

Working title: Spatial separation of catches in highly mixed fisheries

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- 1 Mixed fisheries capture a mix of species at the same time and are the dominant type of**
- 2 fishery worldwide. Overexploitation in mixed fisheries occurs when catches continue for**
- 3 available quota species while low quota species are discarded¹. As EU fisheries manage-**
- 4 ment moves to count all fish caught against quota (the ‘landings obligation’), the challenge**
- 5 is to catch available quota within new constraints, else lose productivity.**

- 6 A mechanism for decoupling exploitation of species caught together is spatial targeting,**
- 7 but this remains challenging due to complex fishery and population dynamics in space and**
- 8 time^{2,3}. How far spatial targeting can go to practically separate species is often unknown**
- 9 and anecdotal. Here we develop a dimension-reduction framework based on joint species**
- 10 distribution modelling (spatial dynamic factor analysis) to understand how spatial com-**
- 11 munity and fishery dynamics interact to determine species and size composition. In the**
- 12 example application to the highly mixed fisheries of the Celtic Sea, clear common spatial**
- 13 patterns emerge for three distinct species-groups. While distribution varies inter-annually,**
- 14 the same species are consistently found in higher densities together, with more subtle dif-**

15 **ferences within species-groups, where spatial separation may not be practically possible.**
16 **We highlight the importance of dimension reduction techniques to focus management dis-**
17 **cussion on axes of maximal separation in space and time. We propose that spatiotemporal**
18 **modelling of available data is a scientific necessity to address the pervasive and nuanced**
19 **challenges of managing mixed fisheries.**

20

21 **Mixed fisheries and the EU landings obligation** Recent efforts to reduce exploitation rates in
22 commercial fisheries have begun the process of rebuilding depleted fish populations⁴. Improved
23 management of fisheries has the potential to increase population sizes and allow increased sus-
24 tainable catches, yet fisheries catch globally remains stagnant⁵. In light of a projected increase in
25 demand for fish protein⁶ there is an important role for well managed fisheries in supporting future
26 food security⁷ necessitating 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^{2,8,9}. 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 quota¹. There is, therefore, a pressing need for scientific
34 tools which simplify the complexities of mixed fisheries to help avoid discarding.

35 Mixed fisheries require specific management approaches to avoid overfishing. Sustainability of Eu-

36 European fisheries has been hampered by the ‘mixed fishery problem’ for decades with large-scale
37 discarding resulting^{10,11}. A paradigm shift is being introduced under the EU Common Fisheries
38 Policy (CFP) reform of 2012 through two significant management changes. First, by 2019 all fish
39 that are caught are due to be counted against the respective stock quota even if they are dis-
40 carded; second, by 2020 all fish stocks must be fished so as to be able to produce their Maximum
41 Sustainable Yield (MSY)¹². The changes are expected to contribute to attainment of the goal
42 of Good Environmental Status (GES) under the European Marine Strategy Framework Directive
43 (MSFD;¹³) and move Europe towards an ecosystem based approach to fisheries management¹⁴.

44 Conflicts between overall management goals and drivers for individual actors must be overcome
45 to achieve sustainability. Societal objectives for fisheries to achieve MSY across ecosystem com-
46 ponents are paralleled by individual fishers goals to maximise utility; whether that be profit, income
47 or the continuance of traditional practices. Under the new policy, unless fishers can avoid catch
48 of unwanted species they will have to stop fishing when reaching their first restrictive quota. This
49 introduces a potential significant cost to fishers of under-utilised quota^{9,15} and provides a strong
50 incentive to mitigate such losses^{16,17}.

51 The ability align catch with available quota depends on being able to exploit target species while
52 avoiding unwanted catch. Methods by which fishers can alter their fishing patterns include by
53 switching fishing method (e.g. trawling to netting), changing technical gear characteristics (e.g.
54 introducing escapement panels in nets), or altering the timing and location of fishing activity^{18,19}.
55 Otter trawl gears are known to have higher catch rates of roundfish due to the higher headline and
56 wider sweeps which herd demersal fish into the net. Conversely, beam trawls, which employ chain
57 mesh to ‘dig’ benthic flatfish species, have higher catch rates for these species²⁰.

58 Design of spatiotemporal management measures requires an effective framework to reduce and
59 understand the complexities of the system. Spatiotemporal management measures (such as time-
60 limited fishery closures) have been applied to reduce unwanted catch with varying degrees of
61 success (e.g.^{21–24}) while move-on rules have also been proposed or implemented to influence
62 catch rates of particular vulnerable species in order to reduce or eliminate discards (e.g.^{3,25,26}).
63 However, such measures have generally been targeted at individual species without considering
64 associations and interactions among several species. Highly mixed fisheries are complex with
65 spatial, technological and community interactions combining. The design of spatio-temporal man-
66 agement measures which aim to allow exploitation of high quota stocks while protecting low quota
67 stocks requires understanding these interactions at a scale meaningful to managers and fishers.
68 Here, our goal is to develop a framework for understanding these complexities. We do so by 1)
69 implementing a spatio-temporal dimension reduction method that estimates the likely correlation
70 in catches for multiple species at each fishing location, 2) using the results to draw inference on the
71 fishery-community dynamics, 3) creating a framework to identify trends common among species,
72 and 4) describing the potential for and limitation of spatial measures to mitigate unwanted catches
73 in highly mixed fisheries.

74 **Framework for analysing spatio-temporal mixed fisheries interactions** We present a frame-
75 work for analysing how far spatio-temporal avoidance can contribute towards mitigating imbal-
76 ances in quota in mixed fisheries. We use fisheries-independent survey data to characterise the
77 spatiotemporal dynamics of key components of a fish community by employing a geostatistical
78 Vector Autoregressive Spatiotemporal model (VAST). We implement a factor analysis decompo-
79 sition to describe trends in spatiotemporal dynamics of the different species as a function of la-
80 tent variables²⁷ representing spatial variation (9 factors; which we call 'average' spatial variation)

81 and spatio-temporal variation (9 factors) for encounter probability and positive catch rates (which
82 we call 'positive density') separately²⁸. We use the resultant factor analysis to identify commu-
83 nity dynamics and drivers common among 9 species, each analyzed separately for juveniles and
84 adult stages. We refer to each combination of species and size class as a "species group", and
85 present results through transformation of the loading matrices using PCA rotation. By describing
86 the species dynamics through underlying contributory spatiotemporal factors we can take account
87 of how the factors contribute to affect catches of the species in mixed fisheries. We use Gaussian
88 Markov Random Fields (GMRFs) to capture spatial and temporal dependence within and among
89 species groups for both encounter probability and positive density²⁹. VAST is set in a mixed mod-
90 elling framework to allow estimation of fixed effects to account for systematic differences driving
91 encounter and catches, such as differences in sampling efficiency (a.k.a. catchability), while ran-
92 dom effects capture the spatio-temporal dynamics of the fish community.

93 **Dynamics of Celtic Sea fisheries** We use the highly mixed demersal fisheries of the Celtic Sea
94 as a case study. The Celtic Sea is a temperate sea where fisheries are spatially and temporally
95 complex; mixed fisheries are undertaken by several nations using different gear types^{30,31}. Close
96 to 150 species have been identified in the commercial catches of the Celtic Sea, with approxi-
97 mately 30 species dominating the catch³².

98 We parametrise our spatiotemporal model using catch data from seven fisheries-independent
99 surveys undertaken in the Celtic Sea over the period 1990 - 2015 (Table S1) and include nine
100 of the main commercial species: Atlantic cod (*Gadus morhua*), Atlantic haddock (*Melanogram-*
101 *mus aeglefinus*), Atlantic whiting (*Merlangius merlangus*), European Hake (*Merluccius merluc-*
102 *cious*), white-bellied anglerfish (*Lophius piscatorius*), black-bellied anglerfish (*Lophius budegassa*),
103 megrim (*Lepidorhombus whiffiagonis*), European Plaice (*Pleuronectes platessa*) and Common

¹⁰⁴ Sole (*Solea solea*). These species make up >60 % of landings by towed fishing gears for the area
¹⁰⁵ (average 2011 - 2015;³³). Each species was separated into juvenile and adult size classes based
¹⁰⁶ on their legal minimum conservation reference size (Table S2).

¹⁰⁷ We analyse the data to understand how the different associations among emergent species (com-
¹⁰⁸ bination of species and size class) and their potential drivers affect catch compositions in mixed
¹⁰⁹ fisheries. We consider how these have changed over time, and the implications for mixed fisheries
¹¹⁰ in managing catches of quota species under the EU landing obligation.

¹¹¹ **Common average spatial patterns driving species associations** A spatial dynamic factor anal-
¹¹² ysis decomposes the dominant spatial patterns driving differences in encounter probability and
¹¹³ positive density. The first three factors (after PCA rotation) account for 83.7 % of the between
¹¹⁴ species variance in average encounter probability and 69 % of the between species variance in
¹¹⁵ average positive density. A clear spatial pattern can been seen both for encounter probability and
¹¹⁶ positive density, with a positive value associated with the first factor in the inshore north easterly
¹¹⁷ part of the Celtic Sea into the Bristol Channel and Western English Channel, moving to a negative
¹¹⁸ value offshore in the south-westerly waters (Figure 1). The species loadings coefficients show
¹¹⁹ plaice, sole and whiting to be positively associated with the first factor for encounter probability
¹²⁰ while the other species are negatively associated. For average positive density, positive associa-
¹²¹ tions are also found for haddock and juvenile cod. This is indicative of a more inshore distribution
¹²² for these species.

¹²³ On the second spatial factor for encounter probability a north / south split can be seen at approxi-
¹²⁴ mately 49° N while positive density is more driven by a positive value in the deeper westerly waters
¹²⁵ as well as some inshore areas. Species values for the second factor indicate there are positive

126 associations for juvenile monkfish (*L. piscatorius*), juvenile hake, juvenile megrim, plaice and ju-
127 venile whiting with average positive density, which may reflect two different spatial distributions in
128 the more offshore and in the inshore areas (Figure 1).

129 On the third factor, there is a positive association with the easterly waters for encounter probability
130 and negative with the westerly waters. This splits the roundfish species (cod, haddock and whiting,
131 which all have a positive association with the third factor for average encounter probability) from
132 the rest of the species (which have a negative association). Positive density is driven by a north /
133 south split (Figure 1), with positive values in the northerly areas. Juvenile monkfish (*L. budgessa*
134 and *L. piscatorius*), cod, juvenile haddock, hake, adult plaice and whiting are also positively asso-
135 ciated with the third factor towards the north while adult monkfish (*L. budgessa* and *L. piscatorius*),
136 adult haddock, megrims, juvenile plaice and sole are negatively associated reflecting their more
137 southerly distribution (Figure 1).

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

148 It is clear that depth and to a lesser extent substrate are important predictors for the main driver
149 of similarities and differences in distributions and abundances for the different species. The first
150 factor correlates strongly with these variables, despite them not explicitly being incorporated in
151 the model. While depth was incorporated as a covariate in an alternative model formulation (see
152 Methods), it was found not to improve predictions. The utility of these variables as predictors
153 of species distributions has been identified in other marine species distribution models³⁴; the
154 advantage to the approach taken here is that, where such data is unavailable at appropriate spatial
155 resolution, the spatial factor analysis can adequately characterise these influences on species
156 spatial dynamics.

157 **Time-varying species distributions, but stability within species groups** While there are clear
158 spatial patterns in the factor coefficients describing differences in average (over time) encounter
159 probability and positive density (Figure 1), the inter-annual differences in factor coefficients show
160 less structure (Figures S5, S6). These inter-annual differences are important as they reflect the
161 ability of fishers to predict where they can target species from one year to the next, without which
162 it may be difficult to avoid unwanted catch.

163 While spatio-temporal factor coefficients did not show consistent trends from year to year across
164 all species, among species there were clear relationships (Figure 2). The same factors appear
165 to drive spatio-temporal distributions of megrim, anglerfish species and hake (the deeper wa-
166 ter species, species-grouping negatively associated with the second axes of Figure 2a) and the
167 roundfish and flatfish (species-grouping more positively associated with the second axes of Fig-
168 ure 2a). For spatio-temporal positive density (Figure 2b) cod, haddock and whiting (the roundfish
169 species) are separated from plaice, sole (the flatfish) and deeper water species. As such, it can
170 be predicted that higher catches of a species within a group (e.g. cod in roundfish) would be ex-

pected when catching another species within that group (e.g. whiting in roundfish). This suggests that one or more common environmental drivers are influencing the distributions of the species groups, and that driver differentially affects the species groups. Temperature is often included as a covariate in species distribution models, but was found not to contribute to the variance in the first factor values (Figure S6, no correlations found for either encounter probability or positive density) and so was not included as a covariate in the final model.

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

Correlation coefficients for the average positive density (Figure 3b) show fewer significant posi-

194 tive or negative relationships among species than for encounter probability, but still evident are
195 the strong association among the roundfish with higher catches of cod are associated with higher
196 catches of haddock (0.58) and whiting (0.47), as well as the two anglerfish species (0.71 for pisca-
197 torius and 0.44 for budegassa) and hake (0.73). Similarly, plaice and sole are closely associated
198 (0.31) and higher catches of one would expect to see higher catches of the other, but also higher
199 catches of some juvenile size classes of roundfish (whiting and haddock) and anglerfish species.
200 Negative association of juvenile megrim, anglerfish (budegassa) and hake with adult sole (-0.61,
201 -0.61 and -0.47 respectively), plaice (-0.36 and -0.35 for megrim and hake only) indicate high
202 catches of one can predict low catches of the other successfully.

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

217 year to the next (Figures S4 and S5) indicating changes may be driven by temporally changing
218 environmental factors and species behaviour.

219 **Subtle differences in distributions may be important to separate catches within groups**

220 **under the landing obligation:** The analysis shows the interdependence within species-groups of
221 roundfish, flatfish and deeper water species, where catching one species within the group indicates
222 a high probability of catching the other species, which has important implications for how spatial
223 avoidance can be used to support implementation of the EU's landings obligation. If production
224 from mixed fisheries is to be maximised, decoupling catches of species between and within the
225 groups will be key. For example, asking where the maximal separation in the densities of two
226 coupled species is likely to occur? To address this requirement, we map the difference in spatial
227 distribution within a group for each pair of species within a species-groupings for a single year
228 (2015; Figure 4).

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

¹two species combined as they are managed as one

239 Predicted catch distribution from a “typical” otter trawl gear and beam trawl fishing at three different
240 locations highlights the differences fishing gear makes on catches (Figure 4h). As can be seen,
241 both the gear selectivity and area fished play important contributions to the catch compositions;
242 in the inshore area (location ‘A’) plaice and sole are the two main species in catch reflecting their
243 distribution and abundance, though the otter trawl gear catches a greater proportion of plaice to
244 sole than the beam trawl. The area between Britain and Ireland (location ‘B’) has a greater contri-
245 bution of whiting, haddock, cod, hake and anglerfishes in the catch with the otter trawl catching a
246 greater proportion of the roundfish, haddock, whiting and cod while the beam trawl catches more
247 anglerfishes and megrims. The offshore area has a higher contribution of megrim, anglerfishes
248 and hake with the otter trawl catching a greater share of hake and the beam trawl a greater pro-
249 portion of megrim. Megrim dominates the catch for both gears in location ‘C’, reflecting its relative
250 abundance in the area.

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

261 More challenging is within-group spatial separation due to significant overlap in spatial distributions

262 for the species, driven by common environmental factors. Subtle changes may yield some benefit
263 in changing catch composition, yet the outcome is likely to be much more difficult to predict. For
264 example, subtle differences in the distribution of cod, haddock and whiting can be seen in Figures
265 4a-c, showing spatial separation of catches is much more challenging and likely to need to be
266 supported by other measures such as changes to the selectivity characteristics of gear (e.g.³⁵).

267 A role that science can play in supporting effectiveness of spatiotemporal avoidance could be to
268 provide probabilistic advice on hotspots for species occurrence and high species density which
269 can inform fishing decisions. Previous modelling studies have shown how spatiotemporal models
270 could improve predictions of high ratios of bycatch species to target species³⁶⁻³⁸, and geosta-
271 tistical models are well suited to this as they incorporate spatial dependency while providing for
272 probabilities to be drawn from posterior distributions of the parameter estimates. We posit that
273 such advice could be enhanced by integrating data obtained directly from commercial fishing ves-
274 sels rapidly while modeling densities at small time scales (e.g., weekly). Short-term forecasts of
275 distribution could inform fishing choices while also capturing seasonal differences in distributions,
276 akin to weather forecasting. Advice informed by a model including a seasonal or real-time com-
277 ponent could inform optimal policies for time-area closures, move-on rules or even as informal
278 information to be utilised by fishers directly without the need for costly continuous data collection
279 on environmental parameters, but by using the vessels-as-laboratories approach.

280 An important question for the implementation of the EU's landing obligation is how far spatial avoid-
281 ance can go to achieving catch balancing in fisheries. Our model captures differences between
282 location fished for two gear types and their broad scale effect on catch composition, information
283 crucial for managers in implementing the landing obligation. It is likely, however, that this analy-
284 sis reflects a lower bound on the utility of spatial avoidance as fine-scale behavioural decisions

285 such as time-of-day, gear configuration and location choices can also be used to affect catch^{39,40}.

286 Results of empirical studies undertaken elsewhere^{2,8} suggest limits to the effectiveness of spatial
287 avoidance. Differences in ability to change catch composition have also been observed for differ-
288 ent fleets; in the North Sea targeting ability was found to differ between otter and beam trawlers
289 as well as between vessels of different sizes⁴¹.

290 Our framework allows for a quantitative understanding of the broad scale global production set
291 available to fishers⁴² and thus the extent to which they can alter catch compositions while operat-
292 ing in a mixed fishery. Simulations of spatial effort allocation scenarios based on the production
293 sets derived from the model estimates could be used as inputs to fisher behavioural models to al-
294 low for identification of the lower bounds of optimum spatial harvest strategies. This would provide
295 managers with information useful for examining trade-offs in quota setting by integrating poten-
296 tial for spatial targeting in changing catch composition, thus provide a scientific contribution to
297 meeting the goal of maximising catches in mixed fisheries within single stock quota constraints⁹.
298 Further, the correlations among species could provide information on fisheries at risk of capturing
299 protected, endangered or threatened species such as elasmobranches, and allow identification of
300 areas where there are high ratios of protected to target species.

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

308 anecdotal knowledge of single-species distribution in space and time.

309 **Methods**

310 **Model structure:** VAST² implements a delta-generalised linear mixed modelling (GLMM) frame-
311 work that takes account of spatio-temporal correlations among species through implementation of
312 a spatial dynamic factor analysis (SDFA). Spatial variation is captured through a Gaussian Markov
313 Random Field, while we model random variation among species and years. Covariates affecting
314 catchability (to account for differences between fishing surveys) and density (to account for envi-
315 ronmental preferences) can be incorporated for predictions of presence and positive density. The
316 following briefly summarises the key methods implemented in the VAST framework. For full details
317 see Thorson *et al* 2017⁴³.

SDFA: A spatial dynamic factor analysis incorporates advances in joint dynamic species models⁴³ 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:

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

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

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

- 320 linear effect of covariates at each site and time⁴⁴.
- 321 The factor analysis can summarize community dynamics and identify which species and life-stages
 322 have similar spatio-temporal patterns. This allows inference regarding species distributions and
 323 abundance of poorly sampled species through association with other species, and also provides
 324 estimates of spatio-temporal correlations among species⁴⁴.

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- distribution²⁸.

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

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

The Delta-Gamma formulation is then:

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

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

334 **Spatio-temporal variation:** The spatiotemporal variation is modelled using Gaussian Markov
 335 Random Fields (GMRF) where observations are correlated in space through a Matérn covariance
 336 function with the parameters estimated within the model. Here, the correlation decays smoothly
 337 over space the further from the location and includes geometric anisotropy to reflect the fact that
 338 correlations may decline in one direction faster than another (e.g. moving offshore)²⁹. The best
 339 fit estimated an anisotropic covariance where the correlations were stronger in a north-east -
 340 south-west direction, extending approximately 97 km and 140 km before correlations for encounter
 341 probability and positive density reduced to <10 %, respectively (Figure S9). Incorporating the spa-
 342 tiotemporal correlations among species provides more efficient use of the data as inference
 343 can be made about poorly sampled locations from the covariance structure.

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

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

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

346 among locations and \mathbf{V}_* a covariance matrix for encounter probability or positive catch rate among
347 species (modelled within the factor analysis). \otimes represents the Kronecker product so that the cor-
348 relation among any location and species can be computed⁴³.

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

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

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

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

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

370 The following steps were undertaken for data processing: i) data for survey stations and catches
371 were downloaded from ICES Datras ([www.ices.dk/marine-data/data-portals/Pages/
372 DATRAS.aspx](http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx)) or obtained directly from the Cefas Fishing Survey System (FSS); ii) data were
373 checked and any tows with missing or erroneously recorded station information (e.g. tow duration
374 or distance infeasible) removed; iii) swept area for each of the survey tows was estimated based
375 on fitting a GAM to gear variables so that $\text{Doorspread} = s(\text{Depth}) + \text{DoorWt} + \text{WarpLength} +$
376 $\text{WarpDiameter} + \text{SweepLength}$ and a gear specific correction factor taken from the literature⁴⁷; iii)
377 fish lengths were converted to biomass (Kg) through estimating a von bertalanffy length weight
378 relationship, $Wt = a \cdot L^b$, fit to sampled length and weight of fish obtained in the EVHOE survey
379 and aggregated within size classes (adult and juvenile).

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

382 **Data availability** Data used to fit the model is available via the ICES Datras data portal (<http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx>) for two surveys and
383 on request to the author for the remaining five surveys.

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

388 predictor for encounter probability and log-link for the linear predictor for positive density, with an
389 assumed gamma distribution.

390 Three candidate models were identified, i) a base model where the vessel interaction was a ran-
391 dom effect, ii) the base but where the vessel x species effect was estimated as a fixed covariate,
392 iii) with vessel x species effect estimated, but with the addition of estimating fixed density covari-
393 ates for both predominant habitat type at a knot and depth. AIC and BIC model selection favoured
394 the second model (Table S3). The final model included estimating 1,674 fixed parameters and
395 predicting 129,276 random effect values.

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

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Acknowledgements Paul J Dolder acknowledges funding support from the MARES joint doctoral research programme (MARES_14_15) and Cefas seedcorn (DP227AC) and logistical support, desk space and enlightening discussions with Trevor Branch, Peter Kuriyama, Cole Monnahan and John Trochta.

The authors gratefully acknowledge the use of computing facilities at the Irish Centre for High-End Computing (ICHEC; <https://www.ichec.ie>) and the hard-work of many scientists and crew in collecting and storing data through the scientific surveys used in this study without which it would not have been possible.

The manuscript benefited from discussions with D. Stokes, C. Lordan, C. Moore and H. Gerritsen (Marine Institute, Ireland), L. Ready, C. Darby, I. Holmes, S. Shaw and T. Earl (Cefas). We thank J.Hastie, M. McClure and R. Fonner for comments that improved the manuscript and Lisa Ready for provision of the Cefas datasets.

Author contributions P.J.D., C.M and J.T.T. designed the study. P.J.D. conducted the analysis. All authors contributed to writing the manuscript.

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

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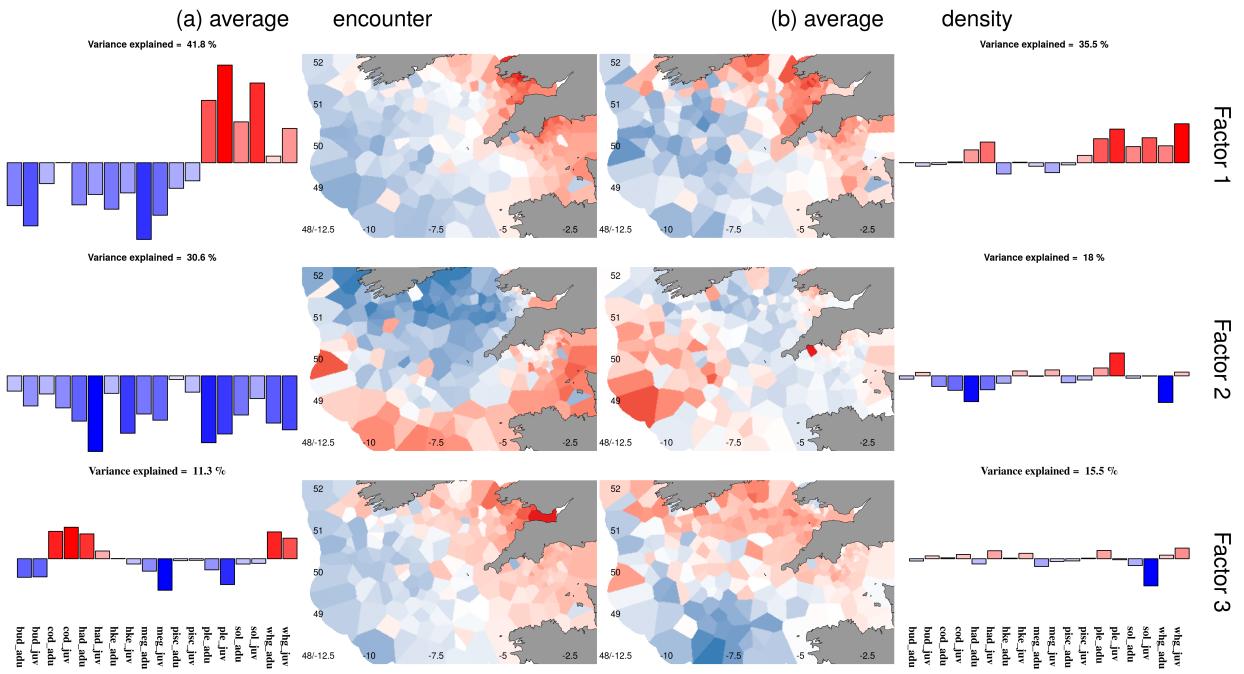


Figure 1: Factor values for the first three factors for (a) Average encounter probability and (b) Average positive density for the species (outer figures) and spatially (inner figures). Red: positive association to the factor, Blue: negative association.

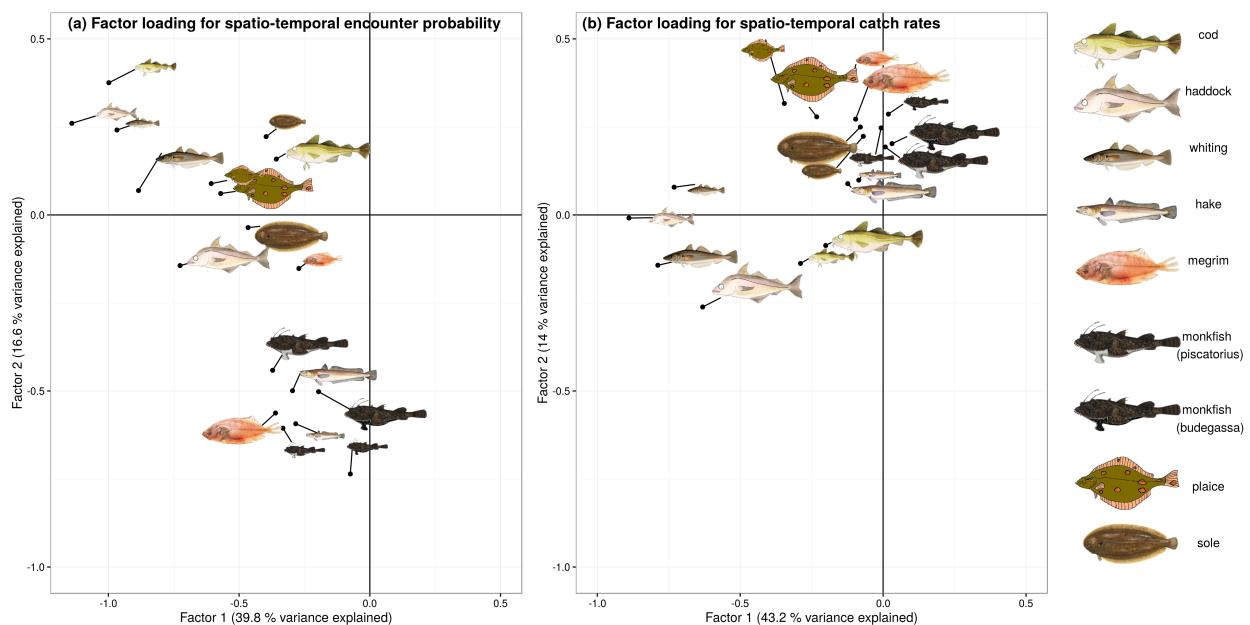


Figure 2: Position of each species on the first two axes from the factor analysis for (a) spatio-temporal encounter probability and (b) spatio-temporal positive density.

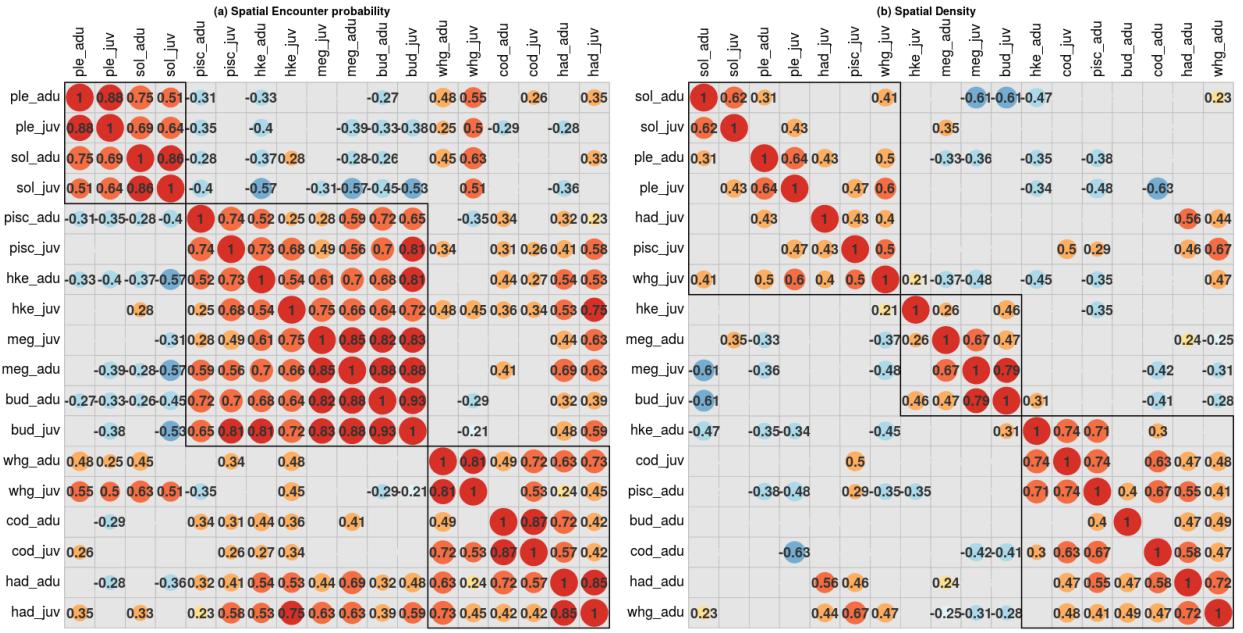


Figure 3: Inter-species correlations for (a) spatial encounter probability over all years and (b) spatial positive density. Species are clustered into three groups based on a hierarchical clustering method with non-significant correlations (the Confidence Interval [$\pm 1.96 * \text{SEs}$] spanned zero)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

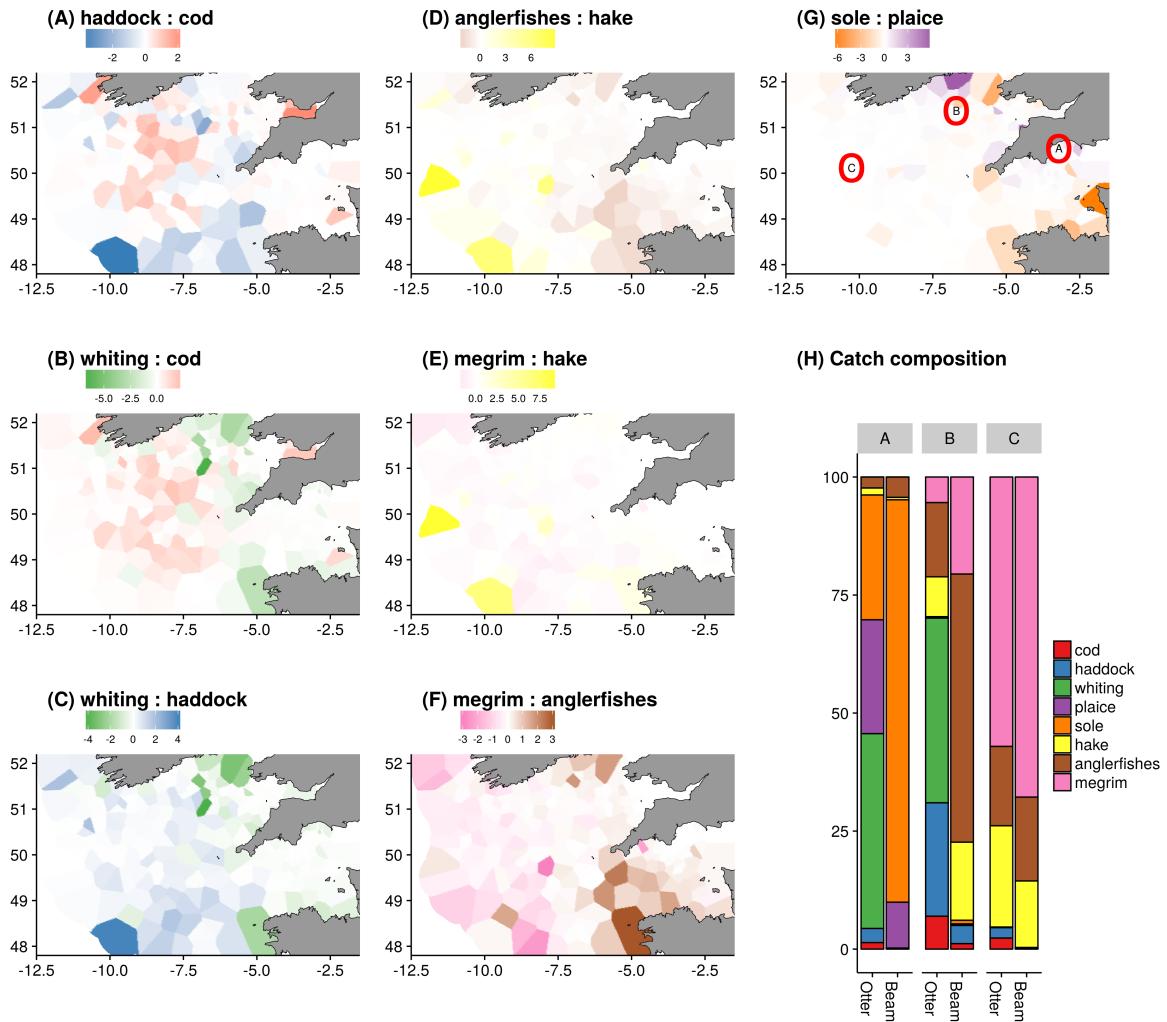


Figure 4: Differences in the standardised spatial density for pairs of species and expected catch rates for two different gears at three different locations in 2015.