# Working title: Spatial separation of catches in highly mixed fisheries

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Mixed fisheries have resulted in overexploitation of weaker stock 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 maximise catches within the new constraints. Failing to achieve this will result in lower productivity 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 an important goal for fisheries sustainability. A potential mechanism for decoupling exploitation is spatial targeting (driven by spatial management or rights-based incentives), but this remains technically challenging due to complex fishery dynamics, the co-occurrence of species at fine spatial and temporal scales and a lack of understanding of how this is driven by community dynamics. We set out a framework to understand how community and fishery spatial dynamics interact to drive species composition in catch by applying to the highly mixed fisheries of the Celtic Sea a spatio-temporal joint species distribution model (VAST). The model is applied to the nine most important demersal quota species, each separated into juvenile and adult size classes to

highlight where challenges in implementing the landings obligation persist.

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8 Clear common drivers for spatial distribution patterns emerge for three species groups (round-

fish flatfish and shelf species) and, while abundance varies from year to year, the same species

groups are commonly found in higher densities together. This indicates common drivers of

distribution and 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.

24 [285 words]

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Mixed fisheries and the EU landings obligation Recent decades have seen efforts to reduce

exploitation rates in fisheries and rebuild depleted fish populations start to bear fruit [1]. Improved

management of fisheries has the potential to increase population sizes and allow increased catches,

29 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 so there remains a need to ensure fisheries are managed efficiently to maximise

32 productivity.

A particular challenge in realising increased catches from rebuilt populations is maximising yields

from mixed fisheries [5–7]. This is because in mixed fisheries, the predominant type of fishery

worldwide, several fish species are caught together in the same net or fishing operation (known

as 'technical interaction'). If managed by individual quotas and catches do not match available

species quotas for a fishing vessel, either the vessel must stop fishing when the first quota is reached

- (the 'choke' species) or there is overexploitation of the weaker species while fishers continue to catch more healthy species and throw back ('discard') the fish for which they have no quota.
- The sustainability of European fisheries have been hampered by this 'mixed fishery problem' for decades with large-scale discarding [8,9]. 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) [10]. The changes are expected to contribute to attainment 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
- Spatio-temporal management measures (such as time-limited fishery closures) have been applied in the past to reduce unwanted catch with varying degrees of success (e.g. [18–21]) while moveon rules have also been proposed or implemented to influence catch rates of particular vulnerable species in order to reduce or eliminate discards (e.g. [22–24]). However, such measures have gen-

nets), or the timing and location of fishing activity [16, 17].

erally been targeted at individual species without considering associations and interactions among several species. Highly mixed fisheries are complex with spatial, technological and community interactions. The design of spatio-temporal management measures which aim to allow exploitation of healthy stocks while protecting weaker stocks requires understanding of these interactions on a meaningful scale for management measures. Here, we set out a framework for understanding these complexities. We do this by implementing a spatio-temporal method for reducing the dimensionality of the problem and use the framework to identify trends common among species groups to describe where spatial measures can contribute to mitigating unwanted catches in the Celtic Sea mixed fisheries.

## 68 [577 words]

Framework for analysing spatio-temporal mixed fisheries interactions We present a framework for analysing how far spatio-temporal avoidance can go 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 Spatio-temporal model (VAST). VAST includes i) a factor analysis decomposition to describe trends in spatio-temporal dynamics of the different species as a function of n
latent variables [25]. This allows for inference of the distribution and density of poorly sampled
species through association with the modelled factors and identification of community dynamics
and drivers common among species groups. In addition, it ii) separately models spatio-temporal
encounter probability and catch rates to allow identification of differences in associations for distribution of the species groups and densities upon encounter [26], it employs iii) Gaussian Markov

- Random Fields (GMRFs) to capture spatial and temporal correlations within and among species groups for both encounter probability and catch rates [27], and iv) the approach 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 integrating across random effects which capture the spatio-temporal properties of the fish community.
- 85 [203 words]
- Dynamics of Celtic Sea fisheries We use the fisheries in 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 [28, 29]. (MORE SPECIFIC details of number of species in typical landings, key species).
- We parametrise our spatio-temporal model using catch data from seven fisheries independent surveys undertaken 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 angler-fish (*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). 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 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's landings obligation.

### 104 [223 words]

Common spatial patterns driving species associations A spatial dynamic factor analysis decom-105 poses the dominant spatial patterns driving differences in encounter probability and abundance. 106 Figure 1 shows the first three factors for (a) average spatial encounter probability and (b) average 107 density. The first three factors account of 83.4 % of the variance in encounter probability and 69.2 108 % of the variance in density, respectively. A clear spatial pattern can been seen both for encounter 109 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. On the second factor a North / South split can be seen for encounter probability at approximately the 49° N while density is more driven 113 by a positive association in the deeper westerly waters. The opposite is evident on the third factor, 114 with a positive association with the Easterly waters for encounter probability and negative with the 115 westerly waters, while density is driven by a North / South split. 116

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 [30]; 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.

### 132 [397 words]

Changes in spatial patterns over time, but stability in species dynamics While there are clear spatial patterns in the factors describing average encounter probability and density, there are interannual differences in factor coefficients which show less structure (Figures S4, S5). While temperature is often included as a covariate in species distribution models it was found not to contribute to the variance in the factor coefficients (Figure S6, correlations for both encounter probability and density  $\sim 0$ ).

While spatio-temporal factor coefficients did not show common trends, among species groups there were common dynamics. Figure 2a shows that 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) on the one hand and the roundfish and flatfish on the
other. 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 the
other roundfish species group would be expected when catching one species group. This suggests
that a common environmental driver is influencing the distributions of the species groups.

#### 147 [178 words]

Correlations show three distinct species-group associations Pearson correlation coefficients 148 for the modelled average spatial encounter probability (Figure 3a) show clear strong associations 149 between adult and juvenile size classes for all species (>0.75 for all species except Hake, 0.56). 150 Among species groups, hierarchical clustering identified three common groups; Roundfish (cod, 151 haddock, whiting) are found closely associated, 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 species found in the deeper waters (hake, megrim and 155 both anglerfish species) with the megrim strongly associated with the budgassa anglerfish species (0.88). Negative relationships were found between plaice and sole and the monkfish species (-0.27, 157 -0.26 for the adult size class with budegassa adults respectively) and hake (-0.33, -0.37) indicating 158 spatial separation in distributions. 159

Correlation coefficients for the average density (Figure 3b) show less significant relationships 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 abundance of one can predict low abundance of the other successfully.

[[In addition to the average correlation, we also estimate how correlations change from one year 170 to the next. The spatial correlations (representing the average correlations across all years) from 171 the population correlations show reasonable alignment with the spatio-temporal population corre-172 lations (representing how correlations change from year to year) indicating generally predictable 173 relationships between species groups from one year to the next (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 do change from one-year to the next. This would have implications for the predictability of the relationship between catches of 178 one species group and another. 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 being driven by temporally changing environmental factors.]] 181

182 [459 words]

Implications for species avoidance in mixed fisheries under the landings obligation The analysis shows the interdependence within species groups (roundfish, flatfish and deeper water species) which has important implications for how spatial avoidance can be used to support implementation of the EU's landings obligation. If mixed fisheries are to maximise productivity, decoupling catches of species between and among the groups will be key. Methods to do this include changes 187 to the selectivity characteristics of gear (e.g. [31]) and spatio-temporal avoidance. Both are likely 188 to play a role but the extent to which they can contribute to fisheries sustainability is unknown. 189 While here we demonstrate the separation of three distinct species groupings (roundfish, flatfish 190 and deeper water species) separating catches within groups is likely to be equally as important. 191 Figure 4 shows the difference in spatial distribution within a group for each of the species group-192 ings for a single year (2015). 193

Figure 4a indicates that cod had a more North-westerly distribution than haddock while cod had 194 more westerly distribution than whiting roughly delineated by the 7° W line. Whiting appeared 195 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 particularly concentrated in two areas compared to anglerfishes<sup>1</sup> 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 200 4f), anglerfishes have a more easterly distribution than megrim. For the flatfish species plaice and 201 sole (Figure 4g), sole appear to be more concentrated along the coastal areas of Ireland and the UK, 202 while Plaice are more concentrated in the Southern part of the English Channel along the coast of 203

<sup>&</sup>lt;sup>1</sup>two species combined as they are managed as one

204 France.

These nuanced differences in distribution can have important implications for fishers seeking to 205 fish in areas which match their quota holdings. Figure 4h shows the predicted catch distribution 206 from a "typical" Otter trawl gear and Beam trawl gear fishing at three different locations. As 207 can be seen, both the gear selectivity and area fished play important contributions to the catch 208 compositions; in the inshore area (66) plaice and sole are the two main species in catch reflecting 209 their distribution and abundance, though the Otter trawl gear catches a greater proportion of plaice 210 than the Beam trawl. The area between the UK and Ireland (79) has a greater contribution of 211 whiting, haddock, cod, hake and anglerfishes in the catch with the Otter trawl catching a greater 212 proportion of the roundfish, haddock, whiting and cod. The offshore area has a higher contribution 213 of megrim, anglerfishes and hake with the Otter trawl catching a greater share of hake and the 214 Beam trawl a greater proportion of megrim. Megrim dominates the catch for both gears in area 215 216, reflecting its relative abundance in the area.

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 [32]. 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...?

225 [573 words]

226 Implications for mixed fishery management under the EU landing obligation Real time?

227 Commercial data? Hotspots & Notspots??

How far can spatial changes in targeting bring you towards achieving the right balance of catch in

229 mixed fisheries to maintain productivity. FOOD SECURITY!!

#### Methods

The model integrates data from seven fisheries independent surveys taking account of correlations

232 among species-group spatio-temporal distributions and abundances to predict spatial density esti-

233 mates consistent with the resolution of the data.

[Model outputs are consistent with stock-level trends abundances over time from international

assessments, yet also provide detailed insight into species co-occurrence and the strength of asso-

ciations in space and time. We use the outputs to draw inference on the challenges in separating

catches of key commercial demersal fish in moving to the EU landing obligation.]]

- 1. Worm, B. et al. Rebuilding Global Fisheries. Science 325, 578-585 (2009). URL http://www.sciencemag.org/cgi/doi/10.1126/science.1173146.
- 2. FAO. The state of world fisheries and aquaculture. Food and Agriculture Oraganization of the United Nations 2014, 218 (2014). URL http://scholar.google.com/scholar? hl=en{\&}btnG=Search{\&}q=intitle:THE+STATE+OF+WORLD+FISHERIES+AND+AQUACULTURE{\#}0.978-92-5-106675-1.
- 3. B??n??, C. *et al.* Contribution of Fisheries and Aquaculture to Food Security and Poverty Reduction: Assessing the Current Evidence. *World Development* **79**, 177–196 (2016).
- 4. Mcclanahan, T., Allison, E. H. & Cinner, J. E. Managing fisheries for human and food security. *Fish and Fisheries* **16**, 78–103 (2015).
- 5. Branch, T. & Hilborn, R. Matching catches to quotas in a multispecies trawl fishery: targeting and avoidance behavior under individual transferable quotas. *Canadian Journal of Fisheries and Aquatic Sciences*65, 1435–1446 (2008). URL http://article.pubs.nrc-cnrc.gc.ca/ppv/RPViewDoc?

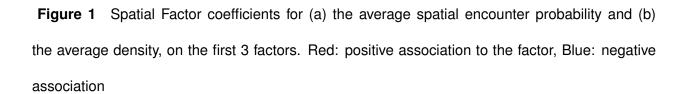
  issn=1205-7533{\&}volume=65{\&}issue=7{\&}startPage=1435{\&}ab=y.
- 6. Kuriyama, P. T., Branch, T. A., Bellman, M. A. & Rutherford, K. Catch shares have not led to catch-quota balancing in two North American multispecies trawl fisheries. *Marine Policy* **71**, 60–70 (2016). URL http://dx.doi.org/10.1016/j.marpol.2016.05.010.
- 7. Ulrich, C. *et al.* Achieving maximum sustainable yield in mixed fisheries: A management approach for the North Sea demersal fisheries. *ICES Journal of Marine Science* **74**, 566–575 (2017). URL https://academic.oup.com/icesjms/article-lookup/doi/10.1093/icesjms/fsw126.
- 8. Borges, L. The evolution of a discard policy in Europe. Fish and Fisheries 534–540 (2015).

- 9. Uhlmann, S. S. *et al.* Discarded fish in European waters: General patterns and contrasts. *ICES Journal of Marine Science* **71**, 1235–1245 (2014).
- 10. European Commission. REGULATION (EU) No 1380/2013 OF THE EUROPEAN PARLIAMENT AND OF THE COUNCIL of 11 December 2013 on the Common Fisheries Policy, amending Council Regulations (EC) No 1954/2003 and (EC) No 1224/2009 and repealing Council Regulations (EC) No 2371/2002 and (EC (2013).
- 11. European Parliament. Directive 2009/28/EC of the European Parliament and of the Council of 23 April 2009. *Official Journal of the European Union* **140**, 16–62 (2009). 534.
- 12. Garcia, S. M., Zerbi, A., C, A., Do Chi, T. & Lasserre, G. The ecosystem approach to fisheries. FAO Fisheries Technical Paper 443, 71 (2003). URL http://www.fao.org/docrep/006/ Y4773E/y4773e05.htm.
- 13. Hoff, A. *et al.* Economic effort management in multispecies fisheries: The FcubEcon model. *ICES Journal of Marine Science* **67**, 1802–1810 (2010).
- 14. Condie, H. M., Grant, A. & Catchpole, T. L. Incentivising selective fishing under a policy to ban discards; lessons from European and global fisheries. *Marine Policy* **45**, 287–292 (2014). URL http://linkinghub.elsevier.com/retrieve/pii/S0308597X1300198X.
- 15. Condie, H. M., Grant, A. & Catchpole, T. L. Does banning discards in an otter trawler fishery create incentives for more selective fishing? *Fisheries Research* **148**, 137–146 (2013). URL http://linkinghub.elsevier.com/retrieve/pii/S016578361300221Xhttp://dx.doi.org/10.1016/j.fishres.2013.09.011.

- 16. Fulton, E. A., Smith, A. D., Smith, D. C. & Van Putten, I. E. Human behaviour: The key source of uncertainty in fisheries management. *Fish and Fisheries* 12, 2–17 (2011). URL http://doi.wiley.com/10.1111/j.1467-2979.2010.00371.x.
- 17. Van Putten, I. E. *et al.* Theories and behavioural drivers underlying fleet dynamics models. *Fish and Fisheries* 13, 216–235 (2012). URL http://doi.wiley.com/10.1111/j.1467-2979.
- 18. Needle, C. L. & Catarino, R. Evaluating the effect of real-time closures on cod targeting. *ICES Journal of Marine Science* **68**, 1647–1655 (2011). URL http://icesjms.oxfordjournals.org/cgi/doi/10.1093/icesjms/fsr092.
- 19. Holmes, S. J. et al. Using fishery-dependent data to inform the development and operation of a comanagement initiative to reduce cod mortality and cut discards. ICES Journal of Marine Science 68, 1679–1688 (2011). URL http://icesjms.oxfordjournals.org/cgi/doi/10.1093/icesjms/fsr101.
- 20. Beare, D. J. et al. Study for the Revision of the plaice box â" Final Report 250– (2010).
- 21. Dinmore, T. A., Duplisea, D. E., Rackham, B. D., Maxwell, D. L. & Jennings, S. Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. *ICES Journal of Marine Science* **60**, 371–380 (2003).
- 22. Gardner, B., Sullivan, P. J., Morreale, S. J. & Epperly, S. P. Spatial and temporal statistical analysis of bycatch data: patterns of sea turtle bycatch in the North Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 2461–2470 (2008). URL http://www.nrcresearchpress.com/doi/abs/10.1139/F08-152.

- 23. Dunn, D. C., Boustany, A. M. & Halpin, P. N. Spatio-temporal management of fisheries to reduce by-catch and increase fishing selectivity. *Fish and Fisheries* **12**, 110–119 (2011). URL http://doi.wiley.com/10.1111/j.1467-2979.2010.00388.x.
- 24. Dunn, D. C. *et al.* Empirical move-on rules to inform fishing strategies: A New England case study. *Fish and Fisheries* **15**, 359–375 (2014). URL http://doi.wiley.com/10.1111/faf.12019.
- 25. Thorson, J. T. *et al.* Spatial factor analysis: A new tool for estimating joint species distributions and correlations in species range. *Methods in Ecology and Evolution* **6**, 627–637 (2015).
- Thorson, J. T., Shelton, A. O., Ward, E. J. & Skaug, H. J. Geostatistical delta-generalized linear mixed models improve precision for estimated abundance indices for West Coast groundfishes. *ICES Journal* of Marine Science 72, 1297–1310 (2015).
- 27. Thorson, J. T. & Ward, E. J. Accounting for space-time interactions in index standardization models. *Fisheries Research* **147**, 426–433 (2013).
- 28. Ellis, J. R., Rogers, S. I. & Freeman, S. M. Demersal Assemblages in the Irish Sea, St George's Channel and Bristol Channel. *Estuarine, Coastal and Shelf Science* **51**, 299–315 (2000). URL http://www.sciencedirect.com/science/article/pii/S0272771400906772.
- 29. Gerritsen, H. D., Lordan, C., Minto, C. & Kraak, S. B. M. Spatial patterns in the retained catch composition of Irish demersal otter trawlers: High-resolution fisheries data as a management tool. *Fisheries Research* **129-130**, 127–136 (2012).
- 30. Robinson, L. M. *et al.* Pushing the limits in marine species distribution modelling: Lessons from the land present challenges and opportunities. *Global Ecology and Biogeography* **20**, 789–802 (2011).
- 31. Santos, J. et al. Reducing flatfish bycatch in roundfish fisheries. Fisheries Research 184, 64–73 (2016).

32. Reimer, M. N., Abbott, J. K. & Wilen, J. E. Fisheries Production: Management Institutions, Spatial Choice, and the Quest for Policy Invariance. *Marine Resource Economics* **32**, 143–168 (2017).



**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