Spatial separation of catches in highly mixed fisheries

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Mixed fisheries capture a mix of species at the same time and are a dominant type of fishery worldwide. Overexploitation in mixed fisheries occurs when catches continue for available quota species while low quota species are discarded. As EU fisheries management moves to count all fish caught against quota (the 'landings obligation'), the challenge is to catch available quota within new constraints, else lose productivity. A mechanism for decoupling exploitation of species caught together is spatial targeting, but this remains challenging due to complex fishery and population dynamics in space and time. How far spatial targeting can go to practically separate species is often unknown and anecdotal. Here we develop a dimension-reduction framework based on joint species distribution modelling (spatial dynamic factor analysis) to understand how spatial community and fishery dynamics interact to determine species and size composition. In the example application to the highly mixed fisheries of the Celtic Sea, clear common spatial patterns emerge for three distinct species-groups and, while distribution varies inter-annually, the same species-groups are consistently found in higher densities together, with more subtle differences within

species-groups - where spatial separation may not be practically possible. ~~The results highlight both opportunities for and limitations of the ability to spatiotemporally separate catches.~~ We highlight the importance of dimension reduction techniques to focus management discussion on axes of maximal separation in space and time. We propose that spatiotemporal modelling of available data is a scientific necessity to address the pervasive and nuanced challenges of managing mixed fisheries.

Mixed fisheries and the EU landings obligation ~~Recent~~ Efforts to reduce exploitation rates in commercial fisheries have begun the process of rebuilding depleted fish populations [1]. Improved fisheries management ~~has the potential to~~ can 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 in supporting future food security [4] ~~and~~[coilin] ~~there~~ necessitating that~~remains a need to ensure~~[coilin] 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 [8]. There is~~, therefore,~~ a pressing need for scientific tools which simplify the complexities of mixed fisheries to help avoid discarding~~managers~~

~~and fishers maximise catches~~[coilin].

Sustainability of European fisheries has been hampered by this ‘mixed fishery problem’ for decades with large-scale discarding resulting [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, 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]~~[coilin].

~~Societal objectives for fisheries to achieve MSY across ecosystem components are paralleled by Individual fishers goals continuance of traditional practices.~~ ~~Under the new policy,~~ 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] and provides a strong incentive to mitigate such losses[13]. 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~~ either 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[14]. ~~For example, 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 while beam trawls employ chain mesh to seabed[15].~~

Spatiotemporal management measures ~~(such as time-limited fishery closures)~~ have been applied to reduce unwanted catch with varying degrees of success[16,17]. 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 high quota stocks while protecting low quota stocks requires understanding of these interactions at a scale meaningful 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. We use this to describe the potential for and limitations of~~where~~[coilin] spatial measures to~~can contribute to~~[coilin] mitigate~~ing~~ unwanted catches in highly 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 [18] 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 [19]. By describing the species dynamics through underlying contributory spatiotemporal factors we can take account of how the factors contribute to affect catches of the species 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[20]. ~~VAST is set in a mixed modelling framework to allow estimation of~~ Fixed effects ~~to~~ account for systematic differences driving 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 [21,22]. Close to 150 species have been identified in the commercial catches of the Celtic Sea, with approximately 30 species dominating the catch [23].

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 (see Table S2, Figure 2) ~~: 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 budegas* megrim (*Lepidorhombus whiffiagonis*), European Plaice (*Pleuronectes platessa*) and Common Sole (*Solea solea*). These species~~ which make up $>$60 % of landings by towed fishing gears for the area (average 2011 - 2015;[24]). 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.~~[coilin]

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 variance in average encounter probability and 69% of the between species 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 loadings coefficients show plaice, sole and whiting to be positively associated with the first factor for encounter probability while the other species 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.~~

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 values for the second factor indicate there are positive associations for juvenile monkfish (*L. 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~~ splits~~ting~~ the roundfish species cod, haddock and whiting which all have a positive association with the third factor for average encounter probability from the rest of the species ~~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 (*L. budgessa* and *L. piscatorius*), cod, juvenile haddock, hake, adult plaice and whiting are also positively associated with the third factor towards the north while adult monkfish (*L. budgessa* and *L. 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),~~[brutus] ~~A random forest classification tree assigned with 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 (random forest classification tree).~~[brutus] ~~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.~~[brutus] ~~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 predictors of species distributions has been, as identified in other marine species distribution models~~ [25]~~; the advantage to the approach taken here is that, where such data is unavailable at appropriate spatial resolution, the spatial factor analysis can adequately characterise these influences on species spatial dynamics.~~[brutus]

Time varying species distributions, but stability within species groups~~**Changes in spatial patterns over time, but stability in species dynamics**~~[Paul] ~~While there are clear spatial patterns in the factor coefficients describing differences in average (over time) encounter probability and positive density (Figure 1),~~ The inter-annual differences in factor coefficients show less structure (Figures S5, S6). These inter-annual differences are important as they reflect the ability of fishers to predict where they can target species from one year to the next~~, without which it may be difficult to avoid unwanted catch~~. ~~There were, however, While spatio-temporal factor coefficients did not show consistent trends from year to year across all species,~~ Common patterns in spatiotemporal factor coefficients among species ~~there were clear relationships (Figure 2)~~ ~~. The same factors appear to~~ drive spatiotemporal distributions of megrim, anglerfish species and hake (the deeper water species, species-group negatively associated with the second axes of Figure 2a) and the roundfish and flatfish (species-group more positively associated with the second axes of Figure 2a). For spatio-temporal positive density (Figure 2b) cod, haddock and whiting (the roundfish species) are separated from plaice, sole (the flatfish) and deeper water species. ~~As such,~~ ~~From this it can be predicted that higher catches of a species within a group (e.g. cod in roundfish) would be expected when catching another species within that group (e.g. whiting in roundfish),~~ ~~. This suggesting that one or more common environmental drivers are influencing the distributions of the species groups, and that driver differentially affects the species groups, but this could not be explained by temperature~~[brutus] ~~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).~~[brutus]

Three clusters of species show similar spatial patterns To~~In order to~~[coilin] gain greater insight into the community dynamics we considered how species covary in space and time through among species 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 (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~~ and 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)~~ showing strong intra-group correlations indicating spatial separation in distributions. This confirms the associations among species seen in the factor loadings, with three distinct species-group assemblages being present. This is also evident in correlation coefficients for the average positive density, with strong associations among the roundfish (Figure 3b) ~~show fewer significant positive or negative relationships among species than 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 *x* and species *y* across all years) are linearly associated with the spatiotemporal population correlations (representing how correlations between species *x* and species *y* change from year to year), indicating generally predictable relationships between species from one year to the next. This suggests that a positive or negative association between two species is likely be persist from one year to the next, and that species 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 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 temporally changing environmental factors and species behaviour.~~

Subtle differences in distributions may be important to separate catches within groups ~~under the landing obligation~~[coilin] : ~~The analysis shows the interdependence within the 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.~~ [coilin]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-group for a single year (2015; Figure 4). This would facilitate discussion on maximal separation, for example, between difficult to separate species such as haddock and whiting (Figure 4c).

~~Cod had a more north-westerly distribution than haddock, while cod was more westerly distributed than whiting roughly delineated by the 7° W line (Figure 4a). Whiting appeared particularly concentrated in an area between 51 and 52 $^\circ$ N and 5 and 7 $^\circ$ 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), hake are more densely distributed in two areas compared to anglerfishes 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 Britain, while sole are more densely distributed in the Southern part of the English Channel along the coast of France.~~

Predicted catch distribution from a “typical” otter trawl gear and beam trawl fishing at three different locations highlights the differences fishing gear and location makes on catches (Figure 4h). ~~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.

Addressing the scientific challenges of the landing obligation in mixed fisheries ~~In application to the Celtic Sea~~ We have identified spatial separation of three distinct species-groups (roundfish, flatfish and deeper water species) while showing that only subtle differences exist in distributions within species-groups. The differences in catch compositions between gears at the same location (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. [26]).

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 [27–29], 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~~. Advice informed by ~~a model including~~ a seasonal or real-time component could inform optimal policies for time-area closures, move-on rules or even as informal information to be utilised by fishers directly without being reliant on costly continuous data collection on environmental parameters~~, but by using the vessels-as-laboratories approach~~.

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 crucial for managers in implementing the landing obligation~~. It is likely~~, however, that~~ this analysis reflects a lower bound on ~~the utility of spatial~~[coilin] avoidance as fine-scale behavioural decisions such as time-of-day, gear configuration and location choices can also be used to affect catch[30,31]. Results of empirical studies undertaken elsewhere[5,6] suggest limits to the effectiveness of spatial avoidance. Differences in ability to change catch composition have also been observed for different fleets; in the North Sea targeting ability was found to differ between otter and beam trawlers as well as between vessels of different sizes[32].

~~Our framework allows for a quantitative understanding of the broad scale global production set available to fishers[33] and thus the extent to which they can alter catch compositions while operating~~

~~in a mixed fishery. Simulations of spatial effort allocation scenarios based on the production sets derived from the model estimates could be used as inputs to fisher behavioural models to allow for identification of the lower bounds of optimum spatial harvest strategies. This would provide managers with information useful for examining trade-offs in quota setting by integrating potential for spatial targeting in changing catch composition, thus provide a scientific contribution to meeting the goal of maximising catches in mixed fisheries within single stock quota constraints[7]. Further, the correlations among species could provide information on fisheries at risk of capturing protected, endangered or threatened species such as elasmobranches, and allow identification of areas where there are high ratios of protected to target species.~~

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. Our analysis identifies where it may be easier to separate catches of species (among groups) and where it is more challenging (within groups). We propose that the framework presented in Figures 1-4 provides a viable route to reducing the complexity of highly mixed systems. This can allow informed management discussion over more traditional anecdotal knowledge of single-species distribution in space and time.

Methods

Model structure: VAST[1] implements a delta-generalised linear mixed modelling (GLMM) framework that takes account of spatio-temporal correlations among species through implementation of

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

a spatial dynamic factor analysis (SDFA). Spatial variation is captured through a Gaussian Markov Random Field, while we model random variation among species and years. Covariates 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 [34].

SDFA: A spatial dynamic factor analysis incorporates advances in joint dynamic species models [34] 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 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 j, $L_{c,j}$ the loading matrix representing association of species c with factor j and $\gamma_{k,c}\chi_k(s,t)$ the linear effect of covariates at each site and time [35].

The factor analysis can identify community dynamics and where species have similar spatio-temporal patterns, allowing inference of species distributions and abundance of poorly sampled species through association with other species and allows for computation of spatio-temporal correlations among species [35].

We use the resultant factor analysis is used to identify community dynamics and drivers common among 18 species and results presented through transformation of the loading matrices using PCA rotation[brutus].

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;

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

and positive catch rates modelling using a gamma- distribution [19].

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

where $p(s_i, c_i, t_i)$ is the predictor for encounter probability for observation i, at location s for species 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 intercept, $\omega_*(s_i, c_i)$ the spatial variation at location s for factor f, with $L_\omega(c_i, f)$ the loading matrix for spatial covariation among species. $\varepsilon_*(s_i, c_i, t_i)$ is the linear predictor for spatio-temporal variation, with $L_\varepsilon(c_i, f)$ the loading matrix for spatio-temporal covariance among species 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 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) [20]. 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 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 that:

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

Here, $vec[\mathbf{E}_*(t)]$ is the stacked columns of the matrices describing $\varepsilon*(s,p,t)$ at every location, species and time, $\mathbf{R}_*$ is a correlation matrix for encounter probability or positive catch rates among locations and $\mathbf{V}_*$ a covariance matrix for encounter probability or positive catch rate among species (modelled within the factor analysis). $\otimes$ represents the Kronecker product so that the correlation among any location and species can be computed [34].

Incorporating covariates Survey catchability (the relative efficiency of a gear catching a species) was estimated as a fixed effect in the model, $\delta_s(v)$, to account for differences in spatial fishing patterns and gear characteristics which affect encounter and capture probability of the sampling gear [36]. Parameter estimates (Figure S10) showed clear differential effects of surveys using otter trawl gears (more effective for round fish species) and beam trawl gears (more effective for flatfish species).

No fixed covariates for habitat quality or other predictors of encounter probability or positive density were included. While incorporation may improve the spatial predictive performance [34], it was not found to be the case here based on model selection with Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC).

Parameter estimation Parameter estimation was undertaken through Laplace approximation of the marginal likelihood for fixed effects while integrating the joint likelihood (which includes the probability of the random effects) with respect to random effects. This was implemented using Template Model Builder (TMB; [37]) 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 correlations among species spatio-temporal distributions and abundances to predict spatial density 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 [38]; 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 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.

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Author contributions XXXX

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

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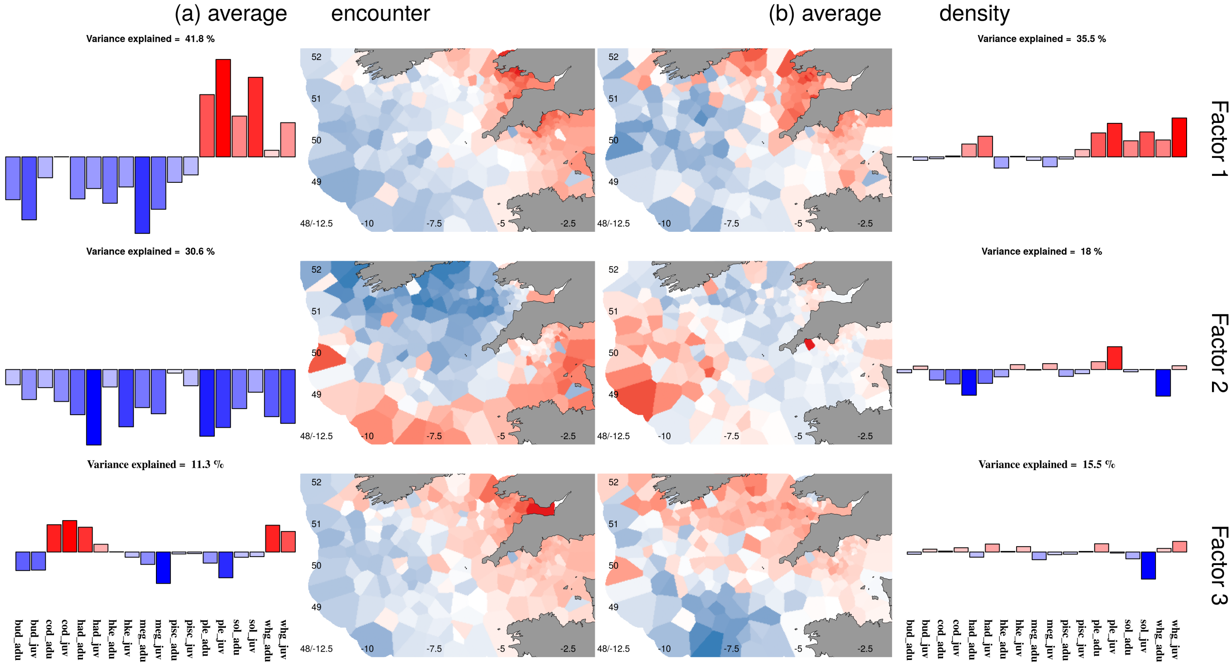

Figure 1: Factor values for the first three factors for (a) Average encounter probability and (b) Average positive density for the species (outer figures) and spatially (inner figures). Red: positive association to the factor, Blue: negative association

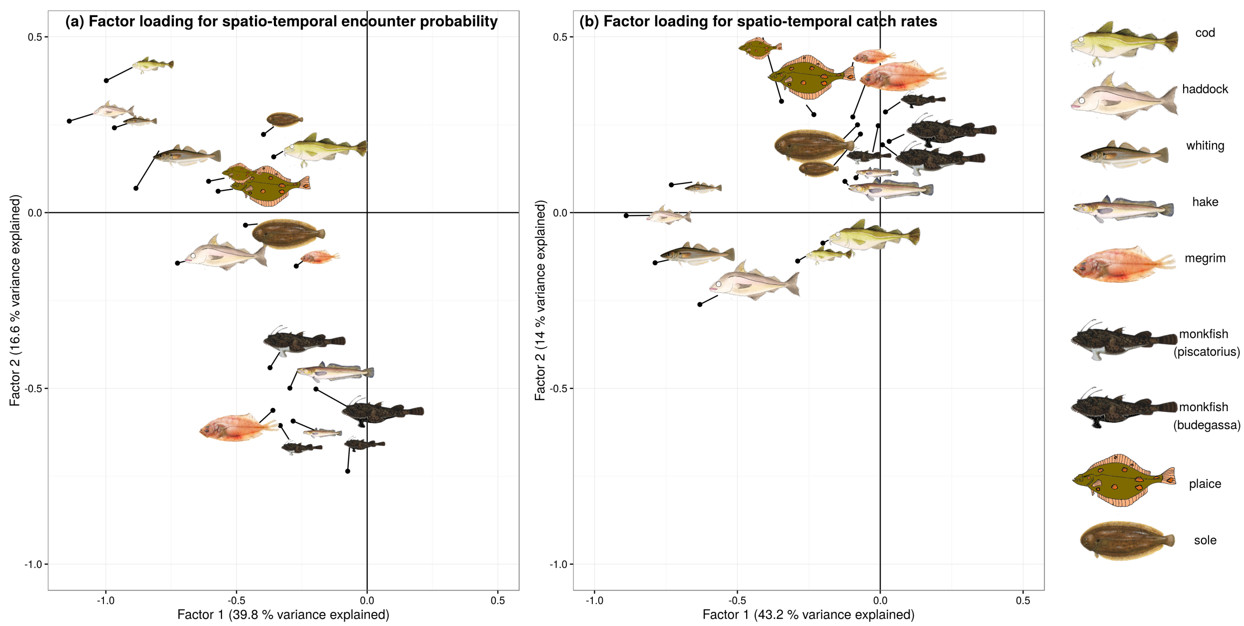

Figure 2: Position of each species on the first two axes from the factor analysis for (a) spatio-temporal encounter probability and (b) spatio-temporal positive density.

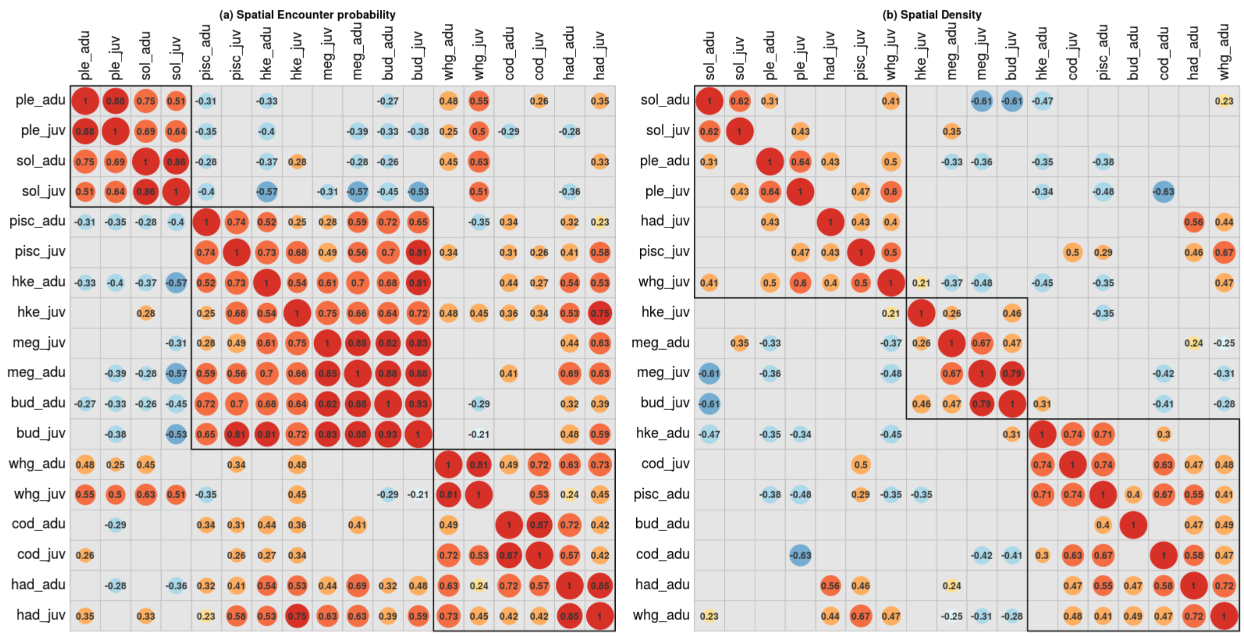

Figure 3: Inter-species correlations for (a) spatial encounter probability over all years and (b) spatial positive density. Species are clustered into three groups based on a hierarchical clustering method with non-significant correlations (the Confidence Interval [+- 1.96 * SEs] spanned zero) left blank.

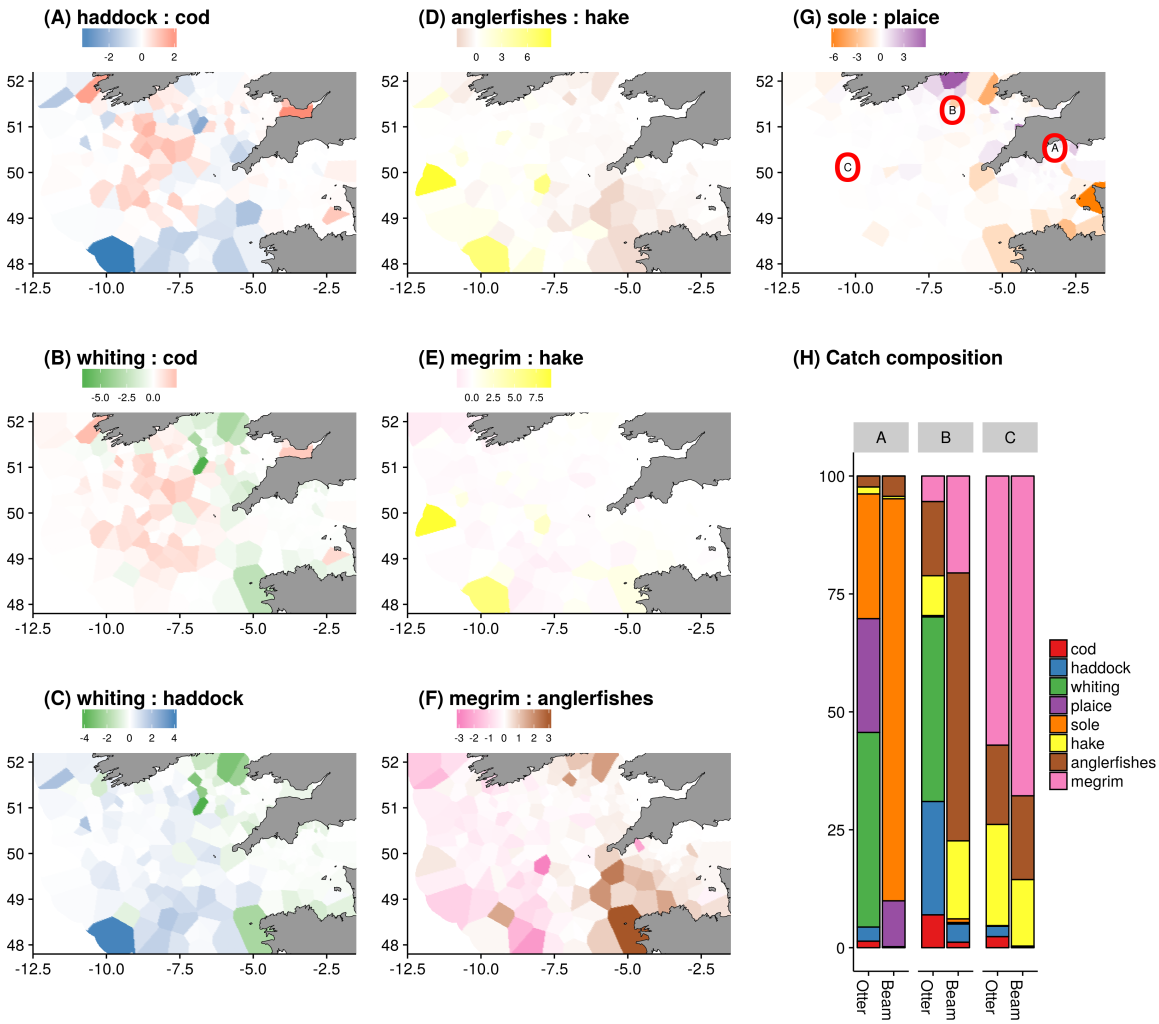

Figure 4: Differences in the standardised spatial density for pairs of species and expected catch rates for two different gears at three different locations in 2015.