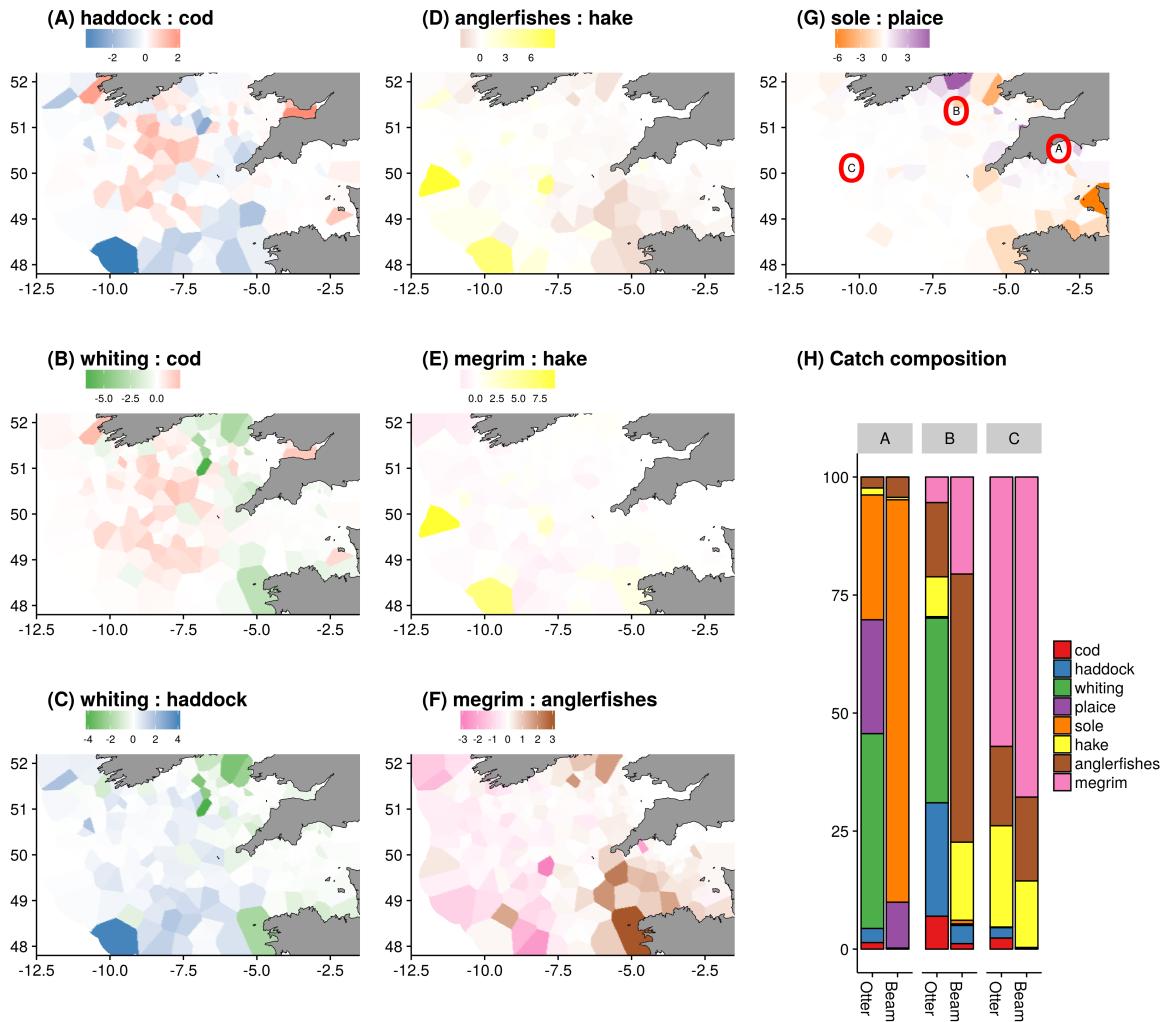


Figure 4: Differences in the standardised spatial density for pairs of species and expected catch rates for two different gears at three different locations in 2015.