

Working title: Spatial separation of catches in highly mixed fisheries

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- 1 Overexploitation of fish populations occurs when catches continue in fisheries pursuing a mix of species and low quota species are discarded. As EU fisheries management moves to count all fish caught against quota (the ‘Landings obligation’), the challenge is to catch available quota within new constraints, else lose productivity.**
- 5 A mechanism for decoupling exploitation of species caught together is spatial targeting, but this remains challenging due to complex fishery dynamics and a lack of understanding of spatiotemporal community dynamics. We develop a framework based on joint species distribution modelling (spatial dynamic factor analysis) to understand how spatial community and fishery dynamics interact to determine species and size composition in the example of the highly mixed fisheries of the Celtic Sea. Clear common spatial patterns emerge for three distinct species-groups and, while distribution varies inter-annually, the same species-groups are consistently found in higher densities together, with more subtle differences within species-groups. The results highlight both opportunities for and limitations of the ability to spatiotemporally separate catches.**

15 We highlight the importance of dimension reduction techniques to focus management dis-
16 cussion on axes of maximal separation in space and time. We propose that spatiotemporal
17 modelling of available data is a scientific requirement to address the pervasive and nu-
18anced challenges of managing mixed fisheries.

19

20 **Mixed fisheries and the EU landings obligation** Recent efforts to reduce exploitation rates in
21 commercial fisheries has begun the process of rebuilding depleted fish populations ¹. Improved
22 management of fisheries has the potential to increase population sizes and allow increased sus-
23 tainable catches, yet fisheries catch globally remains stagnant ². In light of projected increased
24 demand for fish protein ³ there is an important role for well managed fisheries in supporting future
25 food security ⁴ and there remains a need to ensure fisheries are managed efficiently to maximise
26 productivity.

27 A particular challenge in realising increased catches from rebuilt populations is maximising yields
28 from mixed fisheries ^{5–7}. In mixed fisheries, the predominant type of fishery worldwide, several
29 fish species are caught together in the same net or fishing operation (known as a ‘technical inter-
30 action’). If managed by individual quotas, and catches do not match available stock quotas, either
31 a vessel must stop fishing when the first quota is reached (the ‘choke’ species) or overexploitation
32 of the weaker species occurs while fishers continue to catch more healthy species and throw back
33 (‘discard’) the fish for which they have no quota ⁸. There is, therefore, a pressing need for scien-
34 tific tools which simplify the complexities of mixed fisheries to help managers and fishers maximise
35 catches.

36 Sustainability of European fisheries has been hampered by this ‘mixed fishery problem’ for decades
37 with large-scale discarding resulting ^{9,10}. A paradigm shift is being introduced under the EU Com-
38 mon Fisheries Policy (CFP) reform of 2012 through two significant management changes. First,
39 by 2019 all fish that are caught are due to be counted against the respective stock quota; second,
40 by 2020 all fish stocks must be fished so as to be able to produce their Maximum Sustainable Yield
41 (MSY)¹¹. The changes are expected to contribute to attainment of the goal of Good Environmen-
42 tal Status (GES) under the European Marine Strategy Framework Directive (MSFD;¹²) and move
43 Europe towards an ecosystem based approach to fisheries management ¹³.

44 Societal objectives for fisheries to achieve MSY across ecosystem components are paralleled by
45 individual fishers goals to maximise utility; whether that be profit, income or the continuance of
46 traditional practices. Under the new policy, unless fishers can avoid catch of unwanted species
47 they will have to stop fishing when reaching their first restrictive quota. This introduces a potential
48 significant cost to fishers of under-utilised quota^{7,14} and provides a strong incentive to mitigate
49 such losses ^{15,16}. The ability of fishers to align their catch with available quota depends on being
50 able to exploit target species while avoiding unwanted catch. Methods by which fishers can alter
51 their fishing patterns include by switching fishing method (e.g. trawling to netting), changing tech-
52 nical gear characteristics (e.g. introducing escapement panels in nets), or the timing and location
53 of fishing activity ^{17,18}. Otter trawl gears are known to have higher catch rates of roundfish due to
54 the higher headline and wider sweeps which herd demersal fish into the net. Conversely, beam
55 trawls, which employ chain mesh to ‘dig’ benthic flatfish species, have higher catch rates for these
56 species ¹⁹.

57 Spatiotemporal management measures (such as time-limited fishery closures) have been applied
58 to reduce unwanted catch with varying degrees of success (e.g. ^{20–23}) while move-on rules have

59 also been proposed or implemented to influence catch rates of particular vulnerable species in
60 order to reduce or eliminate discards (e.g.^{24–26}). However, such measures have generally been
61 targeted at individual species without considering associations and interactions among several
62 species. Highly mixed fisheries are complex with spatial, technological and community interactions
63 combining. The design of spatio-temporal management measures which aim to allow exploitation
64 of high quota stocks while protecting low quota stocks requires understanding of these interac-
65 tions at a scale meaningful to managers and fishers. Here, our goal is to develop a framework for
66 understanding these complexities. We do so by implementing a spatio-temporal dimension reduc-
67 tion method and use the results to draw inference on the fishery-community dynamics, creating
68 a framework to identify trends common among species-groups. We use this to describe where
69 spatial measures can contribute to mitigating unwanted catches in highly mixed fisheries.

70 **Framework for analysing spatio-temporal mixed fisheries interactions** We present a frame-
71 work for analysing how far spatio-temporal avoidance can contribute towards mitigating imbal-
72 ances in quota in mixed fisheries. We use fisheries-independent survey data to characterise the
73 spatiotemporal dynamics of key components of a fish community by employing a geostatistical
74 Vector Autoregressive Spatiotemporal model (VAST). We implement a factor analysis decomposi-
75 tion to describe trends in spatiotemporal dynamics of the different species as a function of latent
76 variables ²⁷ 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 ²⁸. We use the resultant factor analysis to identify community dy-
79 namics and drivers common among 18 species-groups and present results through transformation
80 of the loading matrices using PCA rotation. By describing the species-groups dynamics through
81 underlying contributory spatiotemporal factors we can take account of how the factors contribute to

82 affect catches of the species-groups in mixed fisheries. We use Gaussian Markov Random Fields
83 (GMRFs) to capture spatial and temporal dependence within and among species groups for both
84 encounter probability and positive density²⁹. VAST is set in a mixed modelling framework to allow
85 estimation of fixed effects to account for systematic differences driving encounter and catches,
86 such as differences in sampling efficiency (a.k.a. catchability), while random effects capture the
87 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^{30,31}. Close
91 to 150 species have been identified in the commercial catches of the Celtic Sea, with approxi-
92 mately 30 species dominating the catch³².

93 We parametrise our spatiotemporal model using catch data from seven fisheries-independent
94 surveys undertaken in the Celtic Sea over the period 1990 - 2015 (Table S1) and include nine
95 of the main commercial species: Atlantic cod (*Gadus morhua*), Atlantic haddock (*Melanogram-*
96 *mus aeglefinus*), Atlantic whiting (*Merlangius merlangus*), European Hake (*Merluccius merlu-*
97 *cious*), 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 make up >60 % of landings by towed fishing gears for the area
100 (average 2011 - 2015;³³). Each species was separated into juvenile and adult size classes based
101 on their legal minimum conservation reference size (Table S2).

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

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

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. budgessa* 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. budgessa* 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 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. The variance
139 explained by these variables dropped to 25 % on the second factor with a more even split between
140 depth and substrate, while explaining 60 % of the variance on the third factor. For positive density,
141 the variables explained less of the variance with 62 %, 35 %, and 31 % for each of the factors,
142 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 identified in other marine species distribution models ³⁴; 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.

158 While spatio-temporal factor coefficients did not show consistent trends from year to year across
159 all species, among species-groups there were clear relationships (Figure 2). The same factors
160 appear to drive spatio-temporal distributions of megrim, anglerfish species and hake (the deeper
161 water species, species-grouping negatively associated with the second axes of Figure 2a) and the
162 roundfish and flatfish (species-grouping more positively associated with the second axes of Figure
163 2a). For spatio-temporal positive density (Figure 2b) cod, haddock and whiting (the roundfish
164 species) are separated from plaice, sole (the flatfish) and deeper water species. As such, it can be
165 predicted that higher catches of a species within a group (e.g. cod in roundfish) would be expected
166 when catching another species within that group (e.g. whiting in roundfish). This suggests that one
167 or more common environmental drivers are influencing the distributions of the species groups, and
168 that driver differentially affects the species groups. Temperature is often included as a covariate in
169 species distribution models, but was found not to contribute to the variance in the first factor values
170 (Figure S6, no correlations found for either encounter probability or positive density).

171 **Three clusters of species show similar spatial patterns** In order to gain greater insight into
172 the community dynamics we considered how species-groups covary in space and time through
173 among species-group correlations. Pearson correlation coefficients for the modelled average spa-
174 tial encounter probability (Figure 3a) show clear strong associations between adult and juvenile
175 size classes for all species (>0.75 for all species except hake, 0.56). Among species-groups, hi-
176 erarchical clustering identified the same three common groups as our visual inspection of factor
177 loadings above, with roundfish (cod, haddock, whiting) closely grouped in their association, with
178 correlations for adult cod with adult haddock and adult whiting of 0.73 and 0.5 respectively, while
179 adult haddock with adult whiting was 0.63 (Figure 3a). Flatfish (plaice and sole) are also strongly
180 correlated with adult plaice and sole having a coefficient of 0.75. The final group are principally the
181 species found in the deeper waters (hake, megrim and both anglerfish species) with the megrim
182 strongly associated with the budegassa anglerfish species (0.88). Negative relationships were
183 found between plaice, sole and the monkfish species (-0.27, -0.26 for the adult size class with
184 budegassa adults respectively) and hake (-0.33, -0.37) (Figure 3a) indicating spatial separation in
185 distributions. This confirms the associations among species seen in the factor loadings, with three
186 distinct species-group assemblages being present.

187 Correlation coefficients for the average positive density (Figure 3b) show fewer significant positive
188 or negative relationships among species-groups than for encounter probability, but still evident
189 are the strong association among the roundfish with higher catches of cod are associated with
190 higher catches of haddock (0.58) and whiting (0.47), as well as the two anglerfish species (0.71
191 for piscatorius and 0.44 for budegassa) and hake (0.73). Similarly, plaice and sole are closely
192 associated (0.31) and higher catches of one would expect to see higher catches of the other,
193 but also higher catches of some juvenile size classes of roundfish (whiting and haddock) and

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

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

213 **Subtle differences in distributions may be important to separate catches within groups un-**
214 **der the landing obligation** : The analysis shows the interdependence within species-groups of
215 roundfish, flatfish and deeper water species, where catching one species within the group indicates
216 a high probability of catching the other species, which has important implications for how spatial

217 avoidance can be used to support implementation of the EU's landings obligation. If production
218 from mixed fisheries is to be maximised, decoupling catches of species between and within the
219 groups will be key. For example, asking where the maximal separation in the densities of two
220 coupled species is likely to occur? To address this requirement, we map the difference in spatial
221 distribution within a group for each pair of species within a species-groupings for a single year
222 (2015; Figure 4).

223 Cod had a more north-westerly distribution than haddock, while cod was more westerly distributed
224 than whiting roughly delineated by the 7° W line (Figure 4a). Whiting appeared particularly con-
225 centrated in an area between 51 and 52 ° N and 5 and 7 ° W, which can be seen by comparing
226 the whiting distribution with both cod (Figure 4b) and haddock (Figure 4c). For the deeper water
227 species (Figures 4d and 4e), hake are more densely distributed in two areas compared to angler-
228 fishes¹ and megrim (though megrim has a stable density across the modelled area as indicated
229 by the large amount of white space). For anglerfishes and megrim (Figure 4f), anglerfishes have a
230 more easterly distribution than megrim. For the flatfish species plaice and sole (Figure 4g), plaice
231 appear to be more densely distributed along the coastal areas of Ireland and Britain, while sole are
232 more densely distributed in the Southern part of the English Channel along the coast of France.

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

¹two species combined as they are managed as one

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

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

255 More challenging is within-group spatial separation due to significant overlap in spatial distributions
256 for the species, driven by common environmental factors. Subtle changes may yield some benefit
257 in changing catch composition, yet the outcome is likely to be much more difficult to predict. For
258 example, subtle differences in the distribution of cod, haddock and whiting can be seen in Figures
259 4a-c, showing spatial separation of catches is much more challenging and likely to need to be
260 supported by other measures such as changes to the selectivity characteristics of gear (e.g. ³⁵).

261 A role that science can play in supporting effectiveness of spatiotemporal avoidance could be to
262 provide probabilistic advice on likely hotspots for species occurrence and high species density
263 which can inform fishing decisions. Previous modelling studies have shown how spatiotemporal
264 models could improve predictions of high ratios of bycatch species to target species^{36–38}, and
265 geostatistical models are well suited to this as they incorporate spatial dependency while providing
266 for probabilities to be drawn from posterior distributions of the parameter estimates. We posit
267 that such advice could be enhanced by integrating data obtained directly from commercial fishing
268 vessels at a higher temporal resolution, providing real-time forecasts to inform fishing choices that
269 also captures seasonal differences in distributions, akin to weather forecasting. Advice informed
270 by a model including a seasonal or real-time component could inform optimal policies for time-area
271 closures, move-on rules or even as informal information to be utilised by fishers directly without the
272 need for costly continuous data collection on environmental parameters, but by using the vessels-
273 as-laboratories approach.

274 An important question for the implementation of the EU's landing obligation is how far spatial avoid-
275 ance can go to achieving catch balancing in fisheries. Our model captures differences between
276 location fished for two gear types and their broad scale effect on catch composition, information
277 crucial for managers in implementing the landing obligation. It is likely, however, that this analy-
278 sis reflects a lower bound on the utility of spatial avoidance as fine-scale behavioural decisions
279 such as time-of-day, gear configuration and location choices can also be used to affect catch^{39,40}.
280 Results of empirical studies undertaken elsewhere^{5,6} suggest limits to the effectiveness of spatial
281 avoidance. Differences in ability to change catch composition have also been observed for differ-
282 ent fleets; in the North Sea targeting ability was found to differ between otter and beam trawlers
283 as well as between vessels of different sizes⁴¹.

284 Our framework allows for a quantitative understanding of the broad scale global production set
285 available to fishers⁴² and thus the extent to which they can alter catch compositions while operat-
286 ing in a mixed fishery. Simulations of spatial effort allocation scenarios based on the production
287 sets derived from the model estimates could be used as inputs to fisher behavioural models to al-
288 low for identification of the lower bounds of optimum spatial harvest strategies. This would provide
289 managers with information useful for examining trade-offs in quota setting by integrating poten-
290 tial for spatial targeting in changing catch composition, thus provide a scientific contribution to
291 meeting the goal of maximising catches in mixed fisheries within single stock quota constraints⁷.
292 Further, the correlations among species could provide information on fisheries at risk of capturing
293 protected, endangered or threatened species such as elasmobranches, and allow identification of
294 areas where there are high ratios of protected to target species.

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

303 **Methods**

304 **Model structure:** VAST² implements a delta-generalised linear mixed modelling (GLMM) frame-
305 work that takes account of spatio-temporal correlations among species-groups through implemen-
306 tation of a spatial dynamic factor analysis (SDFA). Spatial variation is captured through a Gaus-
307 sian Markov Random Field, while we model random variation among species-groups and years.
308 Covariates affecting catchability (to account for differences between fishing surveys) and density
309 (to account for environmental preferences) can be incorporated for predictions of presence and
310 positive density. The following briefly summarises the key methods implemented in the VAST
311 framework. For full details of the model the reader is invited directed to Thorson *et al* 2017⁴³.

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

⁴³ 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:

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

312 Where $\theta_c(s, t)$ represents log-density for species c at site s at time t , ψ_j is the coefficient for factor
313 j , $L_{c,j}$ the loading matrix representing association of species c with factor j and $\gamma_{k,c} \chi_k(s, t)$ the
314 linear effect of covariates at each site and time⁴⁴.

²Software in the R statistical programming language can be found here: www.github.com/james-thorson/VAST

315 The factor analysis can identify community dynamics and where species have similar spatio-
 316 temporal patterns, allowing inference of species distributions and abundance of poorly sampled
 317 species through association with other species and allows for computation of spatio-temporal cor-
 318 relations among species-groups ⁴⁴.

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 ²⁸.

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

319 where $p(s_i, c_i, t_i)$ is the predictor for encounter probability for observation i , at location s for
 320 species-group c and time t and $r(s_i, c_i, t_i)$ is similarly the predictor for the positive density. $\beta_*(c_i, t_i)$
 321 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-
 322 ing matrix for spatial covariation among species-groups. $\varepsilon_*(s_i, c_i, t_i)$ is the linear predictor for
 323 spatio-temporal variation, with $L_\varepsilon(c_i, f)$ the loading matrix for spatio-temporal covariance among
 324 species-groups and $\delta_*(c_i, v_i)$ the contribution of catchability covariates for the linear predictor with
 325 Q_{c_i, v_i} the catchability covariates for species-group c and vessel v ; * can be either p for probability
 326 of encounter or r for positive density.

The Delta-Gamma formulation is then:

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

- 327 for the probability p of a non-zero catch C given a gamma distribution for the positive catch with
 328 a rate parameter λ and shape parameter k .

329 **Spatio-temporal variation:** The spatiotemporal variation is modelled using Gaussian Markov
 330 Random Fields (GMRF) where data is associated to nearby locations through a Matérn covariance
 331 function with the parameters estimated within the model. Here, the correlation decays smoothly
 332 over space the further from the location and includes geometric anisotropy to reflect the fact that
 333 correlations may decline in one direction faster than another (e.g. moving offshore)²⁹. The best
 334 fit estimated an anisotropic covariance where the correlations were stronger in a north-east -
 335 south-west direction, extending approximately 97 km and 140 km before correlations for encounter
 336 probability and positive density reduced to <10 %, respectively (Figure S9). Incorporating the
 337 spatiotemporal correlations among and within species-groups provides more efficient use of the
 338 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:

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

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

341 among locations and \mathbf{V}_* a covariance matrix for encounter probability or positive catch rate among
342 species-groups (modelled within the factor analysis). \otimes represents the Kronecker product so that
343 the correlation among any location and species-group can be computed⁴³.

344 **Incorporating covariates** Survey catchability (the relative efficiency of a gear catching a species-
345 group) was estimated as a fixed effect in the model, $\delta_s(v)$, to account for differences in spatial
346 fishing patterns and gear characteristics which affect encounter and capture probability of the
347 sampling gear⁴⁵. Parameter estimates (Figure S10) showed clear differential effects of surveys
348 using otter trawl gears (more effective for round fish species) and beam trawl gears (more effective
349 for flatfish species).

350 No fixed covariates for habitat quality or other predictors of encounter probability or positive density
351 were included. While incorporation may improve the spatial predictive performance⁴³, it was not
352 found to be the case here based on model selection with Akaike Information Criterion (AIC) and
353 Bayesian Information Criterion (BIC).

354 **Parameter estimation** Parameter estimation was undertaken through Laplace approximation of
355 the marginal likelihood for fixed effects while integrating the joint likelihood (which includes the
356 probability of the random effects) with respect to random effects. This was implemented using
357 Template Model Builder (TMB;⁴⁶) with computation through support by the Irish Centre for High
358 End Computing (ICHEC; <https://www.ichec.ie>) facility.

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

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

365 The following steps were undertaken for data processing: i) data for survey stations and catches
366 were downloaded from ICES Datras ([www.ices.dk/marine-data/data-portals/Pages/
367 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
368 checked and any tows with missing or erroneously recorded station information (e.g. tow duration
369 or distance infeasible) removed; iii) swept area for each of the survey tows was estimated based
370 on fitting a GAM to gear variables so that $\text{Doorspread} = s(\text{Depth}) + \text{DoorWt} + \text{WarpLength} +$
371 $\text{WarpDiameter} + \text{SweepLength}$ and a gear specific correction factor taken from the literature⁴⁷;
372 iii) fish lengths were converted to biomass (Kg) through estimating a von bertalanffy length weight
373 relationship, $Wt = a \cdot L^b$, fit to sampled length and weight of fish obtained in the EVHOE survey
374 and aggregated within size classes (adult and juvenile).

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

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

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

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

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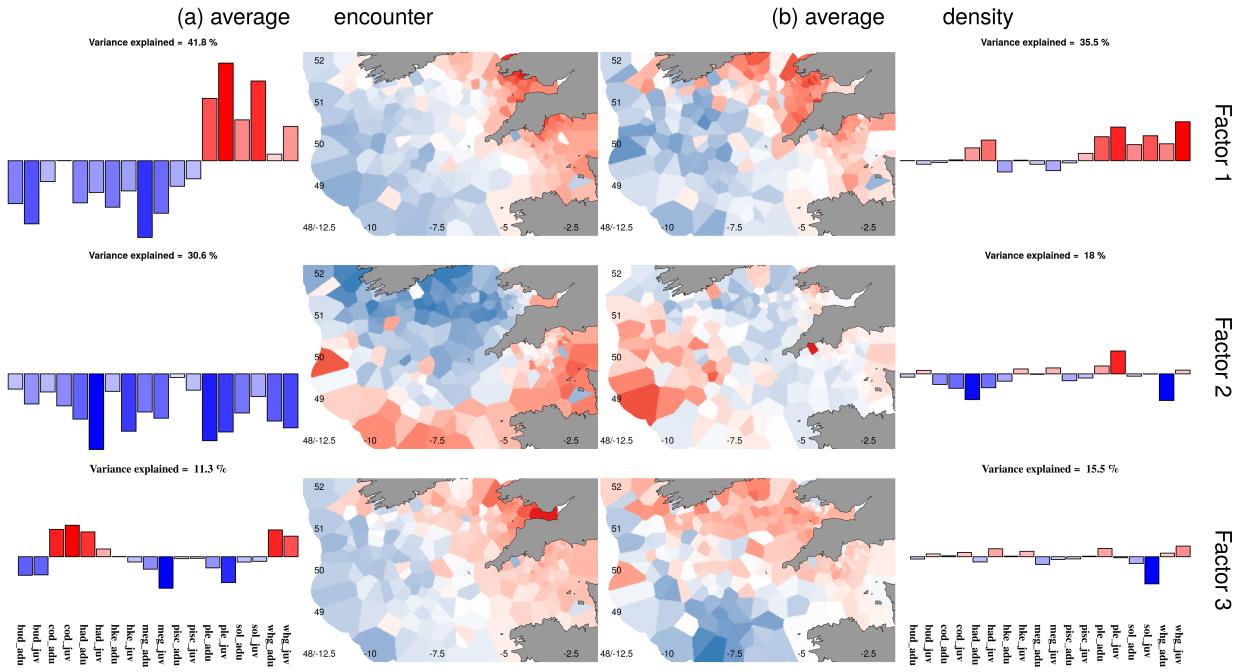


Figure 1: Factor values for the first three factors for (a) Average encounter probability and (b) Average positive density for the species-groups (outer figures) and spatially (inner figures). Red: positive association to the factor, Blue: negative association

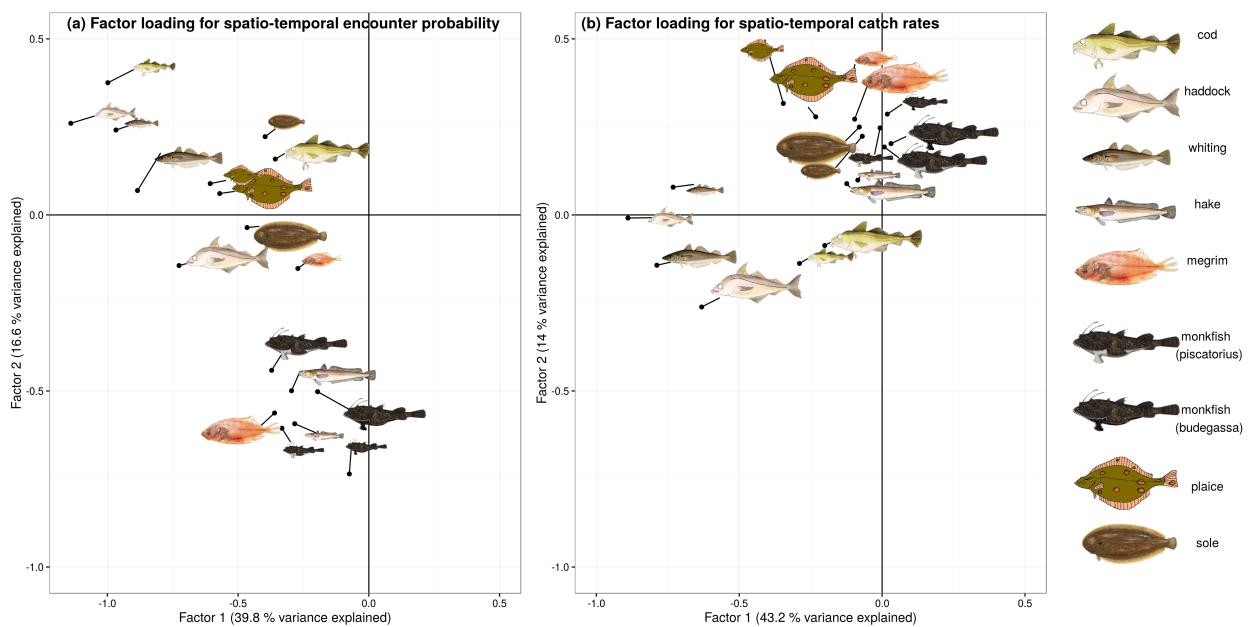


Figure 2: Position of each species-group on the first two axes from the factor analysis for (a) spatio-temporal encounter probability and (b) spatio-temporal positive density.

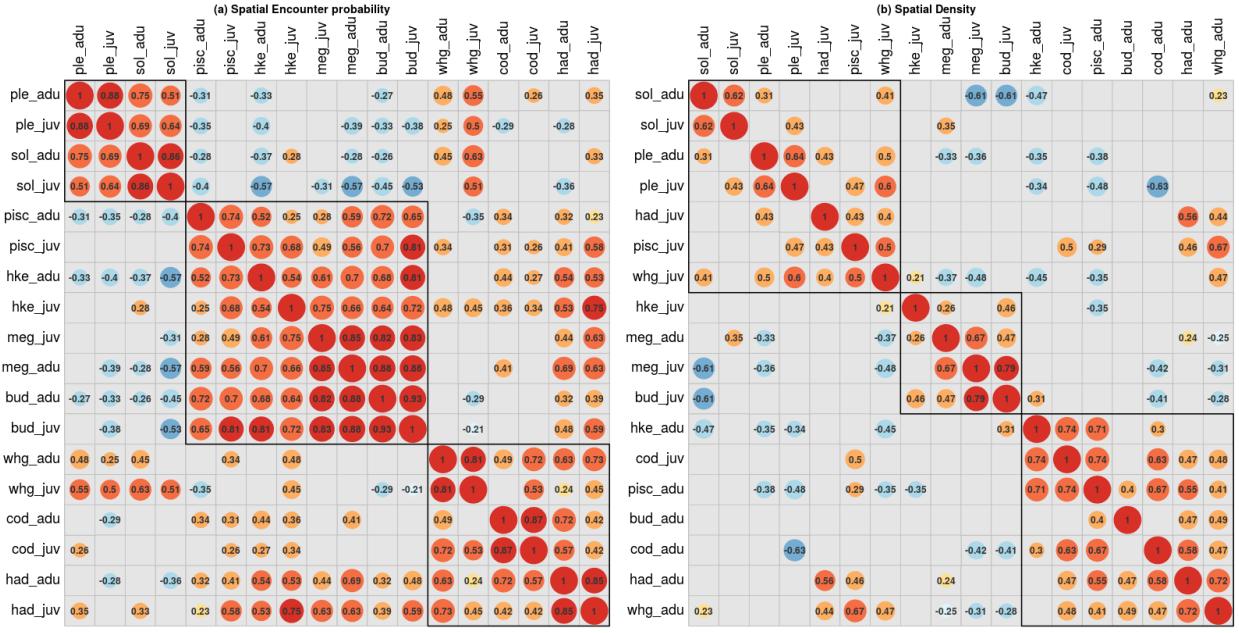


Figure 3: Inter-species correlations for (a) spatial encounter probability over all years and (b) spatial positive density. Species-groups are clustered into three groups based on a hierarchical clustering method with non-significant correlations (the Confidence Interval [$\pm 1.96 \times \text{SEs}$]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

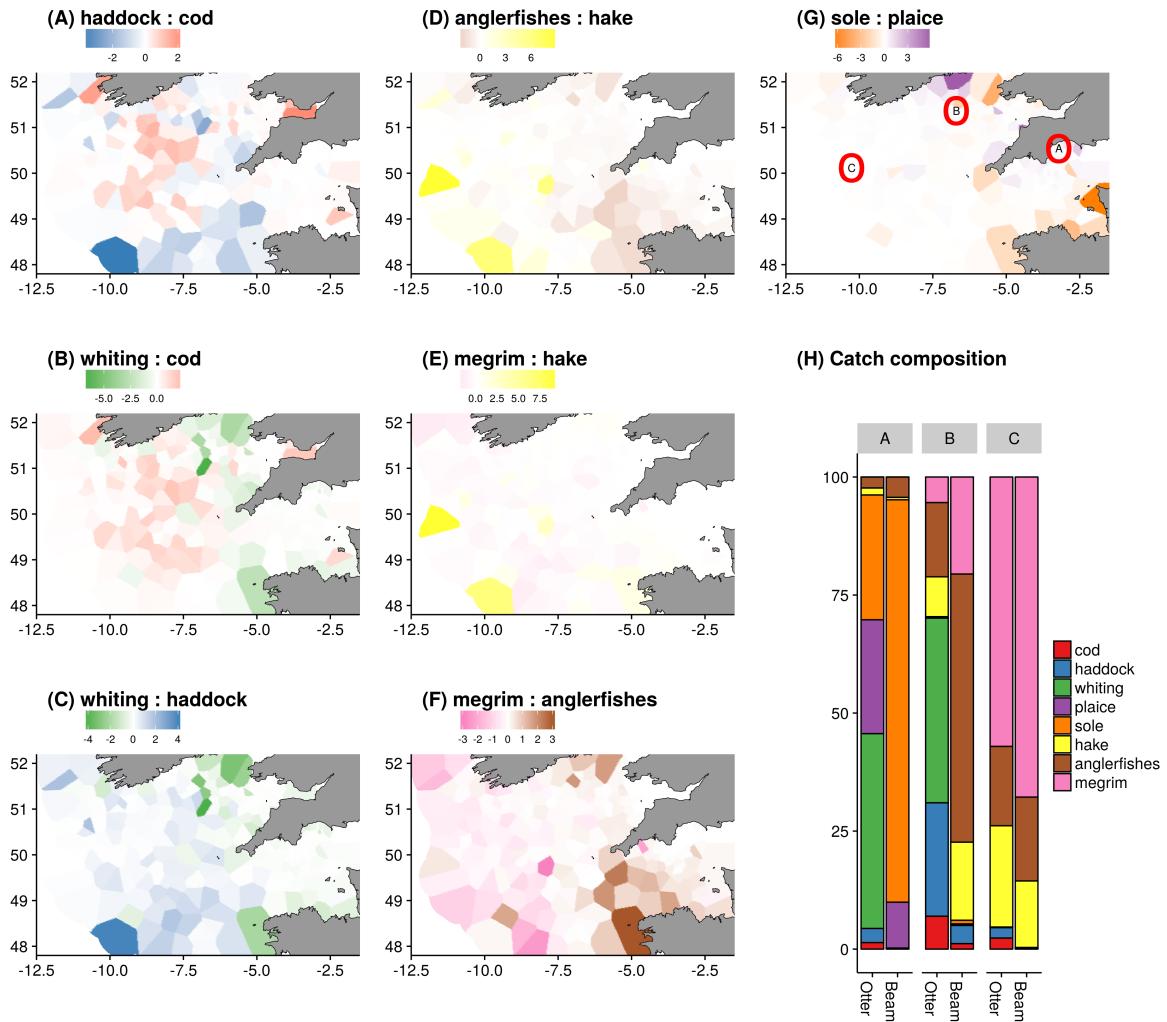


Figure 4: Differences in the standardised spatial density for pairs of species and expected catch rates for two different gears at three different locations in 2015.