Working title: Spatial separation of catches in highly mixed fisheries

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[INCLUDE REFERENCES] Mixed fisheries have resulted in overexploitation of weaker stocks as over-quota catches continue in fisheries pursuing available quota of healthy stocks. As EU fisheries management moves to a system where all fish caught are counted against the quota (the 'Landings obligation'), from 2019 the challenge will be to catch available quota within the new constraints. Failure to achieve this will result in lower production as quota for healthier stocks remains uncaught in order to protect the weaker stocks. Consequently, decoupling exploitation of species caught together in mixed fisheries has become a major goal for fisheries sustainability. A potential mechanism for decoupling exploitation is spatial targeting, but this remains challenging due to complex fishery dynamics and a lack of understanding of community dynamics at fine spatial and temporal scales. We develop a joint species distribution model to understand how spatial community and fishery dynamics interact to determine species and size composition in the highly mixed fisheries of the Celtic Sea.

Clear common patterns for spatial distribution patterns emerge for three species groups commonly targeted (roundfish(gadoids??), flatfish and shelf species) and, while abundance varies inter-annually, the same species groups are commonly found in higher densities together

driven by the same environmental factors (e.g. ??). More subtle differences in distribution are found within a species group, which suggest more limited scope to adjust catch to species composition. Here we highlight the importance of dimension reduction techniques to focus management discussion on axes of maximal separation in space and time.

Common environmental drivers of distribution for groups of species highlights the scale of the challenge in separating catches within the species-groups using spatial management measures, having important implications for management of the mixed fisheries under the EU landings obligation. [FINAL PARAGRAPH NEEDS WORK. Perhaps something like commented section below?]

[296 words]

Mixed fisheries and the EU landings obligation Relatively recent efforts to reduce exploitation rates in industrial fisheries has begun the process of rebuilding depleted fish populations [?]. Improved management of fisheries has the potential to increase population sizes and allow increased sustainable catches, yet fisheries catch globally remains stagnant [?]. In light of projected increased demand for fish protein [?] there is an important role for well managed fisheries to play in supporting future food security [?] and so 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 [?,?,?]. 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 [?,?]. However, 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)[?]. The changes are expected to contribute to attainment of the goals of Good Environmental Status (GES) under the European Marine Strategy Framework Directive (MSFD; [?]) and move Europe towards an ecosystem based approach to fisheries management [?]. 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[?,?] and provides a strong incentive to mitigate such losses [?,?].

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 [?,?].

Spatio-temporal management measures (such as time-limited fishery closures) have been applied to reduce unwanted catch with varying degrees of success (e.g. [?,?,?,?]) 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.[?,?,?]). 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 and create a framework to identify trends common among species groups to describe where spatial measures can contribute to mitigating unwanted catches in mixed fisheries.

[580 words]

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 spatio-temporal dynamics of key components of a fish community by employing a geostatistical Vector Autoregressive Spatio-temporal model (VAST). We implement a factor analysis decomposition to describe trends in spatio-temporal dynamics of the different species as a function of n latent variables [?] to identify community dynamics and drivers common among species groups. Of particular importance for mixed fisheries is the ability to separate species by underlying factors, which can then be investigated for what spatio-temporal separation they pertain to. We separately model spatio-temporal encounter probability and catch rates to allow identification of differences in associations for distribution of the species groups and densities upon encounter [?], by employing Gaussian Markov Random Fields (GMRFs) to capture spatial and temporal dependence within and among species groups for both encounter probability and catch rates [?]. 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 survey catch rate differences while random effects capture the spatio-temporal dynamics of the fish community.

[200 words]

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 a large number of species make up the commercial catches. Fisheries are spatially and temporally complex with mixed fisheries undertaken by several nations using different gear types [?,?]. Close to 150 species have been identified in the commercial catches of the Celtic Sea, with approximately 30 species dominating the catch [Mateo Maria, Pawlowski Lionel, Robert Marianne (2017). Highly mixed fisheries: fine-scale spatial patterns in retained catches of French fisheries in the Celtic Sea . ICES Journal of Marine Science, 74(1), 91-101.].

We parametrise our spatio-temporal 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 (*Melanogram-*

mus 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, STECF data [INCLUDE REF]). 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.

[223 words]

Common spatial patterns driving species associations A spatial dynamic factor analysis decomposes the dominant spatial patterns driving differences in encounter probability and abundance. Figure 1 shows the first three factors for (a) average spatial encounter probability and (b) average density [AVOID SENTENCES SAYING WHAT THE FIGURE/TABLE IS, USE THE SPACE TO SAY SOMETHING ABOUT THE RESULTS - CAPTION DOES THE REST]. The first three factors account of 83.7 % of the variance in encounter probability and 69 % of the variance in density, respectively. A clear spatial pattern can been seen both for encounter probability and density, with a positive association 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 association offshore in the south-westerly waters (Figure 1). On the second factor a North / South split can be seen for encounter probability at approximately 49° N while density is more driven by a positive association in the deeper westerly waters. The opposite is evident on the third factor, with a positive association with the Easterly waters for encounter probability and negative with the westerly waters, while density is driven by a North / South split.

[NEXT TWO PARAGRAPHS CAN BE MOVED LOWER OR SUPPLEMENTARY. DISCUSS HERE TO WHICH SPECIES WERE ASSOCIATED WITH WHICH FACTORS INTRODUCED ABOVE, I.E., FIGURE 2.]In a preliminary investigation of the main observed covariates influencing the factors, the first factor was highly correlated with log(depth) for both encounter probability (-0.85, CI = -0.88 to -0.81; Figure S1) and 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 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. The utility of these variables as predictors of species distributions has been identified in other marine species distribution models [?]; 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.

[397 words]

Changes in spatial patterns over time, but stability in species dynamics While there are clear patterns in the factor coefficients describing spatial differences in average encounter probability and density (Figure 1), the inter-annual differences in factor coefficients show less structure (Figures S4, S5). Temperature is often included as a covariate in species distribution models, but was found not to contribute to the variance in the factor coefficients (Figure S6, correlations for either encounter probability or density ~ 0).

While spatio-temporal factor coefficients did not show consistent trends from year to year, among species groups there were clear relationships (Figure 2). The same factors appear to drive spatio-temporal distributions of megrim, anglerfish species and hake (the deeper water species, species grouping negatively associated with the second axes of Figure 2a) and the roundfish and flatfish (species grouping more positively associated with the second axes of Figure 2a). For spatio-temporal density (Figure 2b) cod, haddock and whiting (the roundfish species) are separated from plaice, sole (the flatfish) and deeper water species. As such, higher catches of a species within a group would be expected when catching another species within that group. This suggests that a common environmental driver is influencing the distributions of the species groups, and that driver differentially affects the species groups.

[178 words]

Spatial correlations show three distinct species-group associations 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 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.

Correlation coefficients for the average density (Figure 3b) show less 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 generally high catches of one can predict low catches of the other successfully.

In addition to the average spatial correlations, we also estimate spatio-temporal correlations. The spatial correlations (representing the average correlations across all years) from the population correlations [DEFINE WHAT IS MEANT BY POPULATION CORRELATION] are linearly associated with the spatio-temporal population correlations (representing how correlations change from year to year), indicating generally predictable relationships between species groups from one year to the next, i.e. a positive or negative association between two species groups is likely be persist from one year to the next. The correlation coefficients were 0.59 (0.52 - 0.66) and 0.47 (0.38 - 0.55) for encounter probability and 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 scores that there are subtle differences in spatial patterns in factor coefficients from one year to the next (Figures S5 and S6) indicating changes may be driven by temporally changing environmental factors.

[459 words]

Subtle differences in distributions may be important to separate catches within groups under the landing obligation The analysis shows the interdependence within species groups (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 he 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 of the 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 for megrim, a fairly even relative distribution elsewhere is 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 the UK, 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 (66 [WHY NOT 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

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

trawl. The area between the UK and Ireland (79) 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. 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 area 216, reflecting its relative abundance in the area.

[[WORK IN PROGRESS, NOT SURE WHETHER TO KEEP OR DEVELOP... [SUGGEST WE JUST CITE THE REFERENCE TO THIS IN THE DISCUSSION PAUL AS WE NEED TO KEEP THE MESSAGE SIMPLE - ‘SPATIOTEMPORAL COMPLEXITY REDUCED’] Figure 5 shows the joint production function for the entire spatial domain, giving the global production sets for the years 2011 - 2015. It gives the space in which vessels have to operate where they can change the relative composition of each species in the catch as a function of changing location fished only. The convex hull of the space is the flexibility vessels have in order to adapt to the changing fishing opportunities given the association of species with each other[?]. As can be seen from Figure 5a which shows the trade-off between cod and haddock for an Otter trawler....

Figure 5b shows the same for plaice and sole for a Beam trawler... STRUGGLING TO DEFINE WHAT IS ’LOTS’ AND WHAT IS ’LITTLE’ SPACE OBJECTIVELY...?]]

[489 words]

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. site 66 in Figure 4) are likely to predominately catch plaice and sole, yet switching to the offshore locations (e.g. site 216) 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. [?]).

A role that science can play in supporting effectiveness of spatio-temporal avoidance could be to provide probabilistic advice on likely hotspots for high probability of species occurrence and high species density which can inform fishing decisions. Such advice could be based also on 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. The framework we develop here could be extended to include commercial data and real-time updates.

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. While this is likely to be fishery specific with differing results observed elsewhere (e.g. BC, East coast US, - will add refs) here we provide a framework that could be used to simulate different management and/or fishing effort scenarios. Such results could inform what additional measures are needed to support transition to the new management system, in order to ensure mixed fisheries can sustainably increased catches consistent with rebuilding fish populations and help support future food security.

[words 416]

Methods

Model structure: VAST[2] implements a delta-generalised linear mixed modelling (GLMM) framework that takes account of spatio-temporal correlations among species-groups through implementation of a spatial dynamic factor analysis (SDFA). In the model, spatio-temporal variation is represented through three-dimensional Gaussian Random Fields while 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 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 [?].

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

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

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 (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:

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

Where $\theta_p(s,t)$ represents log-density for species p at site s at time t, ψ_j is the coefficient for factor j, $L_{p,j}$ the loading matrix representing association of species p with factor j and $\gamma_{k,p}\chi_k(s,t)$ the linear effect of covariates at each site and time [?].

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-groups [?].

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;

$$logit[p(s_i, p_i, t_i)] = \gamma_p(p_i, t_i) + \varepsilon_p(s_i, p_i, t_i) + \delta_p(p_i, v_i) \tag{2}$$

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

$$gamma[r(s_i, p_i, t_i)] = \gamma_p(p_i, t_i) + \varepsilon_p(s_i, p_i, t_i) + \delta_p(p_i, v_i) \tag{3}$$

With $\gamma_*(p_i, t_i)$, $\varepsilon_*(s_i, p_i, t_i)$ and $\delta_*(p_i, v_i)$ representing an intercept, spatio-temporal variation and a vessel effect (v) respectively for for either probability of encounter, $* = p$ or density $* = r$.

Spatio-temporal variation: The spatio-temporal 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/time 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) [?]. 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 density reduced to $<$10 %, respectively (Figure S10). Incorporating the spatio-temporal 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:

$$vec[\mathbf{E}_*(t)] \sim MVN(0, \mathbf{R}_* \otimes \mathbf{V}_{\varepsilon*}) \tag{4}$$

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 correlation 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 [?].

Incorporating covariates Survey catchability (the relative efficiency of a gear catching a species-group) 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 [?]. Parameter estimates (Figure S11) 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 density were include. While incorporation may improve the spatial predictive performance [?], 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; [?]) 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-group 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 S9) 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 [?]; 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.

[1019 words]

Model setup The spatial domain was setup to include 250 knots representing the Gaussian Random Fields. The model was configured to estimate nine factors to describe the spatial and spatio-temporal encounter probability and density parameters, with a log-link between the logit encounter probability and assumed gamma distribution on positive catches.

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 parameters (1,674 fixed and 129,276 random effects).

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 (S12, S13). Further, model outputs are consistent with stock-level trends abundances over time from international assessments (S14), yet also provide detailed insight into species co-occurrence and the strength of associations in space and time.

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Figure 1 Spatial Factor coefficients for (a) the average spatial encounter probability and (b) the average density, on the first 3 factors. 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 density

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

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

Figure 5 Example of technical efficiency space