

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 ¹. 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 ². In light of projected increased
26 demand for fish protein ³ there is an important role for well managed fisheries in supporting fu-
27 ture food security ⁴ and ^{coolin} there necessitating that remains a need to ensure ^{coolin} 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 ⁵⁻⁷. 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 ⁸. 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^{coolin}.

38 Sustainability of European fisheries has been hampered by this 'mixed fishery problem' for decades
39 with large-scale discarding resulting ⁹. ~~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)~~¹⁰. 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;~~¹¹) and move
45 ~~Europe towards an ecosystem based approach to fisheries management~~^{12coolin}.

46 Societal objectives for fisheries to achieve MSY across ecosystem components are paralleled by
47 Individual fishers goals ~~are to~~^{coolin} maximise utility; whether that be profit, income or the contin-
48 uance 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 quota⁷ and provides a strong incentive to
51 mitigate such losses¹³. 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 activity¹⁴. 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~~^{dig}^{'coolin} benthic flatfish species from the seabed¹⁵.
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.^{16,17}). 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 implement-
66 ing a spatio-temporal dimension reduction method and use the results to draw inference on the
67 fishery-community dynamics, creating a framework to identify trends common among species. We
68 use this to describe the potential for and limitations of where^{coolin} spatial measures to can contribute
69 to^{coolin} mitigate^{ing} 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 variables
76 ¹⁸ representing spatial variation (9 factors; which we call 'average' spatial variation) and spatio-
77 temporal variation (9 factors) for encounter probability and positive catch rates (which we call 'pos-
78 itive density') separately ¹⁹. We use The resultant factor analysis is used to identify community
79 dynamics and drivers common among 18 species and results presented through transformation
80 of the loading matrices using PCA rotation. By describing the species dynamics through underly-
81 ing contributory spatiotemporal factors we can take account of how the factors contribute to affect

82 catches of the species in mixed fisheries. We use Gaussian Markov Random Fields (GMRFs) to
83 capture spatial and temporal dependence within and among species groups for both encounter
84 probability and positive density²⁰. VAST is set in a mixed modelling framework to allow estimation
85 of Fixed effects to account for systematic differences driving encounter and catches, such as differ-
86 ences in sampling efficiency (a.k.a. catchability), while random effects capture the spatio-temporal
87 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^{21,22}. Close
91 to 150 species have been identified in the commercial catches of the Celtic Sea, with approxi-
92 mately 30 species dominating the catch²³.

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;²⁴). 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.~~^{coolin}

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

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 values for the second factor indicate there are positive
121 associations for juvenile monkfish (*L. piscatorius*), juvenile hake, juvenile megrim, plaice and ju-
122 venile whiting with average positive density, which may reflect two different spatial distributions in
123 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](#) splits^{ting}

126 the roundfish species cod, haddock and whiting which all have a positive association with the
127 third factor for average encounter probability from the rest of the species ~~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
144 of similarities and differences in distributions and abundances for the different species. ~~The first~~
145 ~~factor correlates strongly with these variables, despite them not explicitly being incorporated in~~
146 ~~the model. While depth was incorporated as a covariate in an alternative model formulation (see~~
147 ~~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 ²⁵; 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 **Time varying species distributions, but stability within species groupsChanges in spatial**
153 **patterns over time, but stability in species dynamics**^{Paul} While there are clear spatial patterns
154 in the factor coefficients describing differences in average (over time) encounter probability and
155 positive density (Figure 1). The inter-annual differences in factor coefficients show less structure
156 (Figures S5, S6). These inter-annual differences are important as they reflect the ability of fishers
157 to predict where they can target species from one year to the next, without which it may be difficult
158 to avoid unwanted catch. There were, however, While spatio-temporal factor coefficients did not
159 show consistent trends from year to year across all species. Common patterns in spatiotemporal
160 factor coefficients among species there were clear relationships (Figure 2). The same factors
161 appear to drive spatiotemporal distributions of megrim, anglerfish species and hake (the deeper
162 water species, species-group negatively associated with the second axes of Figure 2a) and the
163 roundfish and flatfish (species-group more positively associated with the second axes of Figure
164 2a). For spatio-temporal positive density (Figure 2b) cod, haddock and whiting (the roundfish
165 species) are separated from plaice, sole (the flatfish) and deeper water species. As such, From
166 this it can be predicted that higher catches of a species within a group (e.g. cod in roundfish)
167 would be expected when catching another species within that group (e.g. whiting in roundfish),
168 This suggesting that one or more common environmental drivers are influencing the distributions
169 of the species groups, and that driver differentially affects the species groups, but this could not be
170 explained by temperature is often included as a covariate in species distribution models, but was
171 found not to contribute to the variance in the first factor values (Figure S6, no correlations found

172 for either encounter probability or positive density).

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

195 expect to see higher catches of the other, but also higher catches of some juvenile size classes of
196 roundfish (whiting and haddock) and anglerfish species. Negative association of juvenile megrim,
197 anglerfish (budegassa) and hake with adult sole (-0.61, -0.61 and -0.47 respectively), plaice (-0.36
198 and -0.35 for megrim and hake only) indicate high catches of one can predict low catches of the
199 other successfully.

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

216 **Subtle differences in distributions may be important to separate catches within groups**
217 **under the landing obligation**^{coolin} : The analysis shows the interdependence within the species-groups

218 ~~of roundfish, flatfish and deeper water species, where catching one species within the group~~
219 ~~indicates a high probability of catching the other species, which has important implications for~~
220 ~~how spatial avoidance can be used to support implementation of the EU's landings obligation.~~

221 ~~coolin~~ If production from mixed fisheries is to be maximised, decoupling catches of species between
222 and within the groups will be key. For example, asking where the maximal separation in the densi-
223 ties of two coupled species is likely to occur? To address this requirement, we map the difference
224 in spatial distribution ~~within a group~~ for each pair of species within a species-group for a single year
225 (2015; Figure 4). This would facilitate discussion on maximal separation, for example, between
226 difficult to separate species such as haddock and whiting (Figure 4c).

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

237 Predicted catch distribution from a “typical” otter trawl gear and beam trawl fishing at three different
238 locations highlights the differences fishing gear and location makes on catches (Figure 4h). ~~As~~
239 ~~can be seen, both the gear selectivity and area fished play important contributions to the catch~~
240 ~~compositions;~~ In the inshore area (location ‘A’) plaice and sole are the two main species in catch

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

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

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

More challenging is within-group spatial separation due to significant overlap in spatial distributions for the species, driven by common environmental factors. Subtle changes may yield some benefit in changing catch composition, yet the outcome is likely to be much more difficult to predict. **For example,** Subtle differences in the distribution of cod, haddock and whiting can be seen in Figures 4a-c, showing spatial separation of catches is much more challenging and likely to need to be

264 supported by other measures such as changes to the selectivity characteristics of gear (e.g. ²⁶).

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

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

287 as well as between vessels of different sizes³².

288 Our framework allows for a quantitative understanding of the broad-scale global production set
289 available to fishers³³ and thus the extent to which they can alter catch compositions while operating
290 in a mixed fishery. Simulations of spatial effort allocation scenarios based on the production
291 sets derived from the model estimates could be used as inputs to fisher behavioural models to
292 allow for identification of the lower bounds of optimum spatial harvest strategies. This would
293 provide managers with information useful for examining trade-offs in quota setting by integrating
294 potential for spatial targeting in changing catch composition, thus provide a scientific contribution
295 to meeting the goal of maximising catches in mixed fisheries within single stock quota constraints⁷.
296 Further, the correlations among species could provide information on fisheries at risk of capturing
297 protected, endangered or threatened species such as elasmobranches, and allow identification of
298 areas where there are high ratios of protected to target species.

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

307 **Methods**

308 **Model structure:** VAST¹ implements a delta-generalised linear mixed modelling (GLMM) frame-
309 work that takes account of spatio-temporal correlations among species through implementation of
310 a spatial dynamic factor analysis (SDFA). Spatial variation is captured through a Gaussian Markov
311 Random Field, while we model random variation among species and years. Covariates affecting
312 catchability (to account for differences between fishing surveys) and density (to account for envi-
313 ronmental preferences) can be incorporated for predictions of presence and positive density. The
314 following briefly summarises the key methods implemented in the VAST framework. For full details
315 of the model the reader is invited directed to Thorson *et al* 2017³⁴.

SDFA: A spatial dynamic factor analysis incorporates advances in joint dynamic species models³⁴ 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:

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

316 Where $\theta_c(s, t)$ represents log-density for species c at site s at time t , ψ_j is the coefficient for factor
317 j , $L_{c,j}$ the loading matrix representing association of species c with factor j and $\gamma_{k,c} \chi_k(s, t)$ the
318 linear effect of covariates at each site and time³⁵.

¹Software in the R statistical programming language can be found here: www.github.com/james-thorson/VAST

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

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 ¹⁹.

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

323 where $p(s_i, c_i, t_i)$ is the predictor for encounter probability for observation i , at location s for species
 324 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-
 325 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
 326 spatial covariation among species. $\varepsilon_*(s_i, c_i, t_i)$ is the linear predictor for spatio-temporal variation,
 327 with $L_\varepsilon(c_i, f)$ the loading matrix for spatio-temporal covariance among species and $\delta_*(c_i, v_i)$ the
 328 contribution of catchability covariates for the linear predictor with Q_{c_i, v_i} the catchability covariates
 329 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:

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

- 330 for the probability p of a non-zero catch C given a gamma distribution for the positive catch with
 331 a rate parameter λ 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)²⁰. 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 provides more efficient use of the data as
 341 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 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 (modelled within the factor analysis). \otimes represents the Kronecker product so that the cor-
346 relation among any location and species can be computed³⁴.

347 **Incorporating covariates** Survey catchability (the relative efficiency of a gear catching a species)
348 was estimated as a fixed effect in the model, $\delta_s(v)$, to account for differences in spatial fishing
349 patterns and gear characteristics which affect encounter and capture probability of the sampling
350 gear³⁶. Parameter estimates (Figure S10) showed clear differential effects of surveys using otter
351 trawl gears (more effective for round fish species) and beam trawl gears (more effective for flatfish
352 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 performance³⁴, 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;³⁷) 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 spatio-temporal distributions and abundances to predict spatial density
364 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 literature³⁸;
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 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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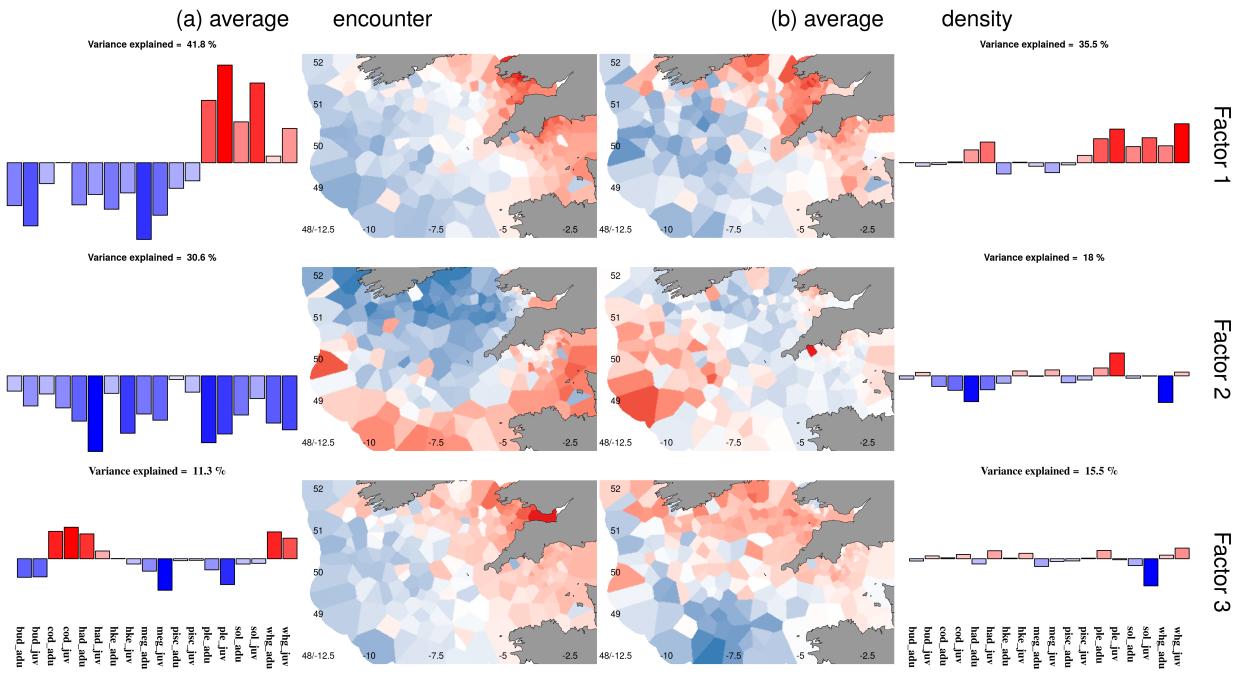


Figure 1: Factor values for the first three factors for (a) Average encounter probability and (b) Average positive density for the species (outer figures) and spatially (inner figures). Red: positive association to the factor, Blue: negative association

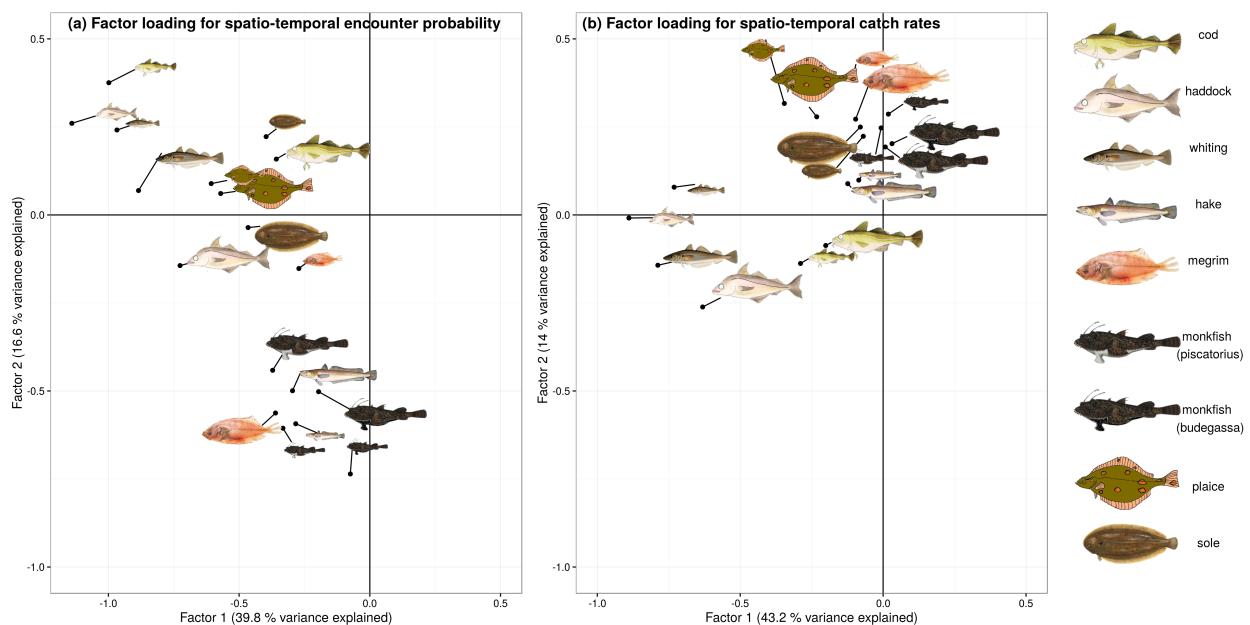


Figure 2: Position of each species on the first two axes from the factor analysis for (a) spatio-temporal encounter probability and (b) spatio-temporal positive density.

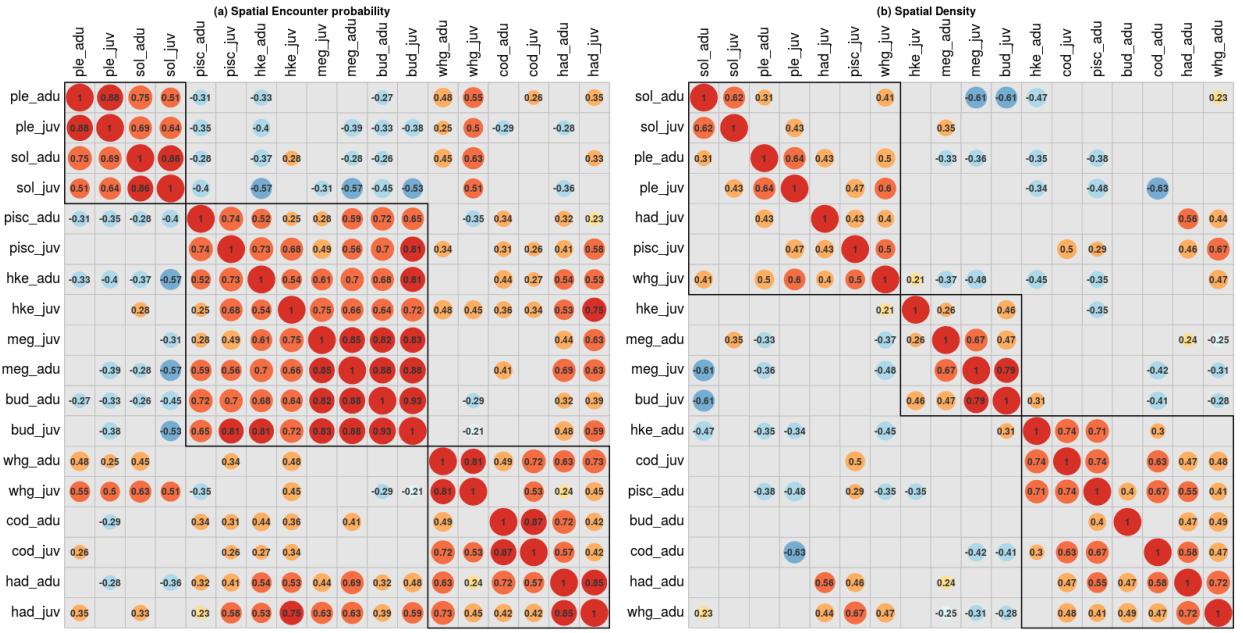


Figure 3: Inter-species correlations for (a) spatial encounter probability over all years and (b) spatial positive density. Species are clustered into three groups based on a hierarchical clustering method with non-significant correlations (the Confidence Interval $[+/- 1.96 * \text{SEs}]$ spanned zero)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

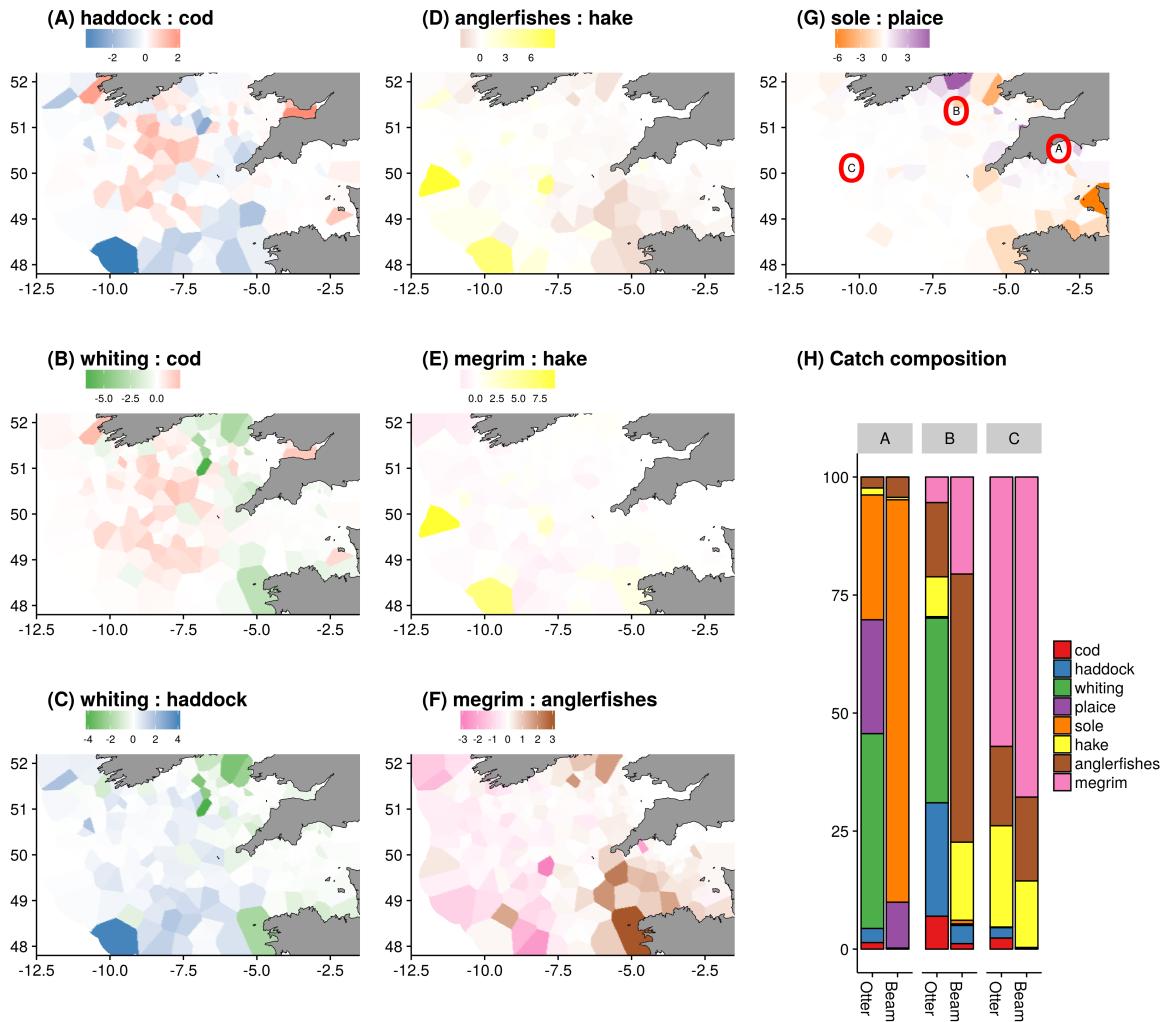


Figure 4: Differences in the standardised spatial density for pairs of species and expected catch rates for two different gears at three different locations in 2015.