

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. We highlight**
16 **the importance of dimension reduction techniques to focus management discussion on**
17 **axes of maximal separation in space and time. We propose that spatiotemporal modelling**
18 **of available data is a scientific necessity to address the pervasive and nuanced challenges**
19 **of managing mixed fisheries.**

20

21 **Mixed fisheries and the EU landings obligation** Efforts to reduce exploitation rates in commer-
22 cial fisheries have begun the process of rebuilding depleted fish populations ¹. Improved fisheries
23 management can increase population sizes and allow increased sustainable catches, yet fisheries
24 catch globally remains stagnant . In light of projected increased demand for fish protein there is
25 an important role for well managed fisheries in supporting future food security ² necessitating that
26 fisheries are managed efficiently to maximise productivity.

27 A particular challenge in realising increased catches from rebuilt populations is maximising yields
28 from mixed fisheries ^{3–5}. In mixed fisheries, several fish species are caught together in the same
29 net or fishing operation . If managed by individual quotas, and catches do not match available stock
30 quotas, either a vessel must stop fishing when the first quota is reached (the ‘choke’ species) or
31 overexploitation of the weaker species occurs while fishers continue to catch more healthy species
32 and throw back (‘discard’) the fish for which they have no quota ⁶. There is a pressing need for
33 scientific tools which simplify the complexities of mixed fisheries to help avoid discarding.

34 Sustainability of European fisheries has been hampered by this ‘mixed fishery problem’ for decades
35 with large-scale discarding resulting ⁷. Under the EU Common Fisheries Policy (CFP) reform of

36 2012 , by 2019 all fish that are caught are due to be counted against the respective stock quota.

37 Individual fishers goals are to maximise utility; whether that be profit, income or the continuance
38 of traditional practices. Unless fishers can avoid catch of unwanted species they will have to stop
39 fishing when reaching their first restrictive quota. This introduces a potential significant cost to fish-
40 ers of under-utilised quota⁵ and provides a strong incentive to mitigate such losses⁸. The ability
41 of fishers to align their catch with available quota depends on being able to exploit target species
42 while avoiding unwanted catch, either by switching fishing method (e.g. trawling to netting), chang-
43 ing technical gear characteristics (e.g. introducing escapement panels in nets), or the timing and
44 location of fishing activity⁹. For example, otter trawl gears are known to have higher catch rates of
45 roundfish due to the higher headline and wider sweeps which herd demersal fish into the net while
46 beam trawls employ chain mesh to lift benthic flatfish species from the seabed¹⁰.

47 Spatiotemporal management measures have been applied to reduce unwanted catch with vary-
48 ing degrees of success (e.g.^{11,12}). However, such measures have been targeted at individual
49 species without considering associations and interactions among several species. Highly mixed
50 fisheries are complex with spatial, technological and community interactions combining. . Our
51 goal is to develop a framework for understanding these complexities. We do so by implementing a
52 spatio-temporal dimension reduction method and use the results to draw inference on the fishery-
53 community dynamics, creating a framework to identify trends common among species. We use
54 this to describe the potential for and limitations of spatial measures to mitigate unwanted catches
55 in highly mixed fisheries.

56 **Framework for analysing spatio-temporal mixed fisheries interactions** We characterise the
57 spatiotemporal dynamics of key components of a fish community by employing a geostatistical

58 Vector Autoregressive Spatiotemporal model (VAST). We implement a factor analysis decom-
59 position to describe trends in spatiotemporal dynamics of the different species as a function of
60 latent variables ¹³ representing spatial variation (9 factors; 'average' spatial variation) and spatio-
61 temporal variation (9 factors) for encounter probability and positive catch rates ('positive density')
62 separately ¹⁴. The resultant factor analysis is used to identify community dynamics and drivers
63 common among 18 species and results presented through PCA rotation. By describing the species
64 dynamics through underlying contributory spatiotemporal factors we can take account of how the
65 factors contribute to affect catches of the species in mixed fisheries. Gaussian Markov Random
66 Fields (GMRFs) capture spatial and temporal dependence within and among species groups for
67 both encounter probability and positive density¹⁵. Fixed effects account for systematic differences
68 driving encounter and catches such as differences in sampling efficiency (a.k.a. catchability), while
69 random effects capture the spatio-temporal dynamics of the fish community.

70 **Dynamics of Celtic Sea fisheries** The Celtic Sea is a temperate sea where fisheries are spatially
71 and temporally complex; mixed fisheries are undertaken by several nations using different gear
72 types ^{16,17}. Close to 150 species have been identified in the commercial catches of the Celtic
73 Sea, with approximately 30 species dominating the catch ¹⁸.

74 We parametrise our model using catch data from seven fisheries-independent surveys undertaken
75 in the Celtic Sea over the period 1990 - 2015 (Table S1) and include nine of the main commercial
76 species (see Table S2, Figure 2) which make up >60 % of landings by towed fishing gears for the
77 area (average 2011 - 2015;¹⁹). Each species was separated into juvenile and adult size classes
78 based on their legal minimum conservation reference size (Table S2).

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

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

96 On the third factor, there is a positive association with the easterly waters for encounter probability
97 and negative with the westerly waters. This splits the roundfish species cod, haddock and whiting
98 which all have a positive association with the third factor for average encounter probability from
99 the rest of the species . Positive density is driven by a north / south split (Figure 1), with positive
100 values in the northerly areas. Juvenile monkfish (*L. budgessa* and *L. piscatorius*), cod, juvenile
101 haddock, hake, adult plaice and whiting are also positively associated with the third factor towards

102 the north while adult monkfish (*L. budgessa* and *L. piscatorius*), adult haddock, megrims, juvenile
103 plaice and sole are negatively associated (Figure 1).

104 We considered what might be driving the differences seen in the spatial factor loadings. The first
105 factor was highly correlated with log(depth) for both encounter probability (-0.85, CI = -0.88 to
106 -0.81; Figure S1) and positive density (-0.71, CI = -0.77 to -0.65; Figure S2), with 80 % of the
107 variance in the first factor for encounter probability to depth and predominant substrate type, with
108 the majority (86 %) of the variance explained by depth (random forest classification tree).

109 It is clear that depth and to a lesser extent substrate are important predictors for the main driver of
110 similarities and differences in distributions and abundances for the different species. , as identified
111 in other marine species distribution models ²⁰; the advantage to the approach taken here is that,
112 where such data is unavailable at appropriate spatial resolution, the spatial factor analysis can
113 adequately characterise these influences on species spatial dynamics.

114 **Time varying species distributions, but stability within species groups** The inter-annual dif-
115 ferences in factor coefficients show less structure (Figures S5, S6). These inter-annual differences
116 are important as they reflect the ability of fishers to predict where they can target species from one
117 year to the next. Common patterns in spatiotemporal factor coefficients among species drive
118 spatiotemporal distributions of megrim, anglerfish species and hake (the deeper water species,
119 species-group negatively associated with the second axes of Figure 2a) and the roundfish and
120 flatfish (species-group more positively associated with the second axes of Figure 2a). For spatio-
121 temporal positive density (Figure 2b) cod, haddock and whiting (the roundfish species) are sepa-
122 rated from plaice, sole (the flatfish) and deeper water species. From this it can be predicted that
123 higher catches of a species within a group (e.g. cod in roundfish) would be expected when catch-

124 ing another species within that group (e.g. whiting in roundfish), suggesting one or more common
125 environmental drivers are influencing the distributions of the species groups, and that driver differ-
126 entially affects the species groups, but this could not be explained by temperature (Figure S6, no
127 correlations found for either encounter probability or positive density).

128 **Three clusters of species show similar spatial patterns** To gain greater insight into the com-
129 munity dynamics we considered how species covary in space and time through among species
130 correlations. Pearson correlation coefficients for the modelled average spatial encounter proba-
131 bility (Figure 3a) show clear strong associations between adult and juvenile size classes for all
132 species (>0.75 for all species except hake, 0.56). Hierarchical clustering identified the same three
133 common groups as our visual inspection of factor loadings above, with roundfish (cod, haddock,
134 whiting) , flatfish (plaice and sole) and species found in the deeper waters (hake, megrim and
135 both anglerfish species) showing strong intra-group correlations indicating spatial separation in
136 distributions. This confirms the associations among species seen in the factor loadings, with three
137 distinct species-group assemblages being present. This is also evident in correlation coefficients
138 for the average positive density, with strong associations among the roundfish (Figure 3b)

139 **Subtle differences in distributions may be important to separate catches within groups** : If
140 production from mixed fisheries is to be maximised, decoupling catches of species between and
141 within the groups will be key. For example, asking where the maximal separation in the densities
142 of two coupled species is likely to occur? To address this requirement, we map the difference in
143 spatial distribution for each pair of species within a species-group for a single year (2015; Figure 4).
144 This would facilitate discussion on maximal separation, for example, between difficult to separate
145 species such as haddock and whiting (Figure 4c).

146 Predicted catch distribution from a “typical” otter trawl gear and beam trawl fishing at three different
147 locations highlights the differences fishing gear and location makes on catches (Figure 4h). . In
148 the inshore area (location ‘A’) plaice and sole are the two main species in catch reflecting their
149 distribution and abundance, though the otter trawl gear catches a greater proportion of plaice to
150 sole than the beam trawl. The area between Britain and Ireland (location ‘B’) has a greater contri-
151 bution of whiting, haddock, cod, hake and anglerfishes in the catch with the otter trawl catching a
152 greater proportion of the roundfish, haddock, whiting and cod while the beam trawl catches more
153 anglerfishes and megrims. The offshore area has a higher contribution of megrim, anglerfishes
154 and hake with the otter trawl catching a greater share of hake and the beam trawl a greater pro-
155 portion of megrim. Megrim dominates the catch for both gears in location ‘C’, reflecting its relative
156 abundance in the area.

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

167 More challenging is within-group spatial separation due to significant overlap in spatial distributions
168 for the species, driven by common environmental factors. Subtle changes may yield some benefit

169 in changing catch composition, yet the outcome is likely to be much more difficult to predict. Subtle
170 differences in the distribution of cod, haddock and whiting can be seen in Figures 4a-c, showing
171 spatial separation of catches is much more challenging and likely to need to be supported by other
172 measures such as changes to the selectivity characteristics of gear (e.g. ²¹).

173 A role that science can play in supporting effectiveness of spatiotemporal avoidance could be to
174 provide probabilistic advice on likely hotspots for species occurrence and high species density
175 which can inform fishing decisions. Previous modelling studies have shown how spatiotemporal
176 models could improve predictions of high ratios of bycatch species to target species ²²⁻²⁴, and
177 geostatistical models are well suited to this as they incorporate spatial dependency while providing
178 for probabilities to be drawn from posterior distributions of the parameter estimates. We posit
179 that such advice could be enhanced by integrating data obtained directly from commercial fishing
180 vessels at a higher temporal resolution, providing real-time forecasts to inform fishing choices
181 that also captures seasonal differences in distributions. Advice informed by a seasonal or real-
182 time component could inform optimal policies for time-area closures, move-on rules or even as
183 informal information to be utilised by fishers directly without being reliant on costly continuous
184 data collection on environmental parameters.

185 An important question for the implementation of the EU's landing obligation is how far spatial avoid-
186 ance can go to achieving catch balancing in fisheries. Our model captures differences between
187 location fished for two gear types and their broad scale effect on catch composition. It is likely this
188 analysis reflects a lower bound on avoidance as fine-scale behavioural decisions such as time-
189 of-day, gear configuration and location choices can also be used to affect catch^{25,26}. Results of
190 empirical studies undertaken elsewhere^{3,4} suggest limits to the effectiveness of spatial avoidance.
191 Differences in ability to change catch composition have also been observed for different fleets;

192 in the North Sea targeting ability was found to differ between otter and beam trawlers as well as
193 between vessels of different sizes²⁷.

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

202 **Methods**

203 **Model structure:** VAST¹ implements a delta-generalised linear mixed modelling (GLMM) frame-
204 work that takes account of spatio-temporal correlations among species through implementation of
205 a spatial dynamic factor analysis (SDFA). Spatial variation is captured through a Gaussian Markov
206 Random Field, while we model random variation among species and years. Covariates affecting
207 catchability (to account for differences between fishing surveys) and density (to account for envi-
208 ronmental preferences) can be incorporated for predictions of presence and positive density. The
209 following briefly summarises the key methods implemented in the VAST framework. For full details
210 of the model the reader is invited directed to Thorson *et al* 2017²⁸.

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

SDFA: A spatial dynamic factor analysis incorporates advances in joint dynamic species models ²⁸ 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:

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

²¹¹ Where $\theta_c(s, t)$ represents log-density for species c at site s at time t , ψ_j is the coefficient for factor
²¹² j , $L_{c,j}$ the loading matrix representing association of species c with factor j and $\gamma_{k,c} \chi_k(s, t)$ the
²¹³ linear effect of covariates at each site and time ²⁹.

²¹⁴ The factor analysis can identify community dynamics and where species have similar spatio-
²¹⁵ temporal patterns, allowing inference of species distributions and abundance of poorly sampled
²¹⁶ species through association with other species and allows for computation of spatio-temporal cor-
²¹⁷ relations among species ²⁹.

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 ¹⁴.

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

218 where $p(s_i, c_i, t_i)$ is the predictor for encounter probability for observation i , at location s for species
 219 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-
 220 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
 221 spatial covariation among species. $\varepsilon_*(s_i, c_i, t_i)$ is the linear predictor for spatio-temporal variation,
 222 with $L_\varepsilon(c_i, f)$ the loading matrix for spatio-temporal covariance among species and $\delta_*(c_i, v_i)$ the
 223 contribution of catchability covariates for the linear predictor with Q_{c_i, v_i} the catchability covariates
 224 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:

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

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

227 **Spatio-temporal variation:** The spatiotemporal variation is modelled using Gaussian Markov
 228 Random Fields (GMRF) where data is associated to nearby locations through a Matérn covariance
 229 function with the parameters estimated within the model. Here, the correlation decays smoothly
 230 over space the further from the location and includes geometric anisotropy to reflect the fact that
 231 correlations may decline in one direction faster than another (e.g. moving offshore) ¹⁵. The best
 232 fit estimated an anisotropic covariance where the correlations were stronger in a north-east -

233 south-west direction, extending approximately 97 km and 140 km before correlations for encounter
234 probability and positive density reduced to <10 %, respectively (Figure S9). Incorporating the
235 spatiotemporal correlations among and within species provides more efficient use of the data as
236 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:

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

237 Here, $\text{vec}[\mathbf{E}_*(t)]$ is the stacked columns of the matrices describing $\varepsilon_*(s, p, t)$ at every location,
238 species and time, \mathbf{R}_* is a correlation matrix for encounter probability or positive catch rates
239 among locations and \mathbf{V}_* a covariance matrix for encounter probability or positive catch rate among
240 species (modelled within the factor analysis). \otimes represents the Kronecker product so that the cor-
241 relation among any location and species can be computed²⁸.

242 **Incorporating covariates** Survey catchability (the relative efficiency of a gear catching a species)
243 was estimated as a fixed effect in the model, $\delta_s(v)$, to account for differences in spatial fishing
244 patterns and gear characteristics which affect encounter and capture probability of the sampling
245 gear³⁰. Parameter estimates (Figure S10) showed clear differential effects of surveys using otter
246 trawl gears (more effective for round fish species) and beam trawl gears (more effective for flatfish
247 species).

248 No fixed covariates for habitat quality or other predictors of encounter probability or positive density
249 were included. While incorporation may improve the spatial predictive performance²⁸, it was not

250 found to be the case here based on model selection with Akaike Information Criterion (AIC) and
251 Bayesian Information Criterion (BIC).

252 **Parameter estimation** Parameter estimation was undertaken through Laplace approximation of
253 the marginal likelihood for fixed effects while integrating the joint likelihood (which includes the
254 probability of the random effects) with respect to random effects. This was implemented using
255 Template Model Builder (TMB; ³¹) with computation through support by the Irish Centre for High
256 End Computing (ICHEC; <https://www.ichec.ie>) facility.

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

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

263 The following steps were undertaken for data processing: i) data for survey stations and catches
264 were downloaded from ICES Datras ([www.ices.dk/marine-data/data-portals/Pages/
265 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
266 checked and any tows with missing or erroneously recorded station information (e.g. tow duration
267 or distance infeasible) removed; iii) swept area for each of the survey tows was estimated based
268 on fitting a GAM to gear variables so that $\text{Doorspread} = s(\text{Depth}) + \text{DoorWt} + \text{WarpLength} +$
269 $\text{WarpDiameter} + \text{SweepLength}$ and a gear specific correction factor taken from the literature ³²;
270 iii) fish lengths were converted to biomass (Kg) through estimating a von bertalanffy length weight

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

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

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

280 Three candidate models were identified, i) a base model where the vessel interaction was a ran-
281 dom effect, ii) the base but where the vessel x species effect was estimated as a fixed covariate, iii)
282 with vessel x species effect estimated, but with the addition of estimating fixed density covariates
283 for both predominant habitat type at a knot and depth. AIC and BIC model selection favoured the
284 second model (Table S3). The final model included estimating 130,950 coefficients (1,674 fixed
285 parameters and 129,276 random effect values).

286 **Model validation** Q-Q plots show good fit between the derived estimates and the data for positive
287 catch rates and between the predicted and observed encounter probability (S11, S12). Further,
288 model outputs are consistent with stock-level trends abundances over time from international as-
289 sessments (S13), yet also provide detailed insight into species co-occurrence and the strength of
290 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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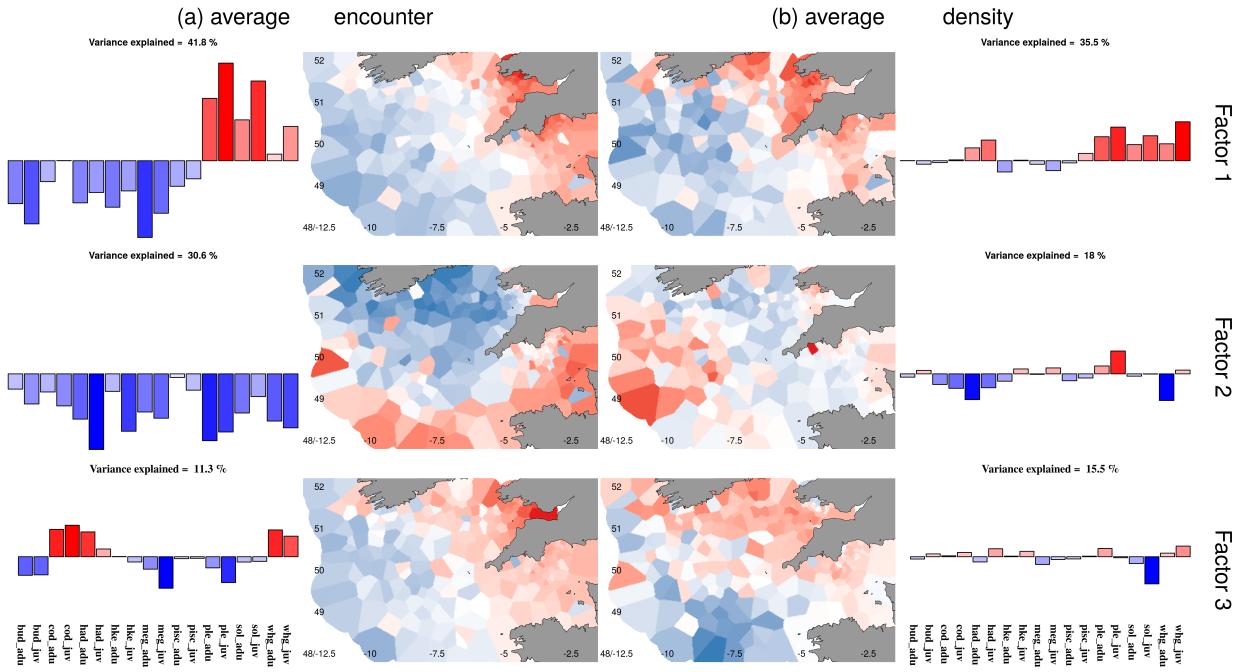


Figure 1: Factor values for the first three factors for (a) Average encounter probability and (b) Average positive density for the species (outer figures) and spatially (inner figures). Red: positive association to the factor, Blue: negative association

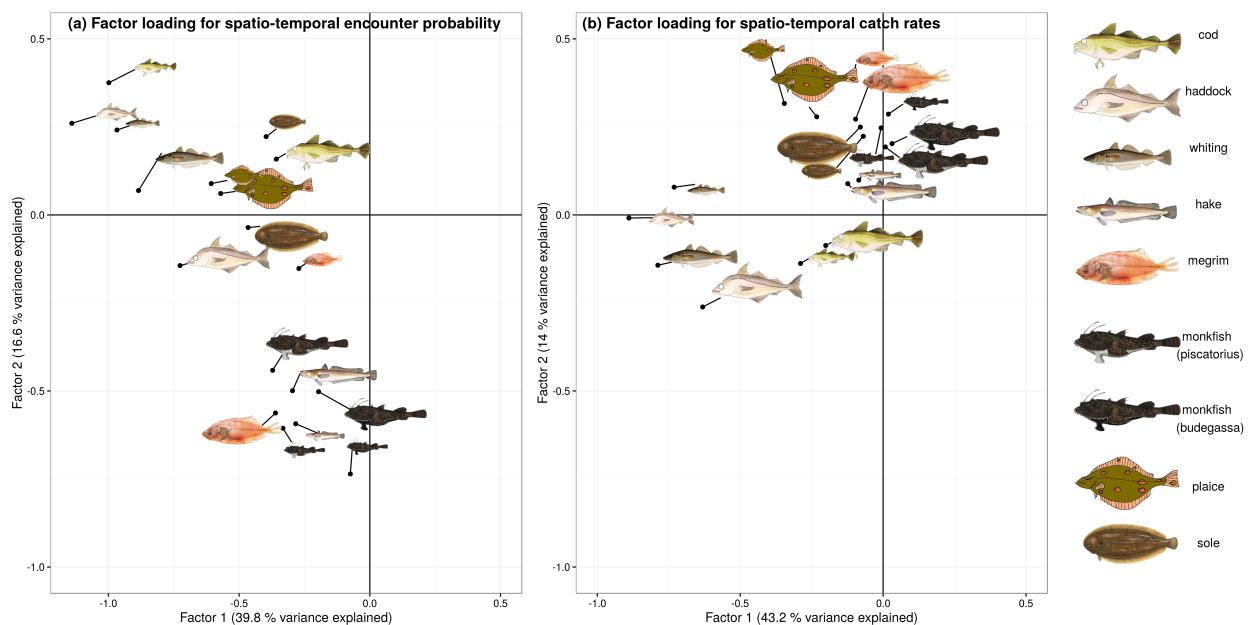


Figure 2: Position of each species on the first two axes from the factor analysis for (a) spatio-temporal encounter probability and (b) spatio-temporal positive density.

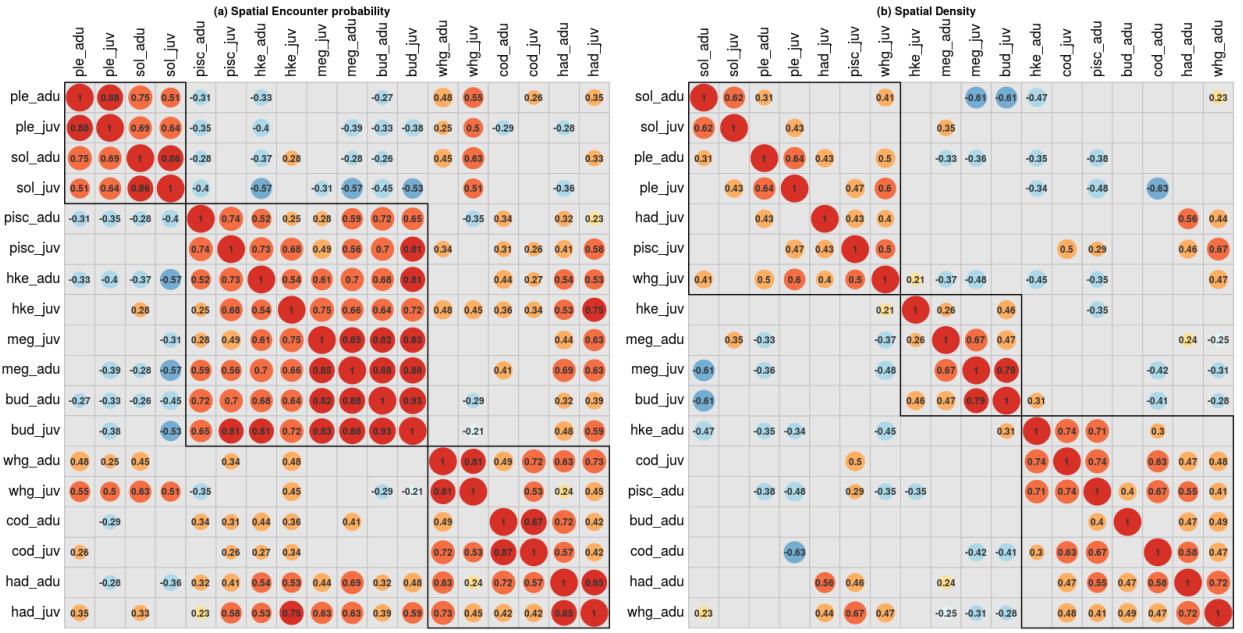


Figure 3: Inter-species correlations for (a) spatial encounter probability over all years and (b) spatial positive density. Species are clustered into three groups based on a hierarchical clustering method with non-significant correlations (the Confidence Interval $[+/- 1.96 * \text{SEs}]$ spanned zero)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

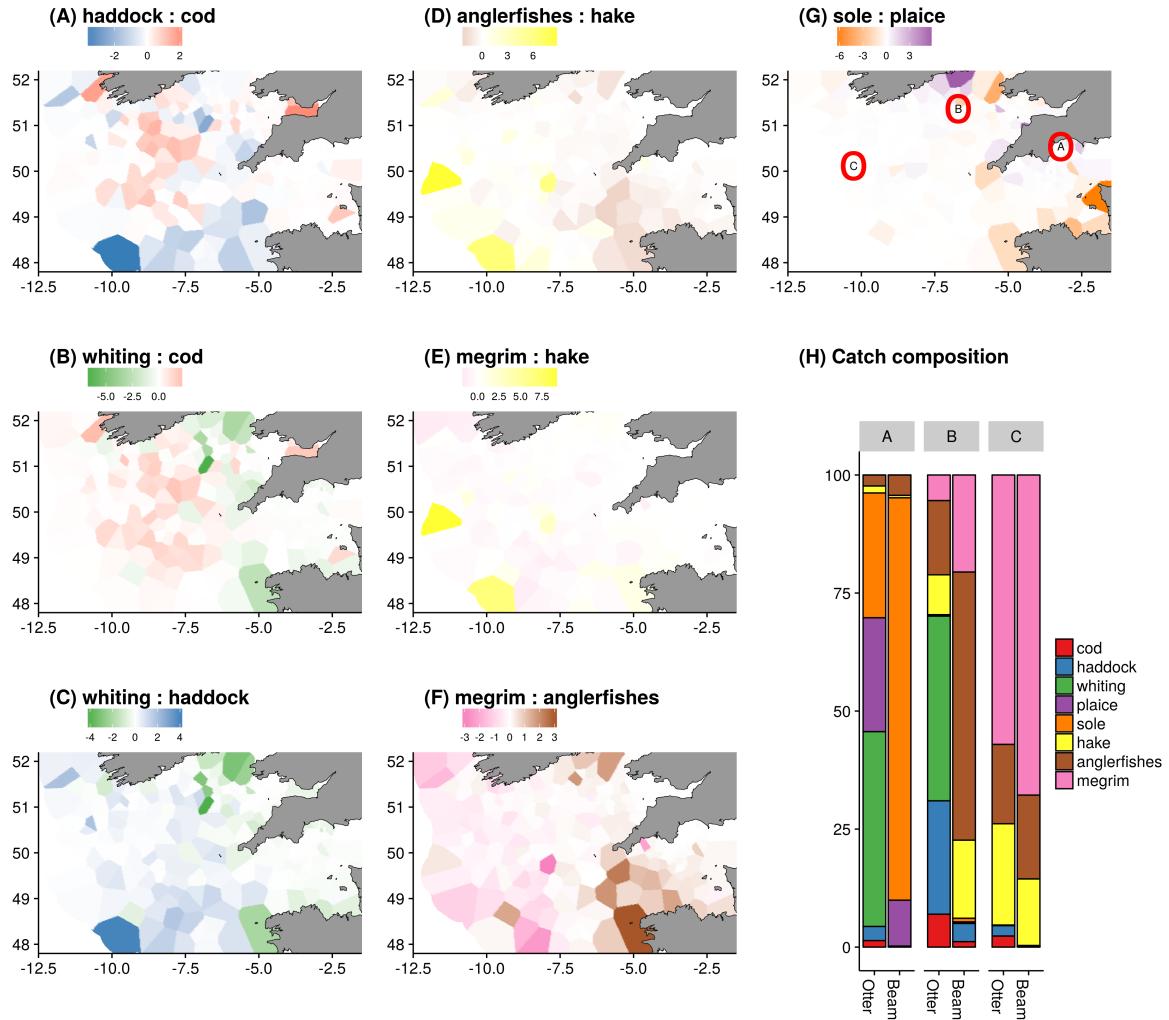


Figure 4: Differences in the standardised spatial density for pairs of species and expected catch rates for two different gears at three different locations in 2015.