

# 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 anecd-  
9 tal. Here we develop a dimension-reduction framework based on joint species distribution  
10 modelling (spatial dynamic factor analysis) to understand how spatial community and fish-  
11 ery dynamics interact to determine species and size composition. In the example applica-  
12 tion to the highly mixed fisheries of the Celtic Sea, clear common spatial patterns emerge  
13 for three distinct species-groups and, 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 **The results highlight both opportunities for and limitations of the ability to spatiotemporally**  
17 **separate catches.** We highlight the importance of dimension reduction techniques to focus  
18 **management discussion on axes of maximal separation in space and time. We propose**  
19 **that spatiotemporal modelling of available data is a scientific necessity to address the per-**  
20 **vasive 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>4</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>5</sup>. With future increased demand for  
26 fish protein <sup>6</sup> there is an important role for well managed fisheries in supporting future food secu-  
27 rity <sup>7</sup> and<sup>coolin</sup> there necessitating remains a need to ensure<sup>coolin</sup> fisheries are managed efficiently  
28 to maximise productivity.

29 A particular<sup>brutus</sup> challenge in realising increased catches from rebuilt populations is maximising  
30 yields from mixed fisheries <sup>2,8,9</sup>. In mixed fisheries, the predominant type of fishery worldwide,  
31 several fish species are caught together in the same net or fishing operation (known as a ‘technical interaction’).  
32 If managed by individual quotas, if and<sup>brutus</sup> catches do not match available stock quotas, either a  
33 vessel must stop fishing when the first quota is reached (the ‘choke’ species) or overexploitation  
34 of the weaker species occurs while fishers continue to catch more healthy species and throw back  
35 (‘discard’) the fish for which they have no quota<sup>1</sup>. There is, therefore, a pressing need for scien-  
36 tific tools which simplify the complexities of mixed fisheries to help avoid discarding managers and

37 fishers maximise catches<sup>coilin</sup>.

38 Sustainability of European fisheries has been hampered by this 'mixed fishery problem' for decades

39 with large-scale discarding<sup>10</sup>. A paradigm shift is being introduced Under the EU Common Fish-

40 eries Policy (CFP) reform of 2012 through two significant management changes. First, by 2019 all

41 fish that are caught are due to be counted against the respective stock quota; second, by 2020 all

42 fish stocks must be fished so as to be able to produce their Maximum Sustainable Yield (MSY)<sup>11</sup>.

43 The changes are, expected to contribute to attainment of the goal of Good Environmental Status

44 (GES) under the European Marine Strategy Framework Directive (MSFD;<sup>12</sup>) and move Europe

45 towards an ecosystem based approach to fisheries management<sup>13coilin</sup>. Societal objectives for

46 fisheries to achieve MSY across ecosystem components are paralleled by individual fishers goals

47 continuance of traditional practices. Under the new policy, Unless fishers can avoid catch of un-

48 wanted species they will have to stop fishing when reaching their first restrictive quota . This

49 introducing a potential significant cost to fishers of under-utilised quota<sup>9</sup> and provides a strong

50 incentive to mitigate such losses<sup>14</sup>. The ability of fishers to align their catch with available quota

51 depends on being able to exploit target species while avoiding unwanted catch. Methods by which

52 fishers can alter their fishing patterns include either by switching fishing method (e.g. trawling

53 to netting), changing technical gear characteristics (e.g. introducing escapement panels in nets),

54 or the timing and location of fishing activity<sup>15</sup>. For example, otter trawl gears are known to have

55 higher catch rates of roundfish due to the higher headline and wider sweeps which herd demersal

56 fish into the net while beam trawls employ chain mesh to seabed<sup>16</sup>.

57 Spatiotemporal management measures (such as time-limited fishery closures) have been applied

58 to reduce unwanted catch with varying degrees of success<sup>3,17</sup>, partly because However, such

59 measures they have generally been targeted at individual species without considering associa-

60 tions ~~and interactions~~ among several species. Highly mixed fisheries are complex with spatial,  
61 technological and community interactions ~~combining; The design of spatio-temporal management~~  
62 ~~measures which aim to allow exploitation of high quota stocks while protecting low quota stocks~~  
63 ~~requires understanding of these interactions at a scale meaningful to managers and fishers.~~ Here,  
64 Our goal is to develop a framework for understanding these complexities. We do so by imple-  
65 menting a spatio-temporal dimension reduction method and use ~~the~~ results to draw inference on  
66 the fishery-community dynamics, creating a framework to identify trends common among species  
67 ~~. We use this to~~ and describe ~~the potential for and limitations of where~~<sup>coolin</sup> spatial measures ~~to an~~  
68 ~~contribute to~~<sup>coolin</sup> mitigate~~ing~~ unwanted catches in highly mixed fisheries.

69 **Framework for analysing spatio-temporal mixed fisheries interactions** We present a framework  
70 ~~for analysing how far spatio-temporal avoidance can contribute towards mitigating imbalances~~  
71 ~~in quota in mixed fisheries.~~ We ~~use fisheries-independent survey data to~~ characterise the spa-  
72 tiotemporal dynamics of key components of a fish community by ~~employing a geostatistical Vector~~  
73 ~~Autoregressive Spatiotemporal model (VAST).~~ We implementing a factor analysis decomposition  
74 to describe trends in spatiotemporal dynamics of the different species as a function of latent vari-  
75 ables <sup>18</sup> representing spatial variation (9 factors; ~~which we call~~ 'average' spatial variation) and  
76 spatio-temporal variation (9 factors) for encounter probability and positive catch rates (~~which we~~  
77 ~~call~~ 'positive density') separately<sup>19</sup>. This allows us to ~~By describing the species dynamics through~~  
78 ~~underlying contributory spatiotemporal factors we can~~ take account of how the factors contribute  
79 to affect catches of the species in mixed fisheries. ~~We use~~ Gaussian Markov Random Fields  
80 (GMRFs) ~~to~~ capture spatial and temporal dependence within and among species groups for both  
81 encounter probability and positive density<sup>20</sup>. ~~VAST is set in a mixed modelling framework to allow~~  
82 ~~estimation of~~ Fixed effects ~~to~~ account for systematic differences driving encounter and catches,

83 such as differences in sampling efficiency (a.k.a. catchability), while random effects capture the  
84 spatio-temporal dynamics of the fish community.

85 **Dynamics of Celtic Sea fisheries** We use the highly mixed demersal fisheries of the Celtic Sea  
86 as a case study. The Celtic Sea is a temperate sea where fisheries are spatially and tempo-  
87 rally complex; mixed fisheries are undertaken by several nations using different gear types<sup>21,22</sup>.  
88 Close to 150 species have been identified in the commercial catches of the Celtic Sea, with ap-  
89 proximately 30 species dominating the catch<sup>23</sup>. We parametrise our spatiotemporal model using  
90 catch data from seven fisheries-independent surveys undertaken in the Celtic Sea over the pe-  
91 riod 1990 - 2015 (Table S1) and include nine of the main commercial species (see Table S2,  
92 Figure 2) : Atlantic cod (*Gadus morhua*), Atlantic haddock (*Melanogrammus aeglefinus*), Atlantic  
93 whiting (*Merlangius merlangus*), European Hake (*Merluccius merluccius*), white-bellied anglerfish  
94 (*Lophius piscatorius*), black-bellied anglerfish (*Lophius budegassa*), megrim (*Lepidorhombus whiffiagonis*),  
95 European Plaice (*Pleuronectes platessa*) and Common Sole (*Solea solea*). These species which  
96 make up >60 % of landings by towed fishing gears for the area (average 2011 - 2015;<sup>24</sup>). Each  
97 species was separated into juvenile and adult size classes based on their legal minimum conser-  
98 vation reference size (Table S2).

99 We analyse the data to understand how the different associations among emergent species groups  
100 (combination of species and size class) and their potential drivers affect catch compositions in  
101 mixed fisheries. We consider how these have changed over time, and the implications for mixed  
102 fisheries in managing catches of quota species under the EU landing obligation.<sup>coolin</sup>

103 **Common average spatial patterns driving species associations** A spatial dynamic factor anal-  
104 ysis decomposes the dominant spatial patterns driving differences in encounter probability and

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

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

121 On the third factor, there is a positive association with the easterly waters for encounter probability  
122 and negative with the westerly waters. This [manifests in the species associations as](#) splitting  
123 the roundfish species cod, haddock and whiting which [all](#) have a positive association with the  
124 third factor for average encounter probability from the rest of the species [which have a negative](#)  
125 [association](#). Positive density is driven by a north / south split (Figure 1), with positive values in the  
126 northerly areas. Juvenile monkfish (*L. budgessa* and *L. piscatorius*), cod, juvenile haddock, hake,  
127 adult plaice and whiting are also positively associated with the third factor in the north while adult

128 monkfish (*L. budgessa* and *L. piscatorius*), adult haddock, megrims, juvenile plaice and sole are  
129 negatively associated reflecting their more southerly distribution (Figure 1).

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

140 It is clear that depth and to a lesser extent substrate are important predictors for the main driver  
141 of similarities and differences in distributions and abundances for the different species.<sup>brutus</sup> The  
142 first factor correlates strongly with these variables, despite them not explicitly being incorporated  
143 in the model. While depth was incorporated as a covariate in an alternative model formulation  
144 (see Methods), it was found not to improve predictions. The utility of these variables as predictors  
145 of species distributions has been, as identified in other marine species distribution models<sup>25</sup>; the  
146 advantage to the approach taken here is that, where such data is unavailable at appropriate spatial  
147 resolution, the spatial factor analysis can adequately characterise these influences on species  
148 spatial dynamics.<sup>brutus</sup>

149 Time varying species distributions, but stability within species groupsChanges in spatial

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

170 **Three clusters of species show similar spatial patterns** To in order to<sup>collin</sup> gain greater in-  
171 sight into the community dynamics we considered how species covary in space and time through  
172 among species correlations. Pearson correlation coefficients for the modelled average spatial en-

173 counter probability (Figure 3a) show clear strong associations between adult and juvenile size  
174 classes for all species (>0.75 for all species except hake, 0.56). ~~Among species groups~~, Hier-  
175 archical clustering identified the same three common groups ~~as our visual inspection of factor~~  
176 ~~loadings above~~,<sup>brutus</sup> with roundfish (cod, haddock, whiting) ~~closely grouped in their association~~,  
177 ~~with correlations for adult cod with adult haddock and adult whiting of 0.73 and 0.5 respectively,~~  
178 ~~while adult haddock with adult whiting was 0.63 (Figure 3a)~~, flatfish (plaice and sole) ~~are also~~  
179 ~~strongly correlated with adult plaice and sole having a coefficient of 0.75. The final group are~~  
180 ~~principally the~~ and species found in the deeper waters (hake, megrim and both anglerfish species)  
181 ~~with the megrim strongly associated with the budegassa anglerfish species (0.88). Negative~~  
182 ~~relationships were found between plaice, sole and the monkfish species (-0.27, -0.26 for the adult~~  
183 ~~size class with budegassa adults respectively) and hake (-0.33, -0.37) (Figure 3a)~~ showing strong  
184 intra-group correlations indicating similar spatial distributions. This confirms the associations  
185 among species seen in the factor loadings, with three distinct species group assemblages being  
186 present. This is also evident in Correlation coefficients for the average positive density also have  
187 strong associations among the roundfish (Figure 3b) ~~show fewer significant positive or negative~~  
188 ~~relationships among species than for encounter probability, but still evident are the strong association~~  
189 ~~among the roundfish with higher catches of cod are associated with higher catches of haddock~~  
190 ~~(0.58) and whiting (0.47), as well as the two anglerfish species (0.71 for piscatorius and 0.44~~  
191 ~~for budegassa) and hake (0.73). Similarly, plaice and sole are closely associated (0.31) and~~  
192 ~~higher catches of one would expect to see higher catches of the other, but also higher catches of~~  
193 ~~some juvenile size classes of roundfish (whiting and haddock) and anglerfish species. Negative~~  
194 ~~association of juvenile megrim, anglerfish (budegassa) and hake with adult sole (-0.61, -0.61 and~~  
195 ~~-0.47 respectively), plaice (-0.36 and -0.35 for megrim and hake only) indicate high catches of one~~  
196 ~~can predict low catches of the other successfully.~~

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

213 **Subtle differences in distributions may be important to separate catches within groups**  
214 **under the landing obligation**<sup>coolin</sup> : The analysis shows the interdependence within the species-groups  
215 of roundfish, flatfish and deeper water species, where catching one species within the group  
216 indicates a high probability of catching the other species, which has important implications for  
217 how spatial avoidance can be used to support implementation of the EU's landings obligation.  
218 <sup>coolin</sup>If production from mixed fisheries is to be maximised, decoupling catches of species between  
219 and within the groups will be key. For example, asking where the maximal separation in the densi-

ties of two coupled species is likely to occur? To address this requirement, We map the difference in spatial distribution ~~within a group~~ for each pair of species within a species-group for a single year (2015; Figure 4) .~~This would to~~ facilitate discussion on maximal separation, for example, between difficult to separate species such as haddock and whiting (Figure 4c). ~~Cod had a more north-westerly distribution than haddock, while cod was more westerly distributed than whiting roughly delineated by the 7° W line (Figure 4a).~~ Whiting appeared particularly concentrated in an area between 51 and 52 ° N and 5 and 7 ° W, which can be seen by comparing the whiting distribution with both cod (Figure 4b) and haddock (Figure 4c). For the deeper water species (Figures 4d and 4e), hake are more densely distributed in two areas compared to anglerfishes and one and megrim (though megrim has a stable density across the modelled area as indicated by the large amount of white space). For anglerfishes and megrim (Figure 4f), anglerfishes have a more easterly distribution than megrim. For the flatfish species plaice and sole (Figure 4g), plaice appear to be more densely distributed along the coastal areas of Ireland and Britain, while sole are more densely distributed in the Southern part of the English Channel along the coast of France.

Predicted catch distribution from a “typical” otter trawl gear and beam trawl fishing at three different locations highlights the differences fishing gear and location makes on catches (Figure 4h). As can be seen, both the gear selectivity and area fished play important contributions to the catch compositions;. In the inshore area (location ‘A’) plaice and sole are the two main species ~~in~~ caught reflecting their distribution and abundance, though the otter trawl gear catches a greater proportion of plaice to sole than the beam trawl. The area between Britain and Ireland (location ‘B’) has a greater contribution of whiting, haddock, cod, hake and anglerfishes in the catch with the otter trawl catching a greater proportion of the roundfish, haddock, whiting and cod while the beam trawl catches more anglerfishes and megrims. The offshore area has a higher contribution of

243 megrim, anglerfishes and hake with the otter trawl catching a greater share of hake and the beam  
244 trawl a greater proportion of megrim. Megrim dominates the catch for both gears in location 'C',  
245 reflecting its relative abundance in the area.

246 **Addressing the scientific challenges of the landing obligation in mixed fisheries** In-application  
247 ~~to the Celtic Sea~~ We have identified spatial separation of three distinct species-groups (roundfish,  
248 flatfish and deeper water species) while showing that only subtle differences exist in distributions  
249 within species-groups. The differences in catch compositions between gears at the same location  
250 (Figure 4h) show that changing fishing methods can go some way to affecting catch, yet that dif-  
251 ferences in catches between locations are likely to be more important. ~~For example, beam trawls~~  
252 ~~fishing at the inshore locations (e.g. location 'A' in Figure 4) are likely to predominately catch plaice~~  
253 ~~and sole, yet switching to the offshore locations (e.g. location 'C') would likely yield greater catches~~  
254 ~~of megrim and anglerfishes. Such~~<sup>brutus</sup> This highlights that changes in spatial fishing patterns are  
255 likely to play an important role in supporting implementation of the landings obligation.

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

263 A role that science can play in supporting effectiveness of spatiotemporal avoidance could be in  
264 providing probabilistic advice on **likely** hotspots for species ~~occurrence and high species density~~

which can inform fishing decisions. Previous modelling studies have shown how spatiotemporal models could improve predictions of high ratios of bycatch species to target species<sup>27–29</sup>, and geostatistical models are well suited ~~to this~~ as they incorporate spatial dependency while providing for probabilities to be drawn from posterior distributions of the parameter estimates. We posit that such advice could be enhanced by integrating data obtained directly from commercial fishing vessels at a higher temporal resolution, providing real-time forecasts to inform fishing choices that also captures seasonal differences in distributions, ~~akin to weather forecasting~~. Such advice informed by a model including a seasonal or real-time component could inform optimal policies for time-area closures, move-on rules or even as informal information ~~to be~~ utilised by fishers directly without being reliant on costly continuous data collection on environmental parameters, ~~but by~~ using the vessels-as-laboratories approach.

An important question for the implementation of the EU's landing obligation is how far spatial avoidance can go to achieve catch balancing in fisheries. Our model captures differences between location fished for two gear types and their broad scale effect on catch composition, ~~information crucial for managers in implementing the landing obligation. Results of~~ Empirical studies undertaken elsewhere<sup>2,8</sup> suggest limits to the effectiveness of spatial avoidance. Differences in ability to change catch composition have also been observed for different fleets; ~~in the North Sea targeting ability was found to differ between otter and beam trawlers as well as between vessels of different sizes~~<sup>30</sup>. It is likely, however, that This analysis likely reflects a lower bound on ~~the utility of spatial~~<sup>coinc</sup> avoidance as fine-scale behavioural decisions such as time-of-day, gear configuration and location choices can also be used to affect catch<sup>31,32</sup>.

~~Our framework allows for a quantitative understanding of the broad scale global production set available to fishers~~<sup>33</sup> and thus the extent to which they can alter catch compositions while operating

288 in a mixed fishery. Simulations of spatial effort allocation scenarios based on the production  
289 sets derived from the model estimates could be used as inputs to fisher behavioural models to  
290 allow for identification of the lower bounds of optimum spatial harvest strategies. This would  
291 provide managers with information useful for examining trade-offs in quota setting by integrating  
292 potential for spatial targeting in changing catch composition, thus provide a scientific contribution  
293 to meeting the goal of maximising catches in mixed fisheries within single-stock quota constraints<sup>9</sup>.  
294 Further, the correlations among species could provide information on fisheries at risk of capturing  
295 protected, endangered or threatened species such as elasmobranches, and allow identification of  
296 areas where there are high ratios of protected to target species.

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

305 **Methods**

306 **Model structure:** We use a geostatistical Vector Autoregressive Spatiotemporal model (VAST)<sup>1</sup>  
307 to implement a delta-generalised linear mixed modelling (GLMM) framework that takes account

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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)

308 of spatio-temporal correlations among species through implementation of a spatial dynamic factor  
309 analysis (SDFA). Spatial variation is captured through a Gaussian Markov Random Field, while we  
310 model random variation among species and years. Covariates affecting catchability (to account for  
311 differences between fishing surveys) and density (to account for environmental preferences) can  
312 be incorporated for predictions of presence and positive density. The following briefly summarises  
313 the key methods implemented in the VAST framework. For full details of the model the reader is  
314 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 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 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>.

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<sup>35</sup>.

322 We use the resultant factor analysis is used to identify community dynamics and drivers common  
 323 among 18 species and results presented through transformation of the loading matrices using  
 324 PCA rotation<sup>brutus</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>.

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

325 where  $p(s_i, c_i, t_i)$  is the predictor for encounter probability for observation  $i$ , at location  $s$  for species  
 326  $c$  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-  
 327 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  
 328 spatial covariation among species.  $\varepsilon_*(s_i, c_i, t_i)$  is the linear predictor for spatio-temporal variation,  
 329 with  $L_\varepsilon(c_i, f)$  the loading matrix for spatio-temporal covariance among species and  $\delta_*(c_i, v_i)$  the  
 330 contribution of catchability covariates for the linear predictor with  $Q_{c_i, v_i}$  the catchability covariates  
 331 for species  $c$  and vessel  $v$ ; \* can be either  $p$  for probability of encounter or  $r$  for positive density.

The Delta-Gamma formulation is then:

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

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

334 **Spatio-temporal variation:** The spatiotemporal variation is modelled using Gaussian Markov  
 335 Random Fields (GMRF) where data is associated to nearby locations through a Matérn covariance  
 336 function with the parameters estimated within the model. Here, the correlation decays smoothly  
 337 over space the further from the location and includes geometric anisotropy to reflect the fact that  
 338 correlations may decline in one direction faster than another (e.g. moving offshore)<sup>20</sup>. The best  
 339 fit estimated an anisotropic covariance where the correlations were stronger in a north-east -  
 340 south-west direction, extending approximately 97 km and 140 km before correlations for encounter  
 341 probability and positive density reduced to <10 %, respectively (Figure S9). Incorporating the  
 342 spatiotemporal correlations among and within species provides more efficient use of the data as  
 343 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:

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

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

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

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

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

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

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

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

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

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

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

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

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

393 **Model validation** Q-Q plots show good fit between the derived estimates and the data for positive  
394 catch rates and between the predicted and observed encounter probability (S11, S12). Further,  
395 model outputs are consistent with stock-level trends abundances over time from international as-  
396 sessments (S13), yet also provide detailed insight into species co-occurrence and the strength of  
397 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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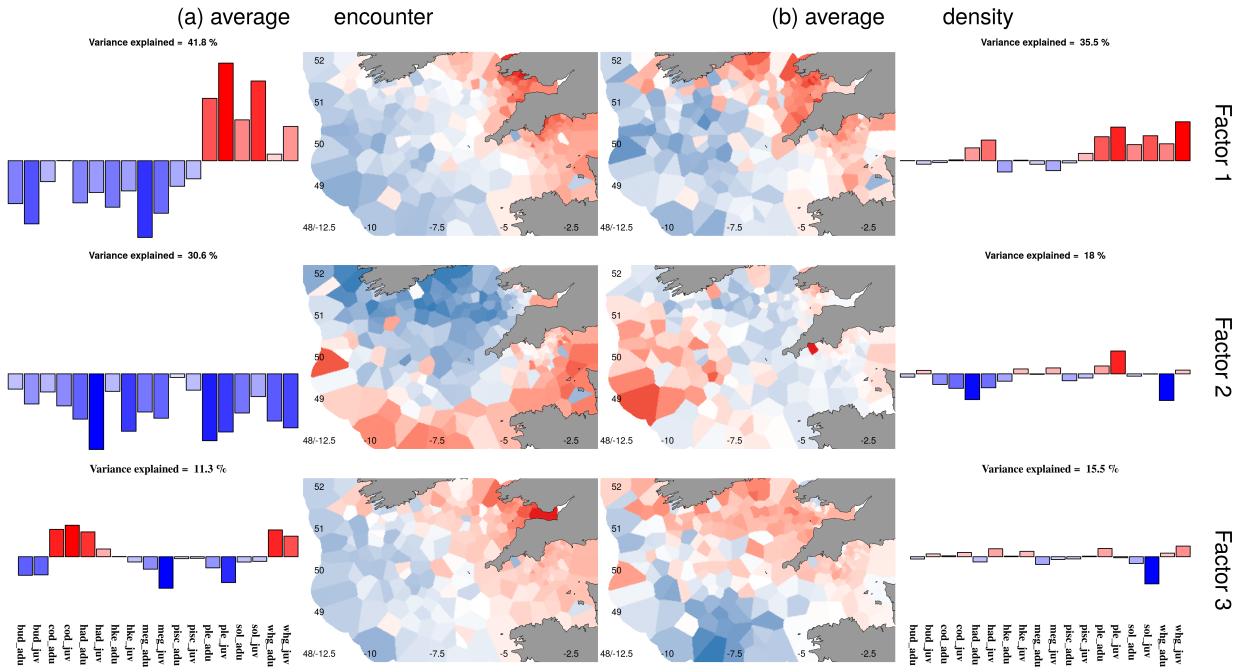


Figure 1: Factor values for the first three factors for (a) Average encounter probability and (b) Average positive density for the species (outer figures) and spatially (inner figures). Red: positive association to the factor, Blue: negative association

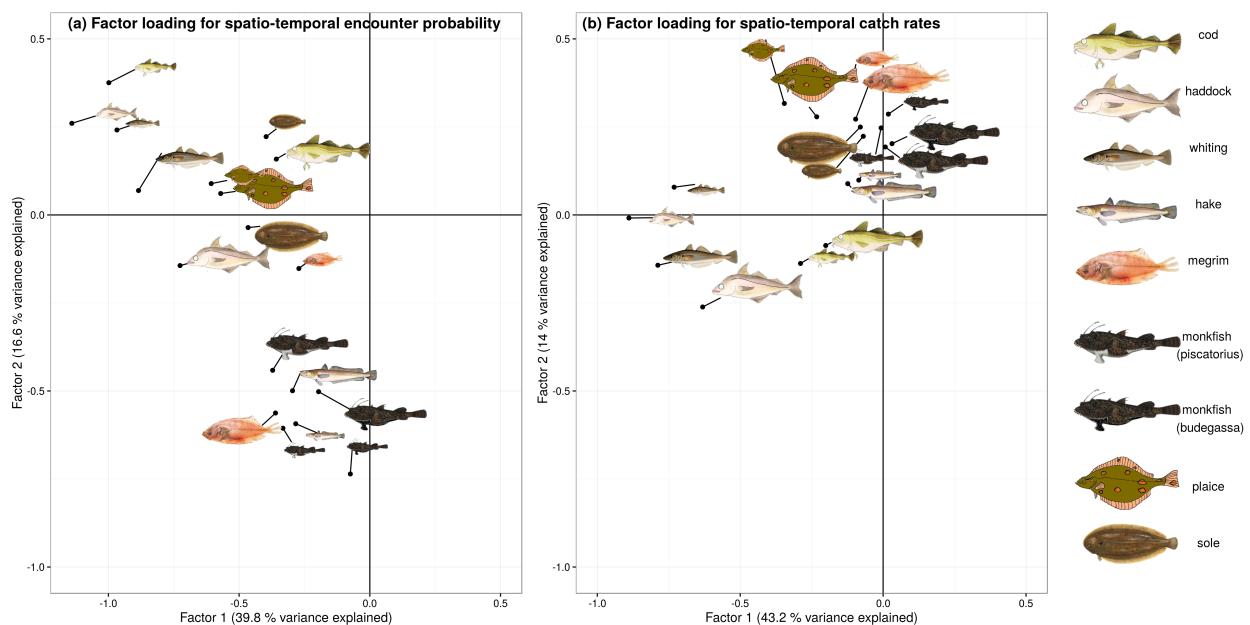


Figure 2: Position of each species on the first two axes from the factor analysis for (a) spatio-temporal encounter probability and (b) spatio-temporal positive density.

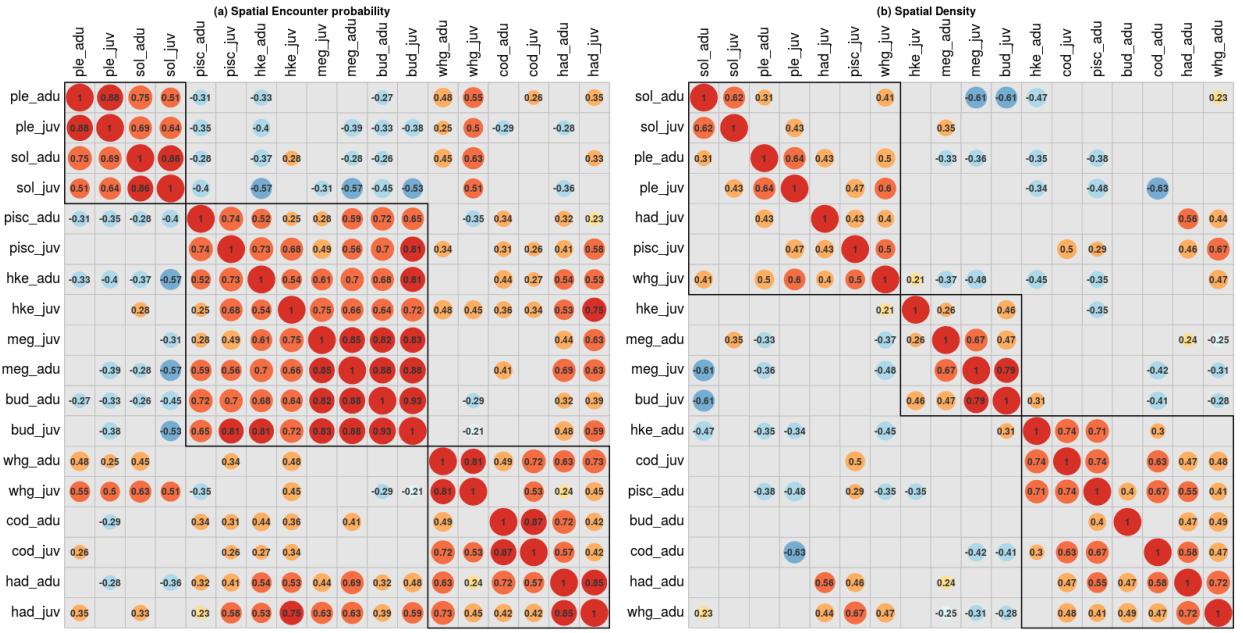


Figure 3: Inter-species correlations for (a) spatial encounter probability over all years and (b) spatial positive density. Species are clustered into three groups based on a hierarchical clustering method with non-significant correlations (the Confidence Interval  $[+/- 1.96 * \text{SEs}]$  spanned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

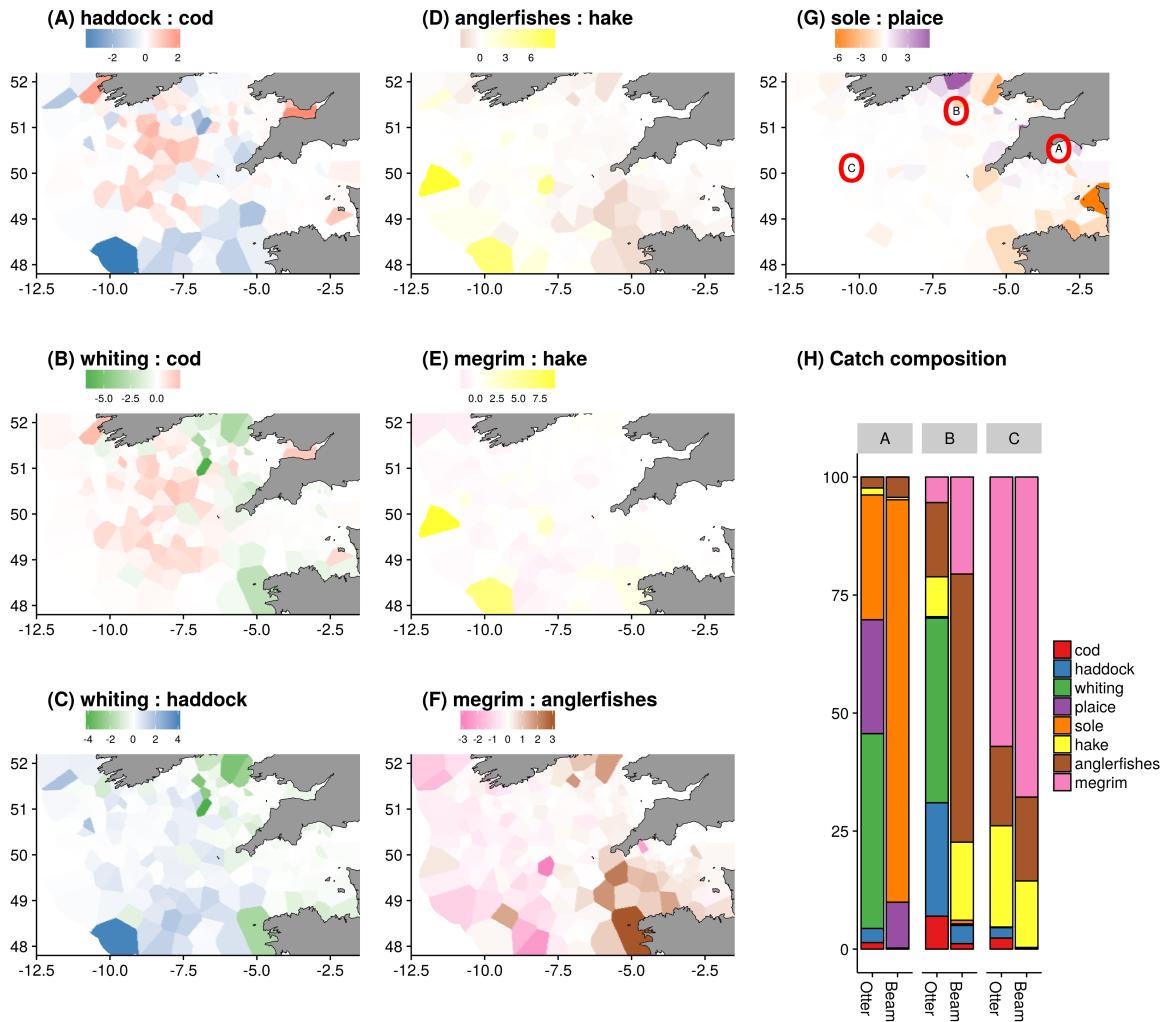


Figure 4: Differences in the standardised spatial density for pairs of species and expected catch rates for two different gears at three different locations in 2015.