Working title: Spatial separation of catches in highly mixed fisheries

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1 **In mixed fisheries overexploitation of weaker stocks results when catches continue in fisheries**

2 **pursuing quota for healthy stocks and these are discarded. As EU fisheries management**

3 **moves to count all fish caught against quota (the 'Landings obligation'), the challenge is to**

4 **catch available quota within new constraints, else lose productivity.**

5 **A mechanism for decoupling exploitation of species caught together is spatial targeting, but**

6 **this remains challenging due to complex fishery dynamics and lack of understanding of spa-**

7 **tiotemporal community dynamics. We apply a joint species distribution model to understand**

8 **how spatial community and fishery dynamics interact to determine species and size composi-**

9 **tion in the highly mixed fisheries of the Celtic Sea. Clear common spatial patterns emerge for**

10 **three distinct species-groups and, while distribution varies inter-annually, the same species-**

11 **groups are consistently found in higher densities together, with more subtle differences within**

12 **species-groups.**

13 **We highlight the importance of dimension reduction techniques to focus management dis-**

14 **cussion on axes of maximal separation in space and time. We propose that spatiotemporal**

15 **modelling of available data is a scientific requirement to address the challenges of managing**

mixed fisheries.

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

A particular challenge in realising increased catches from rebuilt populations is maximising yields from mixed fisheries [5–7]. In mixed fisheries, the predominant type of fishery worldwide, several fish species are caught together in the same net or fishing operation (known as a 'technical interaction'). If managed by individual quotas, and catches do not match available stock quotas, either a vessel must stop fishing when the first quota is reached (the 'choke' species) or overexploitation of the weaker species occurs while fishers continue to catch more healthy species and throw back ('discard') the fish for which they have no quota.

Sustainability of European fisheries has been hampered by this 'mixed fishery problem' for decades with large-scale discarding resulting [8,9]. A paradigm shift is being introduced under the EU Common Fisheries Policy (CFP) reform of 2012 through two significant management changes. First, by 2019 all fish that are caught are due to be counted against the respective stock quota; second,

2

by 2020 all fish stocks must be fished so as to be able to produce their Maximum Sustainable Yield (MSY)[10]. The changes are expected to contribute to attainment of the goal of Good Environmental Status (GES) under the European Marine Strategy Framework Directive (MSFD; [11]) and move Europe towards an ecosystem based approach to fisheries management [12]. Unless fishers can avoid catch of unwanted species they will have to stop fishing when reaching their first restrictive quota. This introduces a potential significant cost to fishers of under-utilised quota[7,13] and provides a strong incentive to mitigate such losses [14,15].

The ability of fishers to align their catch with available quota depends on being able to exploit target species while avoiding unwanted catch. Methods by which fishers can alter their fishing patterns include by switching fishing method (e.g. trawling to netting), changing technical gear characteristics (e.g. introducing escapement panels in nets), or the timing and location of fishing activity [16,17]. Otter trawl gears are known to have higher catch rates of roundfish due to the higher headline and wider sweeps which herd demersal fish into the net. Conversely, beam trawls, which employ chain mesh to 'dig' benthic flatfish species, have higher catch rates for these species [18].

Spatiotemporal management measures (such as time-limited fishery closures) have been applied to reduce unwanted catch with varying degrees of success (e.g. [19–22]) while move-on rules have also been proposed or implemented to influence catch rates of particular vulnerable species in order to reduce or eliminate discards (e.g.[23–25]). However, such measures have generally been targeted at individual species without considering associations and interactions among several species. Highly mixed fisheries are complex with spatial, technological and community interactions combining. The design of spatio-temporal management measures which aim to allow exploitation of healthy

stocks while protecting weaker stocks requires understanding of these interactions at a meaningful scale to managers and fishers. Here, our goal is to develop a framework for understanding these complexities. We do so by implementing a spatio-temporal dimension reduction method and use the results to draw inference on the fishery-community dynamics, creating a framework to identify trends common among species-groups. We use this to describe where spatial measures can contribute to mitigating unwanted catches in mixed fisheries.

Framework for analysing spatio-temporal mixed fisheries interactions We present a framework for analysing how far spatio-temporal avoidance can contribute towards mitigating imbalances in quota in mixed fisheries. We use fisheries-independent survey data to characterise the spatiotemporal dynamics of key components of a fish community by employing a geostatistical Vector Autoregressive Spatiotemporal model (VAST). We implement a factor analysis decomposition to describe trends in spatiotemporal dynamics of the different species as a function of latent variables [26] representing spatial variation (9 factors; which we call 'average' spatial variation) and spatio-temporal variation (9 factors) for encounter probability and positive catch rates (which we call 'positive density') separately [27]. We use the resultant exploratory factor analysis to identify community dynamics and drivers common among 18 species-groups and present results through transformation of the loading matrices using PCA rotation. By describing the species-groups dynamics through underlying contributory spatiotemporal factors we can take account of how the factors contribute to affect catches of the species-groups in mixed fisheries. We use Gaussian Markov Random Fields (GMRFs) to capture spatial and temporal dependence within and among species groups for both encounter probability and positive density[28]. VAST is set in a mixed modelling framework to allow estimation of fixed effects to account for systematic differences driving

4

encounter and catches, such as differences in sampling efficiency (a.k.a. catchability), while random effects capture the spatio-temporal dynamics of the fish community.

Dynamics of Celtic Sea fisheries We use the highly mixed demersal fisheries of the Celtic Sea as a case study. The Celtic Sea is a temperate sea where fisheries are spatially and temporally complex; mixed fisheries are undertaken by several nations using different gear types [29,30]. Close to 150 species have been identified in the commercial catches of the Celtic Sea, with approximately 30 species dominating the catch [31].

We parametrise our spatiotemporal model using catch data from seven fisheries independent surveys undertaken in the Celtic Sea over the period 1990 - 2015 (Table S1) and include nine of the main commercial species: Atlantic cod (*Gadus morhua*), Atlantic haddock (*Melanogrammus aeglefinus*), Atlantic whiting (*Merlangius merlangus*), European Hake (*Merluccius merluccius*), white-bellied anglerfish (*Lophius piscatorius*), black-bellied anglerfish (*Lophius budegassa*), megrim (*Lepidorhombus whiffiagonis*), European Plaice (*Pleuronectes platessa*) and Common Sole (*Solea solea*). These species make up >60 % of landings by towed fishing gears for the area (average 2011 - 2015;[32]). Each species was separated into juvenile and adult size classes based on their legal minimum conservation reference size (Table S2).

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

5

Common average spatial patterns driving species associations A spatial dynamic factor analysis decomposes the dominant spatial patterns driving differences in encounter probability and positive density. The first three factors (after PCA rotation) account for 83.7 % of the between species-group variance in average encounter probability and 69 % of the between species-group variance in average positive density. A clear spatial pattern can been seen both for encounter probability and positive density, with a positive value associated with the first factor in the inshore North Easterly part of the Celtic Sea into the Bristol Channel and Western English Channel, moving to a negative value offshore in the south-westerly waters (Figure 1). The species-group loadings coefficients show plaice, sole and whiting to be positively associated with the first factor for encounter probability while the other species-groups are negatively associated. For average positive density, positive associations are also found for haddock and juvenile cod. This is indicative of a more inshore distribution for these species-groups.

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

On the third factor, there is a positive association with the Easterly waters for encounter probability and negative with the westerly waters. This manifests in the species associations as splitting the roundfish species cod, haddock and whiting which all have a positive association with the third

6

factor for average encounter probability from the rest of the species-groups which have a negative association. Positive density is driven by a North / South split (Figure 1), with positive values in the Northerly areas. Juvenile monkfish (budgessa and piscatorius), cod, juvenile haddock, hake, adult plaice and whiting are also positively associated with the third factor towards the North while adult monkfish (budegassa and piscatorius), adult haddock, megrims, juvenile plaice and sole are negatively associated reflecting their more southerly distribution (Figure 1).

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

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

7

141 tors of species distributions has been identified in other marine species distribution models [33]; the

142 advantage to the approach taken here is that, where such data is unavailable at appropriate spa-

143 tial resolution, the spatial factor analysis can adequately characterise these influences on species

144 dynamics.

145 **Changes in spatial patterns over time, but stability in species dynamics** While there are clear

146 spatial patterns in the factor coefficients describing differences in average encounter probability

147 and positive density (Figure 1), the inter-annual differences in factor coefficients show less struc-

148 ture (Figures S5, S6). These inter-annual differences are important as they reflect the ability of

149 fishers to predict where they can target species from one year to the next, without which it may be

150 difficult to avoid unwanted catch.

151 While spatio-temporal factor coefficients did not show consistent trends from year to year, among

152 species-groups there were clear relationships (Figure 2). The same factors appear to drive spatio-

153 temporal distributions of megrim, anglerfish species and hake (the deeper water species, species-

154 grouping negatively associated with the second axes of Figure 2a) and the roundfish and flatfish

155 (species-grouping more positively associated with the second axes of Figure 2a). For spatio-

156 temporal positive density (Figure 2b) cod, haddock and whiting (the roundfish species) are sep-

157 arated from plaice, sole (the flatfish) and deeper water species. As such, it can be predicted that

158 higher catches of a species within a group (e.g. cod in roundfish) would be expected when catch-

159 ing another species within that group (e.g. whiting in roundfish). This suggests that one or more

160 common environmental drivers are influencing the distributions of the species groups, and that

161 driver differentially affects the species groups. Temperature is often included as a covariate in

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species distribution models, but was found not to contribute to the variance in the first factor values (Figure S6, correlations for either encounter probability or positive density ~ 0).

Spatial correlations show three distinct species-group associations In order to gain greater insight into the community dynamics we considered how species-groups covary in space and time through among species-group correlations. 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-groups, 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. 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) 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 positive or negative relationships among species-groups then for encounter probability, but still evident are the strong association among the roundfish with higher catches of cod are associated with

higher catches of haddock (0.58) and whiting (0.47), as well as the two anglerfish species (0.71 for piscatorius and 0.44 for budegassa) and hake (0.73). Similarly, plaice and sole are closely associated (0.31) and higher catches of one would expect to see higher catches of the other, but also higher catches of some juvenile size classes of roundfish (whiting and haddock) and anglerfish species. Negative association of juvenile megrim, anglerfish (budegassa) and hake with adult sole (-0.61, -0.61 and -0.47 respectively), plaice (-0.36 and -0.35 for megrim and hake only) indicate high catches of one can predict low catches of the other successfully.

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

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temporally changing environmental factors.

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

Figure 4a indicates that cod had a more North-westerly distribution than haddock, while cod was more westerly distributed than whiting roughly delineated by the $7°$ W line. Whiting appeared particularly concentrated in an area between 51 and 52 $°$ N and 5 and 7 $°$ W, which can be seen by comparing the whiting distribution with both cod (Figure 4b) and haddock (Figure 4c). For the deeper water species Figures 4d and 4e indicate that hake are more densely distributed in two areas compared to anglerfishes[1] and megrim (though megrim has a stable density across the modelled area as indicated by the large amount of white space). For anglerfishes and megrim (Figure 4f), anglerfishes have a more easterly distribution than megrim. For the flatfish species plaice and sole (Figure 4g), plaice appear to be more densely distributed along the coastal areas of Ireland and

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[1]two species combined as they are managed as one

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Britain, while sole are more densely distributed in the Southern part of the English Channel along the coast of France.

Figure 4h shows the predicted catch distribution from a "typical" Otter trawl gear and Beam trawl gear fishing at three different locations. As can be seen, both the gear selectivity and area fished play important contributions to the catch compositions; in the inshore area (location 'A') plaice and sole are the two main species in catch reflecting their distribution and abundance, though the otter trawl gear catches a greater proportion of plaice to sole than the beam trawl. The area between Britain and Ireland (location 'B') has a greater contribution of whiting, haddock, cod, hake and anglerfishes in the catch with the Otter trawl catching a greater proportion of the roundfish, haddock, whiting and cod while the beam trawl catches more anglerfishes and megrims. The offshore area has a higher contribution of megrim, anglerfishes and hake with the Otter trawl catching a greater share of hake and the Beam trawl a greater proportion of megrim. Megrim dominates the catch for both gears in location 'C', reflecting its relative abundance in the area.

Application of framework to support implementation landing obligation in mixed fisheries : In application to the Celtic Sea we have identified spatial separation of three distinct species-groupings (roundfish, flatfish and deeper water species) while showing that only subtle differences in distributions within species-groups. The differences in catch compositions between gears at the same location in Figure 4h show that changing fishing methods can go some way to affecting catch, yet that differences in catches between locations are likely to be more important. For example, beam trawls fishing at the inshore locations (e.g. location 'A' in Figure 4) are likely to predominately catch plaice and sole, yet switching to the offshore locations (e.g. location 'C')

would likely yield greater catches of megrim and anglerfishes. Such changes in spatial fishing patterns are likely to play an important role in supporting implementation of the landings obligation.

More challenging is within-group spatial separation due to significant overlap in spatial distributions for the species, driven by common environmental factors. Subtle changes may yield some benefit in changing catch composition, yet the outcome is likely to be much more difficult to predict. For example, subtle differences in the distribution of cod, haddock and whiting can be seen in Figures 4a-c, showing spatial separation of catches is much more challenging and likely to need to be supported by other measures such as changes to the selectivity characteristics of gear (e.g. [34]).

A role that science can play in supporting effectiveness of spatiotemporal avoidance could be to provide probabilistic advice on likely hotspots for species occurrence and high species density which can inform fishing decisions. Previous modelling studies have shown how spatiotemporal models could improve predictions of high ratios of bycatch species to target species [35–37], and geostatistical models are well suited to this as they incorporate spatial dependency while providing for probabilities to be drawn from posterior distributions of the parameter estimates. We posit that such advice could be enhanced by integrating data obtained directly from commercial fishing vessels at a higher temporal resolution, providing real-time forecasts to inform fishing choices that also captures seasonal differences in distributions, akin to weather forecasting.

An important question for the implementation of the EU's landing obligation is how far spatial avoidance can go to achieving catch balancing in fisheries. Our model captures differences between location fished for two gear types and their broad scale effect on catch composition; information which could be used to inform decisions on the contribution spatial avoidance can make

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in implementing the landing obligation. However, it likely the analysis reflects a lower bound on the utility of spatial avoidance as fine scale behavioural decisions such as time-of-day, gear configuration and location choices can also be used to affect catch[38,39]. Results of empirical studies undertaken elsewhere[5,6] suggest limits to the effectiveness of spatial avoidance and our framework could be used to simulate different fishing effort scenarios to identify lower bounds for optimum spatial avoidance[40] to support management decisions[7]. Identifying the limits of spatial targeting and avoidance could support scientific contribution to meeting the goal of maximising catches in mixed fisheries within single stock quota constraints. It may also inform the extent to which measures such as gear changes and time-area closures are needed to support transition to the new management system.

Complex environmental, fishery and community drivers of distribution for groups of species highlights the scale of the challenge in separating catches within the species-groups using spatial management measures. This has important implications for management of the mixed fisheries under the EU landings obligation and our analysis identifies where it may be easier to separate catches of species (among groups) and where it is more challenging (within groups). The framework we propose reduces the complexity of the system to it's major components and thus allows informed management discussion over more traditional anecdotal knowledge of single-species distribution in space and time.

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Methods

Model structure: VAST[2] implements a delta-generalised linear mixed modelling (GLMM) frame-

work that takes account of spatio-temporal correlations among species-groups through implemen-

tation of a spatial dynamic factor analysis (SDFA). Spatial variation is captured through a Gaussian

Markov Random Field, while we model random variation among species-groups and years. Co-

variates affecting catchability (to account for differences between fishing surveys) and density (to

account for environmental preferences) can be incorporated for predictions of presence and positive

density. The following briefly summarises the key methods implemented in the VAST framework.

For full details of the model the reader is invited directed to Thorson *et al* 2017 [41].

SDFA: A spatial dynamic factor analysis incorporates advances in joint dynamic species models
[41] to take account of associations among species-groups by modelling response variables as a mul-

tivariate process. This is achieved through implementing a factor analysis decomposition where

common latent trends are estimated so that the number of common trends (M) is less than the

number of species-groups (N) modelled ($1 \leq N \leq M$). 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 be described as a linear combination

of factors and loadings:

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

Where $\theta_c(s,t)$ represents log-density for species c at site s at time t, ψ_j is the coefficient for factor

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

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295 j, $L_{c,j}$ the loading matrix representing association of species c with factor j and $\gamma_{k,c}\chi_k(s,t)$ the

296 linear effect of covariates at each site and time [42].

297 The factor analysis can identify community dynamics and where species have similar spatio-

298 temporal patterns, allowing inference of species distributions and abundance of poorly sampled

299 species through association with other species and allows for computation of spatio-temporal cor-

300 relations among species-groups [42].

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;

$$
\begin{aligned}
logit[p(s_i, c_i, t_i)] = \beta_p(c_i, t_i) + \sum_{f=1}^{n_\omega} L_\omega(c_i, f)\omega_p(s_i, f) + \sum_{f=1}^{n_\varepsilon} L_\varepsilon(c_i, f)\varepsilon_p(s_i, f, t_i) + \\
\sum_{v=1}^{n_v} \delta_p(v)Q_p(c_i, v_i)
\end{aligned}
\tag{2}
$$

and positive catch rates modelling using a gamma- distribution [27].

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

301 where $p(s_i, c_i, t_i)$ is the predictor for encounter probability for observation i, at location s for

302 species-group c and time t and $r(s_i, c_i, t_i)$ is similarly the predictor for the positive density. $\beta_*(c_i, t_i)$

303 is the intercept, $\omega_*(s_i, c_i)$ the spatial variation at location s for factor f, with $L_\omega(c_i, f)$ the load-

304 ing matrix for spatial covariation among species-groups. $\varepsilon_*(s_i, c_i, t_i)$ is the linear predictor for

305 spatio-temporal variation, with $L_\varepsilon(c_i, f)$ the loading matrix for spatio-temporal covariance among

16

species-groups and $\delta_*(c_i, v_i)$ the contribution of catchability covariates for the linear predictor with Q_{c_i,v_i} the catchability covariates for species-group c and vessel v; $*$ can be either p for probability of encounter or r for positive density.

The Delta-Gamma formulation is then:

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

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

Spatio-temporal variation: The spatiotemporal variation is modelled using Gaussian Markov Random Fields (GMRF) where data is associated to nearby locations through a Matérn covariance function with the parameters estimated within the model. Here, the correlation decays smoothly over space the further from the location and includes geometric anisotropy to reflect the fact that correlations may decline in one direction faster than another (e.g. moving offshore) [28]. The best fit estimated an anisotropic covariance where the correlations were stronger in a North-East - South-West direction, extending approximately 97 km and 140 km before correlations for encounter probability and positive density reduced to <10 %, respectively (Figure S9). Incorporating the spatiotemporal correlations among and within species-groups provides more efficient use of the data as inference can be made about poorly sampled locations from the covariance structure.

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

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that:

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

321 Here, $vec[\mathbf{E}_*(t)]$ is the stacked columns of the matrices describing $\varepsilon*(s, p, t)$ at every location,

322 species-group and time, $\mathbf{R}_*$ is a correlation matrix for encounter probability or positive catch rates

323 among locations and $\mathbf{V}_*$ a covariance matrix for encounter probability or positive catch rate among

324 species-groups (modelled within the factor analysis). $\otimes$ represents the Kronecker product so that

325 the correlation among any location and species-group can be computed [41].

326 ***Incorporating covariates*** Survey catchability (the relative efficiency of a gear catching a species-

327 group) was estimated as a fixed effect in the model, $\delta_s(v)$, to account for differences in spatial

328 fishing patterns and gear characteristics which affect encounter and capture probability of the sam-

329 pling gear [43]. Parameter estimates (Figure S10) showed clear differential effects of surveys using

330 otter trawl gears (more effective for round fish species) and beam trawl gears (more effective for

331 flatfish species).

332 No fixed covariates for habitat quality or other predictors of encounter probability or positive den-

333 sity were include. While incorporation may improve the spatial predictive performance [41], it was

334 not found to be the case here based on model selection with Akaike Information Criterion (AIC)

335 and Bayesian Information Criterion (BIC).

336 ***Parameter estimation*** Parameter estimation was undertaken through Laplace approximation of

337 the marginal likelihood for fixed effects while integrating the joint likelihood (which includes the

338 probability of the random effects) with respect to random effects. This was implemented using

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Template Model Builder (TMB; [44]) with computation through support by the Irish Centre for High

End Computing (ICHEC; https://www.ichec.ie) facility.

Data The model integrates data from seven fisheries independent surveys taking account of corre-

lations among species-group spatio-temporal distributions and abundances to predict spatial den-

sity estimates consistent with the resolution of the data.

The model was been fit to nine species separated into adult and juvenile size classes (Table S2) to

seven survey series (Table S1) in the Celtic Sea bound by 48° N to 52 ° N latitude and 12 ° W to

2° W longitude (Figure S8) for the years 1990 - 2015 inclusive.

The following steps were undertaken for data processing: i) data for survey stations and catches

were downloaded from ICES Datras (www.ices.dk/marine-data/data-portals/Pages/

DATRAS.aspx) or obtained directly from the Cefas Fishing Survey System (FSS); ii) data were

checked and any tows with missing or erroneously recorded station information (e.g. tow duration

or distance infeasible) removed; iii) swept area for each of the survey tows was estimated based

on fitting a GAM to gear variables so that Doorspread = s(Depth) + DoorWt + WarpLength +

WarpDiameter + SweepLength and a gear specific correction factor taken from the literature [45]; iii)

fish lengths were converted to biomass (Kg) through estimating a von bertalanffy length weight

relationship, $Wt = a \cdot L^b$, fit to sampled length and weight of fish obtained in the EVHOE survey

and aggregated within size classes (adult and juvenile).

The final dataset comprised of estimates of catches (including zeros) for each station and species-

group and estimated swept area for the tow.

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

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

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

Total words:

Abstract: 182

Intro: 624

Outline: 223

Case study desc: 229

Results 1: 636

Results 2: 252

Results 3: 568

Discussion: 461

Conclusions: 635

Methods: 1430

TOTAL: 5240

Total - abstract 5058

Figures: 4

References: 45

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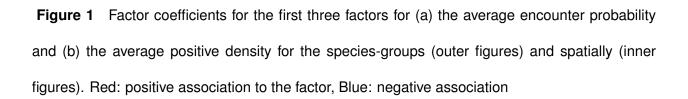
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Competing Interests   The authors declare that they have no competing financial interests.

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Figure 1 Factor coefficients for the first three factors for (a) the average encounter probability and (b) the 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 * 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