

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 pur-**
- 2 suing a mix of species and low quota species are discarded. As EU fisheries man-**
- 3 agement moves to count all fish caught against quota (the ‘Landings obligation’),**
- 4 the challenge is to catch available quota within new constraints, else lose produc-**
- 5 tivity.**

- 6 A mechanism for decoupling exploitation of species caught together is spatial tar-**
- 7 geting, but this remains challenging due to complex fishery dynamics and a lack of**
- 8 understanding of spatiotemporal community dynamics. We develop application of**
- 9 a joint species distribution model (spatial dynamic factor analysis) to understand**
- 10 how spatial community and fishery dynamics interact to determine species and**
- 11 size composition in the example of the highly mixed fisheries of the Celtic Sea.**
- 12 Clear common spatial patterns emerge for three distinct species-groups and, while**

13 **distribution varies inter-annually, the same species-groups are consistently found**
14 **in higher densities together, with more subtle differences within species-groups.**

15 **The results highlight both opportunities for and limitations of the ability to spa-**
16 **tiotemporally separate catches.**

17 **We highlight the importance of dimension reduction techniques to focus manage-**
18 **ment discussion on axes of maximal separation in space and time. We propose**
19 **that spatiotemporal modelling of available data is a scientific requirement to ad-**
20 **dress the pervasive and nuanced challenges of managing mixed fisheries.**

21

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

29 A particular challenge in realising increased catches from rebuilt populations is maximis-
30 ing yields from mixed fisheries ⁵⁻⁷. In mixed fisheries, the predominant type of fishery
31 worldwide, several fish species are caught together in the same net or fishing operation
32 (known as a ‘technical interaction’). If managed by individual quotas, and catches do not
33 match available stock quotas, either a vessel must stop fishing when the first quota is

³⁴ reached (the ‘choke’ species) or overexploitation of the weaker species occurs while fish-
³⁵ ers continue to catch more healthy species and throw back (‘discard’) the fish for which
³⁶ they have no quota⁸. There is, therefore, a pressing need for scientific tools which simplify
³⁷ the complexities of mixed fisheries to help managers and fishers maximise catches.

³⁸ Sustainability of European fisheries has been hampered by this ‘mixed fishery problem’ for
³⁹ decades with large-scale discarding resulting^{9,10}. A paradigm shift is being introduced
⁴⁰ under the EU Common Fisheries Policy (CFP) reform of 2012 through two significant
⁴¹ management changes. First, by 2019 all fish that are caught are due to be counted
⁴² against the respective stock quota; second, by 2020 all fish stocks must be fished so
⁴³ as to be able to produce their Maximum Sustainable Yield (MSY)¹¹. The changes are
⁴⁴ expected to contribute to attainment of the goal of Good Environmental Status (GES)
⁴⁵ under the European Marine Strategy Framework Directive (MSFD;¹²) and move Europe
⁴⁶ towards an ecosystem based approach to fisheries management¹³.

⁴⁷ Societal objectives for fisheries to achieve MSY across ecosystem components are par-
⁴⁸ alleled by individual fishers goals to maximise utility; whether that be profit, income or
⁴⁹ the continuance of traditional practices. Under the new policy, unless fishers can avoid
⁵⁰ catch of unwanted species they will have to stop fishing when reaching their first restrictive
⁵¹ quota. This introduces a potential significant cost to fishers of under-utilised quota^{7,14} and
⁵² provides a strong incentive to mitigate such losses^{15,16}. The ability of fishers to align their
⁵³ catch with available quota depends on being able to exploit target species while avoid-
⁵⁴ ing unwanted catch. Methods by which fishers can alter their fishing patterns include by

55 switching fishing method (e.g. trawling to netting), changing technical gear characteris-
56 tics (e.g. introducing escapement panels in nets), or the timing and location of fishing
57 activity^{17,18}. Otter trawl gears are known to have higher catch rates of roundfish due to
58 the higher headline and wider sweeps which herd demersal fish into the net. Conversely,
59 beam trawls, which employ chain mesh to 'dig' benthic flatfish species, have higher catch
60 rates for these species¹⁹.

61 Spatiotemporal management measures (such as time-limited fishery closures) have been
62 applied to reduce unwanted catch with varying degrees of success (e.g.^{20–23}) while move-
63 on rules have also been proposed or implemented to influence catch rates of particular
64 vulnerable species in order to reduce or eliminate discards (e.g.^{24–26}). However, such
65 measures have generally been targeted at individual species without considering asso-
66 ciations and interactions among several species. Highly mixed fisheries are complex
67 with spatial, technological and community interactions combining. The design of spatio-
68 temporal management measures which aim to allow exploitation of high quota stocks
69 while protecting low quota stocks requires understanding of these interactions at a scale
70 meaningful to managers and fishers. Here, our goal is to develop a framework for un-
71 derstanding these complexities. We do so by implementing a spatio-temporal dimension
72 reduction method and use the results to draw inference on the fishery-community dy-
73 namics, creating a framework to identify trends common among species-groups. We use
74 this to describe where spatial measures can contribute to mitigating unwanted catches in
75 highly mixed fisheries.

76 **Framework for analysing spatio-temporal mixed fisheries interactions** We present
77 a framework for analysing how far spatio-temporal avoidance can contribute towards miti-
78 gating imbalances in quota in mixed fisheries. We use fisheries-independent survey data
79 to characterise the spatiotemporal dynamics of key components of a fish community by
80 employing a geostatistical Vector Autoregressive Spatiotemporal model (VAST). We im-
81 plement a factor analysis decomposition to describe trends in spatiotemporal dynamics
82 of the different species as a function of latent variables ²⁷ representing spatial variation
83 (9 factors; which we call 'average' spatial variation) and spatio-temporal variation (9 fac-
84 tors) for encounter probability and positive catch rates (which we call 'positive density')
85 separately ²⁸. We use the resultant factor analysis to identify community dynamics and
86 drivers common among 18 species-groups and present results through transformation
87 of the loading matrices using PCA rotation. By describing the species-groups dynam-
88 ics through underlying contributory spatiotemporal factors we can take account of how
89 the factors contribute to affect catches of the species-groups in mixed fisheries. We use
90 Gaussian Markov Random Fields (GMRFs) to capture spatial and temporal dependence
91 within and among species groups for both encounter probability and positive density²⁹.
92 VAST is set in a mixed modelling framework to allow estimation of fixed effects to account
93 for systematic differences driving encounter and catches, such as differences in sampling
94 efficiency (a.k.a. catchability), while random effects capture the spatio-temporal dynamics
95 of the fish community.

96 **Dynamics of Celtic Sea fisheries** We use the highly mixed demersal fisheries of the
97 Celtic Sea as a case study. The Celtic Sea is a temperate sea where fisheries are spatially

98 and temporally complex; mixed fisheries are undertaken by several nations using different
99 gear types^{30,31}. Close to 150 species have been identified in the commercial catches of
100 the Celtic Sea, with approximately 30 species dominating the catch³².

101 We parametrise our spatiotemporal model using catch data from seven fisheries-independent
102 surveys undertaken in the Celtic Sea over the period 1990 - 2015 (Table S1) and include
103 nine of the main commercial species: Atlantic cod (*Gadus morhua*), Atlantic haddock
104 (*Melanogrammus aeglefinus*), Atlantic whiting (*Merlangius merlangus*), European Hake
105 (*Merluccius merluccius*), white-bellied anglerfish (*Lophius piscatorius*), black-bellied an-
106 glerfish (*Lophius budegassa*), megrim (*Lepidorhombus whiffiagonis*), European Plaice
107 (*Pleuronectes platessa*) and Common Sole (*Solea solea*). These species make up >60
108 % of landings by towed fishing gears for the area (average 2011 - 2015;³³). Each species
109 was separated into juvenile and adult size classes based on their legal minimum conser-
110 vation reference size (Table S2).

111 We analyse the data to understand how the different associations among emergent species-
112 groups (combination of species and size class) and their potential drivers affect catch
113 compositions in mixed fisheries. We consider how these have changed over time, and
114 the implications for mixed fisheries in managing catches of quota species under the EU
115 landing obligation.

116 **Common average spatial patterns driving species associations** A spatial dynamic
117 factor analysis decomposes the dominant spatial patterns driving differences in encounter
118 probability and positive density. The first three factors (after PCA rotation) account for 83.7

119 % of the between species-group variance in average encounter probability and 69 % of
120 the between species-group variance in average positive density. A clear spatial pattern
121 can been seen both for encounter probability and positive density, with a positive value
122 associated with the first factor in the inshore north easterly part of the Celtic Sea into the
123 Bristol Channel and Western English Channel, moving to a negative value offshore in the
124 south-westerly waters (Figure 1). The species-group loadings coefficients show plaice,
125 sole and whiting to be positively associated with the first factor for encounter probability
126 while the other species-groups are negatively associated. For average positive density,
127 positive associations are also found for haddock and juvenile cod. This is indicative of a
128 more inshore distribution for these species-groups.

129 On the second spatial factor for encounter probability a north / south split can be seen at
130 approximately 49° N while positive density is more driven by a positive value in the deeper
131 westerly waters as well as some inshore areas. Species-group values for the second fac-
132 tor indicate there are positive associations for juvenile monkfish (*L. piscatorius*), juvenile
133 hake, juvenile megrim, plaice and juvenile whiting with average positive density, which
134 may reflect two different spatial distributions in the more offshore and in the inshore areas
135 (Figure 1).

136 On the third factor, there is a positive association with the easterly waters for encounter
137 probability and negative with the westerly waters. This manifests in the species associa-
138 tions as splitting the roundfish species cod, haddock and whiting which all have a positive
139 association with the third factor for average encounter probability from the rest of the

140 species-groups which have a negative association. Positive density is driven by a north
141 / south split (Figure 1), with positive values in the northerly areas. Juvenile monkfish
142 (*L. budgessa* and *L. piscatorius*), cod, juvenile haddock, hake, adult plaice and whiting
143 are also positively associated with the third factor towards the north while adult monkfish
144 (*L. budgessa* and *L. piscatorius*), adult haddock, megrims, juvenile plaice and sole are
145 negatively associated reflecting their more southerly distribution (Figure 1).

146 While this exploratory factor analysis is modelling unobserved drivers of distribution, we
147 considered what might be driving the differences seen in the spatial factor loadings. The
148 first factor was highly correlated with log(depth) for both encounter probability (-0.85, CI
149 = -0.88 to -0.81; Figure S1) and positive density (-0.71, CI = -0.77 to -0.65; Figure S2). A
150 random forest classification tree assigned 80 % of the variance in the first factor for en-
151 counter probability to depth and predominant substrate type, with the majority (86 %) of
152 the variance explained by depth. The variance explained by these variables dropped to 25
153 % on the second factor with a more even split between depth and substrate, while explain-
154 ing 60 % of the variance on the third factor. For positive density, the variables explained
155 less of the variance with 62 %, 35 %, and 31 % for each of the factors, respectively.

156 It is clear that depth and to a lesser extent substrate are important predictors for the
157 main driver of similarities and differences in distributions and abundances for the different
158 species-groups. The first factor correlates strongly with these variables, despite them not
159 explicitly being incorporated in the model. While depth was incorporated as a covariate in
160 an alternative model formulation (see Methods), it was found not to improve predictions.

¹⁶¹ The utility of these variables as predictors of species distributions has been identified in
¹⁶² other marine species distribution models ³⁴; the advantage to the approach taken here
¹⁶³ is that, where such data is unavailable at appropriate spatial resolution, the spatial factor
¹⁶⁴ analysis can adequately characterise these influences on species spatial dynamics.

¹⁶⁵ **Changes in spatial patterns over time, but stability in species dynamics** While there
¹⁶⁶ are clear spatial patterns in the factor coefficients describing differences in average (over
¹⁶⁷ time) encounter probability and positive density (Figure 1), the inter-annual differences in
¹⁶⁸ factor coefficients show less structure (Figures S5, S6). These inter-annual differences
¹⁶⁹ are important as they reflect the ability of fishers to predict where they can target species
¹⁷⁰ from one year to the next, without which it may be difficult to avoid unwanted catch.

¹⁷¹ While spatio-temporal factor coefficients did not show consistent trends from year to year
¹⁷² across all species, among species-groups there were clear relationships (Figure 2). The
¹⁷³ same factors appear to drive spatio-temporal distributions of megrim, anglerfish species
¹⁷⁴ and hake (the deeper water species, species-grouping negatively associated with the sec-
¹⁷⁵ ond axes of Figure 2a) and the roundfish and flatfish (species-grouping more positively
¹⁷⁶ associated with the second axes of Figure 2a). For spatio-temporal positive density (Fig-
¹⁷⁷ ure 2b) cod, haddock and whiting (the roundfish species) are separated from plaice, sole
¹⁷⁸ (the flatfish) and deeper water species. As such, it can be predicted that higher catches of
¹⁷⁹ a species within a group (e.g. cod in roundfish) would be expected when catching another
¹⁸⁰ species within that group (e.g. whiting in roundfish). This suggests that one or more com-
¹⁸¹ mon environmental drivers are influencing the distributions of the species groups, and

182 that driver differentially affects the species groups. Temperature is often included as a
183 covariate in species distribution models, but was found not to contribute to the variance in
184 the first factor values (Figure S6, no correlations found for either encounter probability or
185 positive density).

186 **Three clusters of species show similar spatial patterns** In order to gain greater in-
187 sight into the community dynamics we considered how species-groups covary in space
188 and time through among species-group correlations. Pearson correlation coefficients for
189 the modelled average spatial encounter probability (Figure 3a) show clear strong associa-
190 tions between adult and juvenile size classes for all species (>0.75 for all species except
191 hake, 0.56). Among species-groups, hierarchical clustering identified the same three
192 common groups as our visual inspection of factor loadings above, with roundfish (cod,
193 haddock, whiting) closely grouped in their association, with correlations for adult cod with
194 adult haddock and adult whiting of 0.73 and 0.5 respectively, while adult haddock with
195 adult whiting was 0.63 (Figure 3a). Flatfish (plaice and sole) are also strongly correlated
196 with adult plaice and sole having a coefficient of 0.75. The final group are principally
197 the species found in the deeper waters (hake, megrim and both anglerfish species) with
198 the megrim strongly associated with the budegassa anglerfish species (0.88). Negative
199 relationships were found between plaice-sole and the monkfish species (-0.27, -0.26 for
200 the adult size class with budegassa adults respectively) and hake (-0.33, -0.37) (Figure
201 3a) indicating spatial separation in distributions. This confirms the associations among
202 species seen in the factor loadings, with three distinct species-group assemblages being
203 present.

204 Correlation coefficients for the average positive density (Figure 3b) show fewer significant
205 positive or negative relationships among species-groups than for encounter probability,
206 but still evident are the strong association among the roundfish with higher catches of
207 cod are associated with higher catches of haddock (0.58) and whiting (0.47), as well as
208 the two anglerfish species (0.71 for *piscatorius* and 0.44 for *budegassa*) and hake (0.73).
209 Similarly, plaice and sole are closely associated (0.31) and higher catches of one would
210 expect to see higher catches of the other, but also higher catches of some juvenile size
211 classes of roundfish (whiting and haddock) and anglerfish species. Negative association
212 of juvenile megrim, anglerfish (*budegassa*) and hake with adult sole (-0.61, -0.61 and -
213 0.47 respectively), plaice (-0.36 and -0.35 for megrim and hake only) indicate high catches
214 of one can predict low catches of the other successfully.

215 In addition to the average spatial correlations, we also estimate spatiotemporal corre-
216 lations. Spatial population correlations (representing the average correlations between
217 pairs for species-group *x* and species group *y* across all years) are linearly associated
218 with the spatiotemporal population correlations (representing how correlations between
219 species-group *x* and species-group *y* change from year to year), indicating generally pre-
220 dictable relationships between species-groups from one year to the next. This suggests
221 that a positive or negative association between two species-groups is likely to persist
222 from one year to the next, and that species-groups are consistently associated with each
223 other in the catch. The correlation coefficients were 0.59 (0.52 - 0.66) and 0.47 (0.38
224 - 0.55) for encounter probability and positive density respectively. However, a linear re-
225 gression between the spatial correlations and the spatio-temporal correlations shows high

226 variance ($R^2 = 0.36$ and 0.22 respectively), indicating that the scale of these relationships
227 does change from one-year to the next. This would have implications for the predictability
228 of the relationship between catches of one species-group and another when trying to bal-
229 ance catch with quotas in mixed fisheries. It can also be seen in the spatial factor maps
230 that there are subtle differences in spatial patterns in factor loading values from one year
231 to the next (Figures S4 and S5) indicating changes may be driven by temporally changing
232 environmental factors and species behaviour.

233 **Subtle differences in distributions may be important to separate catches within**
234 **groups under the landing obligation** : The analysis shows the interdependence within
235 species-groups of roundfish, flatfish and deeper water species, where catching one species
236 within the group indicates a high probability of catching the other species, which has im-
237 portant implications for how spatial avoidance can be used to support implementation
238 of the EU's landings obligation. If production from mixed fisheries is to be maximised,
239 decoupling catches of species between and within the groups will be key. For example,
240 asking where the maximal separation in the densities of two coupled species is likely to
241 occur? To address this requirement, we map the difference in spatial distribution within a
242 group for each pair of species within a species-groupings for a single year (2015; Figure
243 4).

244 Cod had a more north-westerly distribution than haddock, while cod was more westerly
245 distributed than whiting roughly delineated by the 7° W line (Figure 4a). Whiting appeared
246 particularly concentrated in an area between 51 and 52° N and 5 and 7° W, which can

247 be seen by comparing the whiting distribution with both cod (Figure 4b) and haddock
248 (Figure 4c). For the deeper water species (Figures 4d and 4e), hake are more densely
249 distributed in two areas compared to anglerfishes¹ and megrim (though megrim has a
250 stable density across the modelled area as indicated by the large amount of white space).
251 For anglerfishes and megrim (Figure 4f), anglerfishes have a more easterly distribution
252 than megrim. For the flatfish species plaice and sole (Figure 4g), plaice appear to be
253 more densely distributed along the coastal areas of Ireland and Britain, while sole are
254 more densely distributed in the Southern part of the English Channel along the coast of
255 France.

256 Predicted catch distribution from a “typical” otter trawl gear and beam trawl fishing at three
257 different locations highlights the differences fishing gear makes on catches (Figure 4h).
258 As can be seen, both the gear selectivity and area fished play important contributions to
259 the catch compositions; in the inshore area (location ‘A’) plaice and sole are the two main
260 species in catch reflecting their distribution and abundance, though the otter trawl gear
261 catches a greater proportion of plaice to sole than the beam trawl. The area between
262 Britain and Ireland (location ‘B’) has a greater contribution of whiting, haddock, cod, hake
263 and anglerfishes in the catch with the otter trawl catching a greater proportion of the
264 roundfish, haddock, whiting and cod while the beam trawl catches more anglerfishes
265 and megrims. The offshore area has a higher contribution of megrim, anglerfishes and
266 hake with the otter trawl catching a greater share of hake and the beam trawl a greater
267 proportion of megrim. Megrism dominates the catch for both gears in location ‘C’, reflecting

¹two species combined as they are managed as one

268 its relative abundance in the area.

269 **Addressing the scientific challenges of the landing obligation in mixed fisheries** In
270 application to the Celtic Sea we have identified spatial separation of three distinct species-
271 groupings (roundfish, flatfish and deeper water species) while showing that only subtle
272 differences exist in distributions within species-groups. The differences in catch composi-
273 tions between gears at the same location (Figure 4h) show that changing fishing methods
274 can go some way to affecting catch, yet that differences in catches between locations are
275 likely to be more important. For example, beam trawls fishing at the inshore locations (e.g.
276 location 'A' in Figure 4) are likely to predominately catch plaice and sole, yet switching to
277 the offshore locations (e.g. location 'C') would likely yield greater catches of megrim and
278 anglerfishes. Such changes in spatial fishing patterns are likely to play an important role
279 in supporting implementation of the landings obligation.

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

287 A role that science can play in supporting effectiveness of spatiotemporal avoidance
288 could be to provide probabilistic advice on likely hotspots for species occurrence and

289 high species density which can inform fishing decisions. Previous modelling studies have
290 shown how spatiotemporal models could improve predictions of high ratios of bycatch
291 species to target species^{36–38}, and geostatistical models are well suited to this as they in-
292 corporate spatial dependency while providing for probabilities to be drawn from posterior
293 distributions of the parameter estimates. We posit that such advice could be enhanced
294 by integrating data obtained directly from commercial fishing vessels at a higher temporal
295 resolution, providing real-time forecasts to inform fishing choices that also captures sea-
296 sonal differences in distributions, akin to weather forecasting. Advice informed by a model
297 including a seasonal or real-time component could inform optimal policies for time-area
298 closures, move-on rules or even as informal information to be utilised by fishers directly
299 without the need for costly continuous data collection on environmental parameters, but
300 by using the vessels-as-laboratories approach.

301 An important question for the implementation of the EU’s landing obligation is how far
302 spatial avoidance can go to achieving catch balancing in fisheries. Our model captures
303 differences between location fished for two gear types and their broad scale effect on
304 catch composition, information crucial for managers in implementing the landing obliga-
305 tion. It is likely, however, that this analysis reflects a lower bound on the utility of spatial
306 avoidance as fine-scale behavioural decisions such as time-of-day, gear configuration and
307 location choices can also be used to affect catch^{39,40}. Results of empirical studies under-
308 taken elsewhere^{5,6} suggest limits to the effectiveness of spatial avoidance. Differences
309 in ability to change catch composition have also been observed for different fleets; in the
310 North Sea targeting ability was found to differ between otter and beam trawlers as well as

311 between vessels of different sizes⁴¹.

312 Our framework allows for a quantitative understanding of the broad scale global produc-

313 tion set available to fishers⁴² and thus the extent to which they can alter catch composi-

314 tions while operating in a mixed fishery. Simulations of spatial effort allocation scenarios

315 based on the production sets derived from the model estimates could be used as inputs

316 to fisher behavioural models to allow for identification of the lower bounds of optimum

317 spatial harvest strategies. This would provide managers with information useful for exam-

318 ining trade-offs in quota setting by integrating potential for spatial targeting in changing

319 catch composition, thus provide a scientific contribution to meeting the goal of maximis-

320 ing catches in mixed fisheries within single stock quota constraints⁷. Further, the correla-

321 tions among species could provide information on fisheries at risk of capturing protected,

322 endangered or threatened species such as elasmobranches, and allow identification of

323 areas where there are high ratios of protected to target species.

324 Complex environmental, fishery and community drivers of distribution for groups of species

325 highlights the scale of the challenge in separating catches within the species-groups us-

326 ing spatial management measures. This has important implications for management of

327 the mixed fisheries under the EU landings obligation. Our analysis identifies where it may

328 be easier to separate catches of species (among groups) and where it is more challeng-

329 ing (within groups). We propose that the framework presented in Figures 1-4 provides a

330 viable route to reducing the complexity of highly mixed systems. This can allow informed

331 management discussion over more traditional anecdotal knowledge of single-species dis-

332 tribution in space and time.

333 **Methods**

334 **Model structure:** VAST² implements a delta-generalised linear mixed modelling (GLMM)
335 framework that takes account of spatio-temporal correlations among species-groups through
336 implementation of a spatial dynamic factor analysis (SDFA). Spatial variation is captured
337 through a Gaussian Markov Random Field, while we model random variation among
338 species-groups and years. Covariates affecting catchability (to account for differences
339 between fishing surveys) and density (to account for environmental preferences) can be
340 incorporated for predictions of presence and positive density. The following briefly sum-
341 marises the key methods implemented in the VAST framework. For full details of the
342 model the reader is invited directed to Thorson *et al* 2017 ⁴³.

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

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

is then be described as a linear combination of factors and loadings:

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

343 Where $\theta_c(s, t)$ represents log-density for species c at site s at time t , ψ_j is the coefficient
 344 for factor j , $L_{c,j}$ the loading matrix representing association of species c with factor j and
 345 $\gamma_{k,c} \chi_k(s, t)$ the linear effect of covariates at each site and time ⁴⁴.

346 The factor analysis can identify community dynamics and where species have similar
 347 spatio-temporal patterns, allowing inference of species distributions and abundance of
 348 poorly sampled species through association with other species and allows for computation
 349 of spatio-temporal correlations 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.

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

350 where $p(s_i, c_i, t_i)$ is the predictor for encounter probability for observation i , at location
 351 s for species-group c and time t and $r(s_i, c_i, t_i)$ is similarly the predictor for the positive

352 density. $\beta_*(c_i, t_i)$ is the intercept, $\omega_*(s_i, c_i)$ the spatial variation at location s for factor f , with
 353 $L_\omega(c_i, f)$ the loading matrix for spatial covariation among species-groups. $\varepsilon_*(s_i, c_i, t_i)$ is the
 354 linear predictor for spatio-temporal variation, with $L_\varepsilon(c_i, f)$ the loading matrix for spatio-
 355 temporal covariance among species-groups and $\delta_*(c_i, v_i)$ the contribution of catchability
 356 covariates for the linear predictor with Q_{c_i, v_i} the catchability covariates for species-group
 357 c and vessel v ; * can be either p for probability of encounter or r for positive density.

The Delta-Gamma formulation is then:

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

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

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

370 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:

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

371 Here, $vec[\mathbf{E}_*(t)]$ is the stacked columns of the matrices describing $\varepsilon_*(s, p, t)$ at every loca-
372 tion, species-group and time, \mathbf{R}_* is a correlation matrix for encounter probability or positive
373 catch rates among locations and \mathbf{V}_* a covariance matrix for encounter probability or pos-
374 itive catch rate among species-groups (modelled within the factor analysis). \otimes represents
375 the Kronecker product so that the correlation among any location and species-group can
376 be computed ⁴³.

377 **Incorporating covariates** Survey catchability (the relative efficiency of a gear catching
378 a species-group) was estimated as a fixed effect in the model, $\delta_s(v)$, to account for dif-
379 ferences in spatial fishing patterns and gear characteristics which affect encounter and
380 capture probability of the sampling gear ⁴⁵. Parameter estimates (Figure S10) showed
381 clear differential effects of surveys using otter trawl gears (more effective for round fish
382 species) and beam trawl gears (more effective for flatfish species).

383 No fixed covariates for habitat quality or other predictors of encounter probability or pos-
384 itive density were included. While incorporation may improve the spatial predictive per-
385 formance ⁴³, it was not found to be the case here based on model selection with Akaike

³⁸⁶ Information Criterion (AIC) and Bayesian Information Criterion (BIC).

³⁸⁷ **Parameter estimation** Parameter estimation was undertaken through Laplace approx-
³⁸⁸ imation of the marginal likelihood for fixed effects while integrating the joint likelihood
³⁸⁹ (which includes the probability of the random effects) with respect to random effects. This
³⁹⁰ was implemented using Template Model Builder (TMB;⁴⁶) with computation through sup-
³⁹¹ port by the Irish Centre for High End Computing (ICHEC; <https://www.ichec.ie>)
³⁹² facility.

³⁹³ **Data** The model integrates data from seven fisheries independent surveys taking ac-
³⁹⁴ count of correlations among species-group spatio-temporal distributions and abundances
³⁹⁵ to predict spatial density estimates consistent with the resolution of the data.

³⁹⁶ The model was been fit to nine species separated into adult and juvenile size classes
³⁹⁷ (Table S2) to seven survey series (Table S1) in the Celtic Sea bound by 48° N to 52 ° N
³⁹⁸ latitude and 12 ° W to 2° W longitude (Figure S8) for the years 1990 - 2015 inclusive.

³⁹⁹ The following steps were undertaken for data processing: i) data for survey stations and
⁴⁰⁰ catches were downloaded from ICES Datras (www.ices.dk/marine-data/data-portals/
⁴⁰¹ Pages/DATRAS.aspx) or obtained directly from the Cefas Fishing Survey System (FSS);
⁴⁰² ii) data were checked and any tows with missing or erroneously recorded station informa-
⁴⁰³ tion (e.g. tow duration or distance infeasible) removed; iii) swept area for each of the
⁴⁰⁴ survey tows was estimated based on fitting a GAM to gear variables so that Doorspread
⁴⁰⁵ = s(Depth) + DoorWt + WarpLength + WarpDiameter + SweepLength and a gear specific

406 correction factor taken from the literature⁴⁷; iii) fish lengths were converted to biomass
407 (Kg) through estimating a von bertalanffy length weight relationship, $Wt = a \cdot L^b$, fit to
408 sampled length and weight of fish obtained in the EVHOE survey and aggregated within
409 size classes (adult and juvenile).

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

412 **Model setup** The spatial domain was setup to include 250 knots representing the Gaussian
413 Random Fields. The model was configured to estimate nine factors each to describe
414 the spatial and spatiotemporal encounter probability and positive density parameters, with
415 a logit-link for the linear predictor for encounter probability and log-link for the linear predictor
416 for positive density, with an assumed gamma distribution.

417 Three candidate models were identified, i) a base model where the vessel interaction
418 was a random effect, ii) the base but where the vessel x species effect was estimated
419 as a fixed covariate, iii) with vessel x species effect estimated, but with the addition of
420 estimating fixed density covariates for both predominant habitat type at a knot and depth.

421 AIC and BIC model selection favoured the second model (Table S3). The final model
422 included estimating 130,950 coefficients (1,674 fixed parameters and 129,276 random
423 effect values).

424 **Model validation** Q-Q plots show good fit between the derived estimates and the data for
425 positive catch rates and between the predicted and observed encounter probability (S11,

⁴²⁶ S12). Further, model outputs are consistent with stock-level trends abundances over time
⁴²⁷ from international assessments (S13), yet also provide detailed insight into species co-
⁴²⁸ occurrence and the strength of associations in space and time.

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Author contributions XXXX

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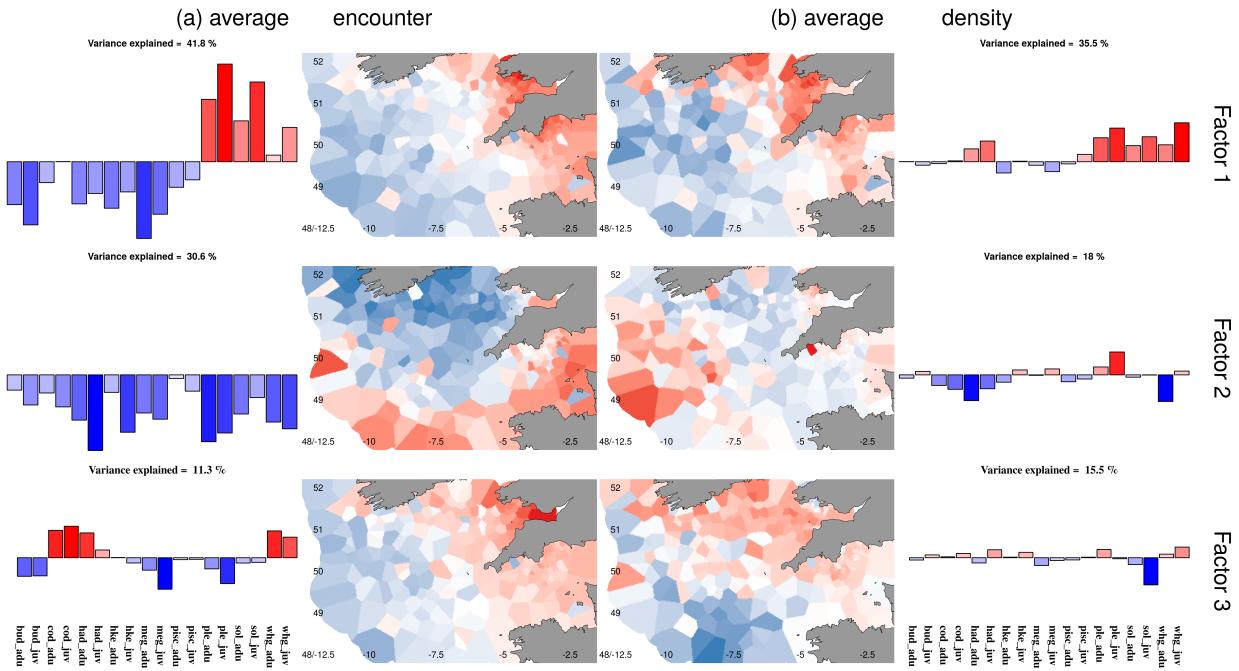


Figure 1: Factor values for the first three factors for (a) Average encounter probability and (b) Average positive density for the species-groups (outer figures) and spatially (inner figures). Red: positive association to the factor, Blue: negative association

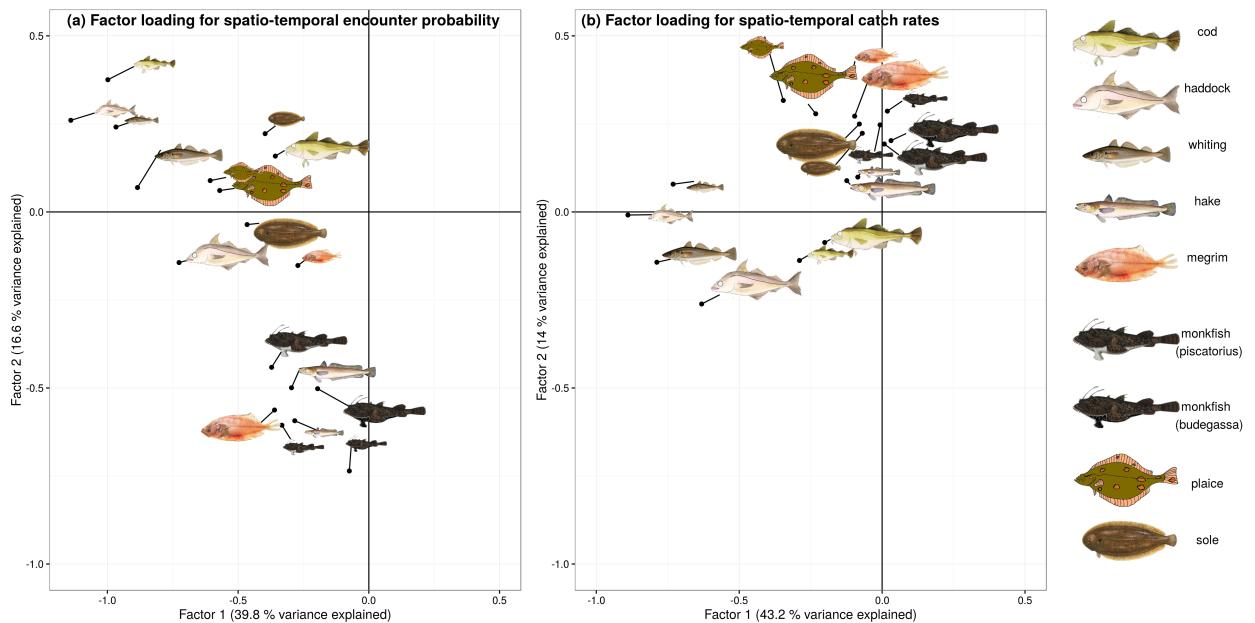


Figure 2: Position of each species-group on the first two axes from the factor analysis for
 (a) spatio-temporal encounter probability and (b) spatio-temporal positive density.

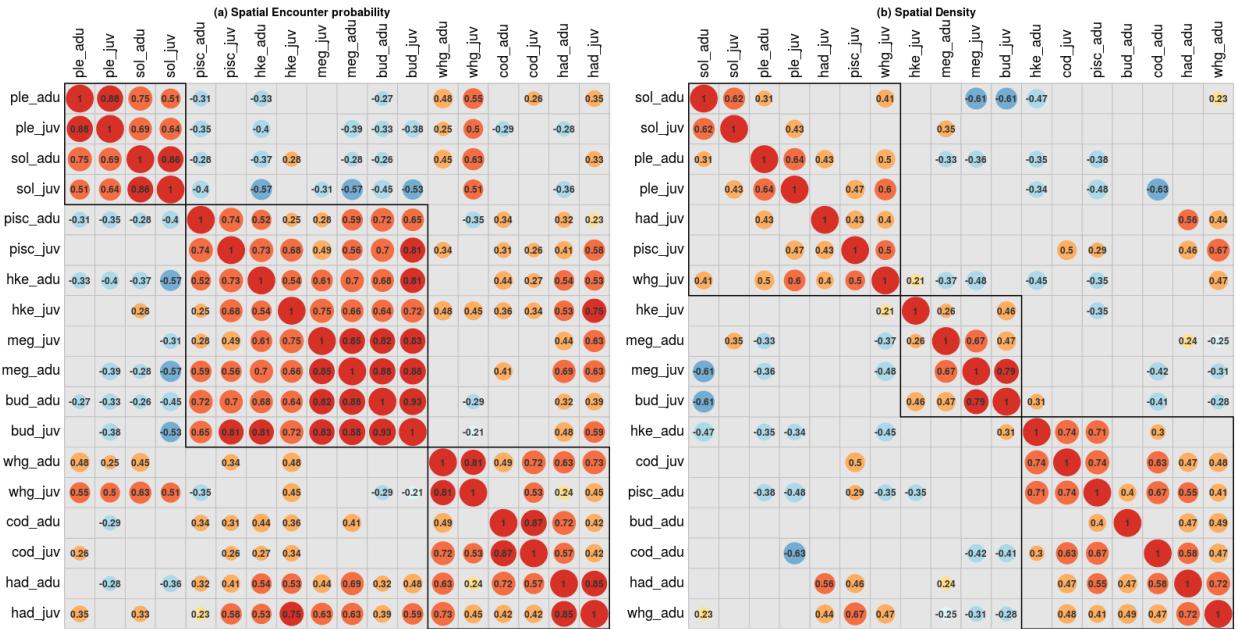


Figure 3: Inter-species correlations for (a) spatial encounter probability over all years and (b) spatial positive density. Species-groups are clustered into three groups based on a hierarchical clustering method with non-significant correlations (the Confidence Interval $[+/- 1.96 * \text{SEs}]$ spanned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

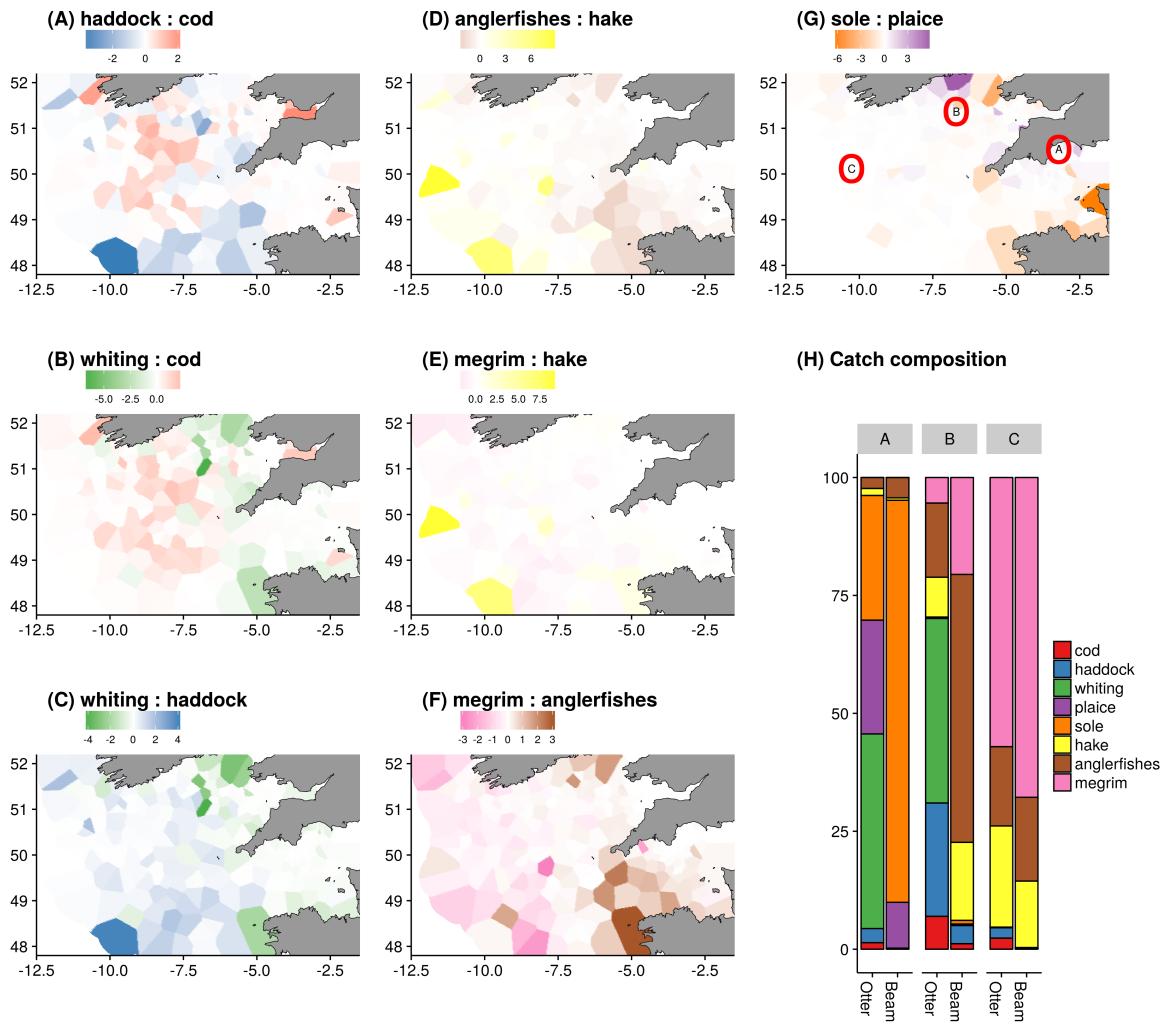


Figure 4: Differences in the standardised spatial density for pairs of species and expected catch rates for two different gears at three different locations in 2015.