

A simulation framework for exploring spatio-temporal dynamics in mixed fisheries

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Abstract

[Guidance: A concise and factual abstract is required. The abstract should state briefly the purpose of the research, the principal results and major conclusions. An abstract is often presented separately from the article, so it must be able to stand alone. For this reason, References should be avoided, but if essential, then cite the author(s) and year(s). Also, non-standard or uncommon abbreviations should be avoided, but if essential they must be defined at their first mention in the abstract itself. Graphical abstract: Although a graphical abstract is optional, its use is encouraged as it draws more attention to the online article. The graphical abstract should summarize the contents of the article in a concise, pictorial form designed to capture the attention of a wide readership. Graphical abstracts should be submitted as a separate file in the online submission system. Image size: Please provide an image with a minimum of 531 X 1328 pixels (h X w) or proportionally more. The image should be readable at a size of 5 x 13 cm using a regular screen resolution of 96 dpi. Preferred file types: TIFF, EPS, PDF or MS Office files.]

Fishing exploits spatio-temporally heterogeneous fish populations without fully selective gear which can result in unintended, unwanted catch of low quota or

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protected species. Reducing these unwanted catches is crucial for biological and economic sustainability of 'mixed fisheries' and implementation of an ecosystem approach to fishing.

In order to implement effective spatial measures to reduce discards there needs to be a good understanding of spatio-temporal fishery dynamics. However, scientific advice is limited by a lack of knowledge of population distribution, movement and how fishers interact with different fish populations. This is because data on location of fish at high temporal and spatial resolutions is expensive and difficult to collect and therefore proxy inferred from either scientific survey or commercial catch data is often used to model distributions, but often limited in its spatial or temporal resolution.

We develop a highly resolved spatio-temporal simulation model that incorporate i) delay-difference population dynamics, ii) population movement dynamics using Gaussian Random Fields to simulate patchy, heterogeneously distributed populations, iii) fishery dynamics for multiple fleet characteristics based on a correlated random walk and learned behaviour.

Using our model we simulation 20 years of exploitation of the fish populations and use the results from the fishing model to draw inference on the underlying population structures. We compare this inference to i) a simulated fixed-site sampling design commonly used for fisheries monitoring purposes, ii) the underlying population structures input to the simulation, to establish whether fishing dependent data, which is obtained from a biased sampling due to fishers targeting, provides a robust picture of spatio-temporal distributions. [We simulate a closure based on areas defined from commercial catch data and assess its effectiveness on reducing catches of a fish population.]

We conclude that...

[233 words]

Keywords: Some, keywords, here. Max 6

2010 MSC: 00-01, 99-00

1 1. Introduction

2 [Guidance:: State the objectives of the work and provide an adequate back-
3 ground, avoiding a detailed literature survey or a summary of the results.]

4

5 Fishers exploit fish populations that are heterogenously distributed in space
6 and time without prior knowledge of species distributions using non-selective
7 fishing gear. Fisheries that catch an assemblage of species, known as mixed fish-
8 eries, when managed by single-species quotas can end up discarding overquota
9 catch leading to overexploitation of fish populations. Reducing discarding is
10 crucial to ensure biological and economic sustainability of fisheries and imple-
11 mentation of an ecosystem approach to fisheries. As such there is increasing
12 interest in technical solutions such as gear, spatial closures as a way of avoiding
13 discards.

14

15 Use of spatial management as a tool has been proposed as a method to re-
16 duce discards. However, its implementation is hampered by lack of knowledge
17 of fish and fishery spatiotemporal dynamics and understanding of the scale at
18 which processes are important for management. Understanding of the correct
19 scale for spatial management is crucial in order to implement measures at a
20 resolution that ensures effective management[?] while minimising economic
21 impact; for example a scale which promotes species avoidance for vulnerable or
22 low quota species while allowing continuation of sustainable fisheries for available
23 quota species.

24

25 Ensuring measures are implemented at an appropriate scale has been a chal-
26 lenge in the past that has led to ineffectual measures with unintended conse-

27 quences such as limited impact towards the management objective or increased
28 benthic impact on previously unexploited areas (e.g. the cod closure in the
29 North Sea[? ?]). Since then more refined spatial information has become
30 available through the combination of logbook and Vessel Monitoring System
31 (VMS) data[? ? ? ?] and more real-time spatial management has been able
32 to be implemented (e.g. [?]), though such information is patchy and derived
33 from an inherently biased sampling programme (i.e. targeted fishing). Further,
34 fishers generally only recorded landings (not catch) on a daily basis. This leads
35 to questions about the validity of inferences that can be drawn from landings
36 data assigned to VMS activity pings.

37

38 In order to test the assumption that VMS associated landings data can be
39 used to draw inference on the underlying population structures we develop a
40 simulation model where population dynamics are known rather than inferred
41 from sampling or commercial catches. Population movement is driven by a
42 random (diffusive) and directed (advection) process and we incorporate charac-
43 terisation of a number of different fisheries exploiting four fish populations with
44 different spatial and population demographics.

45

46 Using our model we simulate 20 years of exploitation of the fish populations
47 and use the results from the fishing model to draw inference on the underlying
48 population structures. We compare this inference to i) a simulated [stratified]
49 fixed-site sampling design commonly used for fisheries monitoring purposes, ii)
50 the underlying population structures input to the simulation.

51

52 [Could fit a geostatistical model (e.g. VAST) to the fisheries-dependent and
53 fisheries-independent data, though may be overkill...]

54

55 We simulate a fishery closure to protect one species based on the fishery-
56 dependent inferred distributions at a spatial and temporal scale typical in fish-
57 eries management, and assess a theoretical "benefit" to the population, and

58 effect on the other three populations. Further, we extend our analysis to a
59 range of spatial and temporal scales to assess the impact of these processes on
60 the success of the management measure.

61

62 2. Materials and Methods

63 [Guidance: Provide sufficient details to allow the work to be reproduced
64 by an independent researcher. Methods that are already published should be
65 summarized, and indicated by a reference. If quoting directly from a previously
66 published method, use quotation marks and also cite the source. Any modifi-
67 cations to existing methods should also be described.]

68

69 We develop a simulation model with a modular event-based approach, where
70 modules are implemented on independent time-scales appropriate to capture the
71 characteristic of the process modelled. The fishing model operated on a tow-by-
72 tow basis, while population dynamics (fishing and natural mortality, growth)
73 operate on a daily time-step. Population movement occurs on a weekly time-
74 step, while recruitment occurs periodically each year for a set time period (e.g.
75 3 weeks) at a specified point individual to a species. The simulation frame-
76 work is implemented in the statistical software package R [?]; available as an
77 R package from the authors github (www.github.com/pdolder/MixFishSim).
78 The overall model structure is summarised in Figure 1.

79

80 In the following section, we describe each of the model components; 1) Popu-
81 lation dynamics, 2) Recruitment dynamics, 3) Population movement, 4) fishery
82 dynamics.

83 2.1. Population dynamics

84 The basic population level processes are simulated using a modified two-
85 stage Deriso-Schnute delay difference model [? ? ?] occurring at a daily

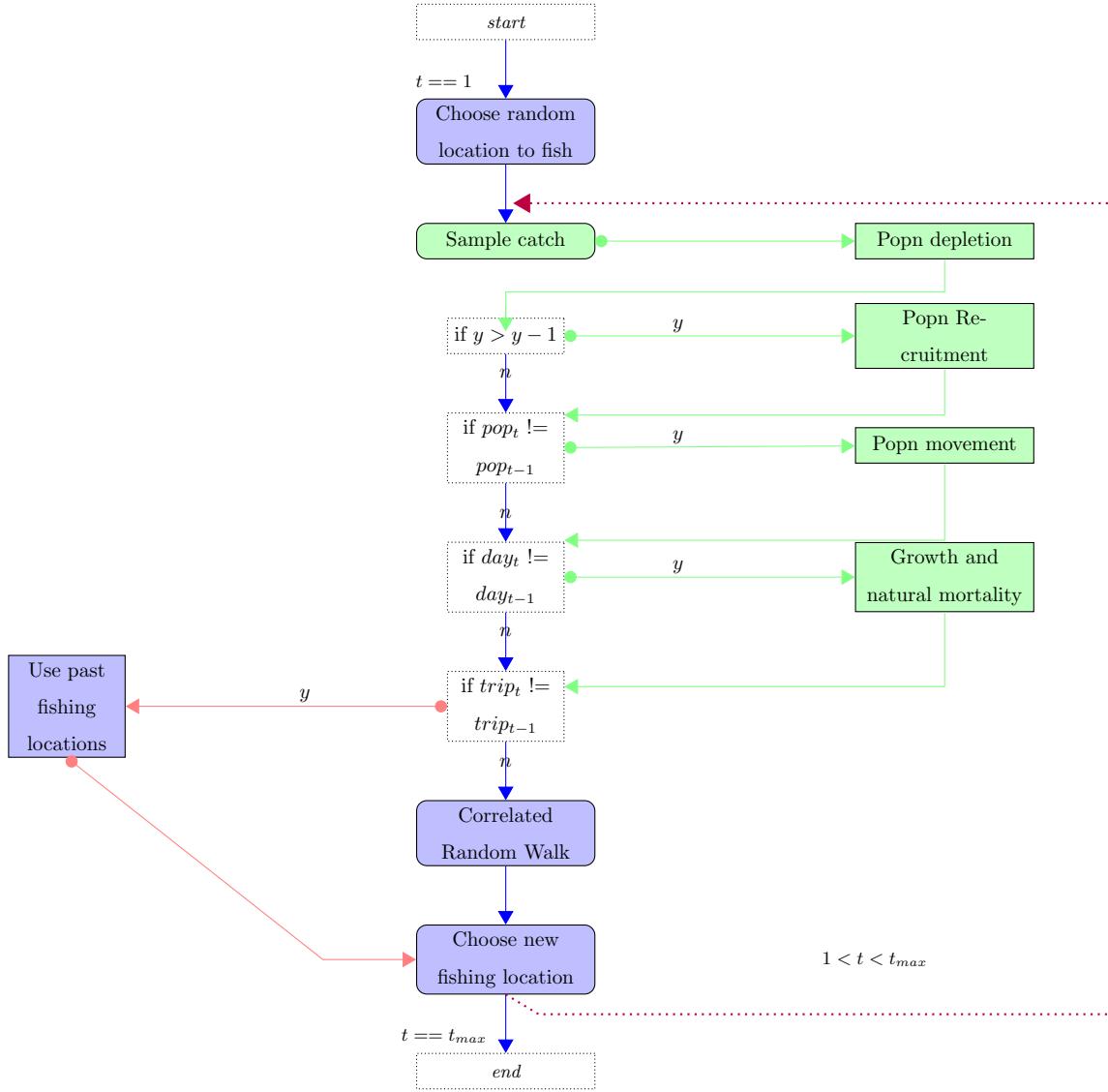


Figure 1: Overview Schematic of simulation model

time-step. Here, population biomass growth and depletion for pre-recruits and fish recruited to the fishery are modelled separately as a function of previous recruited biomass, intrinsic population growth and recruitment:

$$\begin{aligned}
B_{y,d+1} = & \\
& (1 + \rho) B_{y,d} \cdot e^{-Z_{y,d}} - \rho \cdot e^{-Z_{y,d}} \times \\
& (B_{y,d-1} \cdot e^{-Z_{y,d-1}} + Wt_{R-1} \cdot \alpha_{d-1} \cdot R_{\tilde{y}(y,d-1)}) + \\
& Wt_R \cdot \alpha_d \cdot R_{\tilde{y}(y,d)}
\end{aligned}$$

89 where ρ is Brody's coefficient, shown to be approximately equal to $\exp(-K)$,
 90 where K is the growth rate from a von bertalanffy logistic growth model [?].
 91 Wt_{R-1} is the weight of fish prior to recruitment, while Wt_R is the recruited
 92 weight. α_d represents the proportion of fish recruited during that day for the
 93 year, while $R_{\tilde{y}}$ is the annual recruits.

94
 95 Mortality Z can be decomposed to natural mortality, M , and fishing mor-
 96 tality, F , where both M and F are instantaneous rates with M fixed and F
 97 calculated by solving the Baranov catch equation [?] for F :

$$C_d = \frac{F_d}{F_d + M_d} * (1 - e^{-(F_d + M_d)}) * B$$

98 where C is the summed catch from the fishing model across all fleets and
 99 vessels for the population during the day, and B the daily biomass for the species.

100

101 2.2. Recruitment dynamics

102 Recruitment is modelled through a function relating the biomass at time of
 103 recruitment to recruits. In the simulation, it can be modelled either either as a
 104 stochastic Beverton-Holt stock-recruit form ([?]):

$$\begin{aligned}
\bar{R} &= \frac{(\alpha * B)}{(\beta + B)} \\
R &\sim N[(\bar{R}, \sigma^2)]
\end{aligned}$$

105 Where α is the maximum recruitment rate, β the spawning stock biomass
 106 (SSB) required to produce half the maximum, and B current SSB;

107

108 or a stochastic Ricker form [?]

$$\bar{R} = B * e^{(\alpha - \beta * B)}$$

$$R \sim N[(\bar{R}, \sigma^2)]$$

109 where α is the maximum productivity per spawner and β the density dependent reduction in productivity as the SSB increases.

111 *2.3. Population movement*

112 In order to simulate how fish populations might be distributed in space and
113 time, we employed a Gaussian spatial process to model habitat suitability for
114 each of the populations, with an advection-diffusion process to control how the
115 populations moved over time.

116

117 For the habitat we define a Gaussian random field process, $\{S(x) : x \in \mathbb{R}^2\}$,
118 that is a stochastic process where any collection of locations x_1, \dots, x_n where
119 for each $x_i \in \mathbb{R}^2$, the joint distribution of $S = \{S(x_1), \dots, S(x_n)\}$ is multivariate
120 Gaussian. The distribution is specified by its *mean function*, $\mu(x) = E[S(x)]$
121 and its *covariance function*, $\gamma(x, x') = Cov\{S(x), S(x')\}$ [?].

122

123 The covariance structure affects the smoothness of the surfaces which the
124 process generates, and we used the *Matérn* family of covariance structures, one
125 where the correlation strength weakens the further the distance apart (i.e. the
126 correlation between $S(x)$ and $S(x')$ decreases as the distance $u = \|x - x'\|$ increases).
127 The *Matérn* correlation is a two-parameter family where:

128

$$\rho(u) = \{2^{\kappa-1}\Gamma\kappa\}^{-1}(u/\phi)^\kappa K_\kappa(u/\phi)$$

129 $K_\kappa(\cdot)$ is a modified Bessel function of order κ , $\phi > 0$ is a scale parameter
130 with the dimensions of distance, and $\kappa > 0$, called the order, is a shape parameter
131 which determines the smoothness of the underlying process.

132

134 In the simulation model, the habitat for each of the populations is generated
135 through the *RFSimulate* function of the *RandomFields* R package [?], imple-
136 menting different parameter settings to affect the patchiness of the populations.
137 Each population is initialised at a single location, and subsequently moves ac-
138 cording to a probabilistic distribution based on habitat suitability and distance
139 from current cell.

$$Pr(B|A) = \frac{e^{-\lambda * d_{AB}} \cdot Hab_B^2}{\sum_{c=1}^C e^{-\lambda * d} \cdot Hab^2} \quad (1)$$

140 Where d_{AB} is the euclidean distance between cell A and cell B , and λ is a
141 given rate of decay.

142
143 During specified weeks of the year, the habitat quality is modified for spaw-
144 ning habitats, meaning each population has a concentrated area where spawning
145 takes place and the population moves towards this in the weeks prior to spawn-
146 ing.

147

148 2.4. Fleet dynamics

149 The fleet dynamics can be broadly categorised into three components; fleet
150 targeting - which determines the fleet catch efficiency and preference towards
151 a particular species; trip-level decisions, which determine the initial location
152 to be fished at the beginning of a trip; and within-trip decisions, determining
153 movement from one fishing spot to another within a trip.

154 2.4.1. Fleet targeting

155 Each fleet of n vessels is characterised by both a general efficiency, Q , and
156 a population specific efficiency, Q_p . Thus, the product of these parameters
157 affects the overall catch rates for the fleet and the preferential targeting of one
158 population over another. This, in combination with the parameter choice for the
159 step-function (as well as some randomness from the exploratory fishing process)

160 determines the preference of fishing locations for the fleet. All species prices are
161 kept the same, across fleets, though can be made to vary seasonally.

162 *2.4.2. Trip-level decisions*

163 Several studies (e.g.[? ? ?]) have confirmed past activity and past catch
164 rates are strong predictors of fishing location choice. For this reason, the fleet
165 dynamics sub-model includes a learning component, where a vessels initial fish-
166 ing location in a trip is based on selecting from previously successful fishing
167 locations. This is achieved by sorting all previous fishing events in the previous
168 trip as well as the previous time periods in past years, and choosing randomly
169 from the top x % of fishing events in value. Simulation testing indicating this
170 increased the mean value of catches for the vessels, over just relying on the
171 correlated random walk function.

172 *2.4.3. Within-trip decisions*

173 Fishing locations within a trip are determined by a Random Walk process.
174 A Random walk was chosen as it is commonly used in ecology to describe ani-
175 mal movement which searching for homogeneously distributed prey about which
176 there is uncertain knowledge. In a random walk, movement is a stochastic pro-
177 cess through a series of steps that can either be equal in length or take some
178 other functional form. The direction of the random walk can be correlated, a
179 characteristic known as 'persistence', providing some overall location of direc-
180 tional movement [?] or uncorrelated.

181

182 A *lévy walk* is a particular form of random walk characterised by a heavy-
183 tailed distribution of step-length and has received a lot of attention in ecological
184 theory in recent years as having shown to have very similar characteristics as
185 those observed by animals in nature, and being a near optimum searching strat-
186 egy for predators pursuing patchily distributed prey [? ?]. [?] showed that
187 Peruvian anchovy fishermen have a stochastic search pattern similar to that
188 observed with a lévy walk. However, it remains a subject of debate, with the

189 contention that search patterns may be more simply characteristed as random
 190 walks [?] with specific patterns related to the characteristics of the prey field
 191 [?].
 192

We use a modified random walk where directional change is based on a correlated circular distribution where a favourable fishing ground is likely to be "fished back over" by the vessel returning in the direction it came from and step length (i.e. the distance travelled from the current to the next fishing location) is determined by relating recent fishing success, measured as the summed value of fish caught,

$$Rev = \sum_{s=1}^{\infty} C_s \cdot Pr_s$$

193 where C_s is catch of a species, and Pr_s price of a species, to step distance. Here,
 194 when fishing is successful vessels remain in a similar location and continue to
 195 exploit the local fishing grounds. When unsuccessful, they move some distance
 196 away from the current fishing location. The movement distance retains some
 197 degree of stochasticity, which can be controlled separately.

198 The step function takes the form:

$$StepL = e^{\log(\beta_1) + \log(\beta_2) - (\log(\frac{\beta_1}{\beta_3}))} * Rev$$

199 So that, a step from $(x1, y1)$ to $(x2, y2)$ is defined by:

$$(x2, y2) = x1 + StepL \cdot \cos\left(\frac{\pi \cdot Br}{180}\right),$$

$$y1 + StepL \cdot \sin\left(\frac{\pi \cdot Br}{180}\right)$$

$$\text{with } Br_{t-1} < 180, Br_t = 180+ \sim vm[(0, 360), k]$$

$$Br_{t-1} > 180, Br_t = 180- \sim vm[(0, 360), k]$$

200 with k the concentration parameter from the von mises distribution which
 201 we correlate with the revenue so that $k = (Rev + 1/RefRev) * max_k$, where
 202 max_k is the maximum concentration value, k , and RefRev is parameterised as
 203 for β_3 in the step length function.

204 *2.4.4. Local population depletion*

205 Where several fishing vessels are exploiting the same fish population compe-
206 tition is known to play an important role in local distribution of fishing effort
207 [?]. If several vessels are fishing on the same patch of fish, local depletion and
208 interference will affect fishing location choice of the fleet as a whole [? ?]. In
209 order to account for this behaviour, the fishing sub-model operates spatially on
210 a daily time-step so that for future days the biomass available to the fishery
211 is reduced in the areas fished. The cumulative effect is to make heavily fished
212 areas less attractive as future fishing opportunities.

213 *2.5. Fisheries independent survey*

214 A fisheries-independent survey is simulated where fishing on a regular grid
215 begins each year at the same time for a given number of stations (a fixed sta-
216 tion survey design). Catches of the populations present are recorded but not
217 removed from the population. This provides a fishery independent snap shot of
218 the populations at a regular spatial distribution each year, similar to scientific
219 surveys undertaken by fisheries research agencies.

220 **3. Calculation**

221 [Guidance: A Theory section should extend, not repeat, the background to
222 the article already dealt with in the Introduction and lay the foundation for fur-
223 ther work. In contrast, a Calculation section represents a practical development
224 from a theoretical basis.]

225

226 *3.1. Simulation settings*

227 We set up with simulation to run for 20 years based on a 100 X 100 square
228 grid, with five fleets of 20 vessels each and four fish populations. Fishing takes
229 place four times a day per vessel and five days a week, while population move-
230 ment is every week.

231 *3.2. Population parameterisation*

232 We parameterised the simulation model for four populations with differing
233 habitat preference (Figure 2), population demographic and recruitment func-
234 tions; each of the populations also has two defined spawning areas and move-
235 ment rates (Table 1).

236

237 *3.3. Fleet parameterisation*

238 The fleets were parameterised to reflect five different characteristics based
239 on targeting preference and exploitation dynamics (Table 2). This ensures that
240 different fleets have different spatial dynamics, preferentially targeted different
241 fish populations. The stochasticity in the random walk process ensures that
242 different vessels within a fleet have slightly different spatial distributions based
243 on individual experience, while the step function was parameterised dynami-
244 cally so that vessels take smaller steps where the fishing location yields in the
245 top X Quartile of the value available in that year (as defined per fleet in Table 2).

246

247 Each fleet was set so that, after the first year, fishing locations were chosen
248 based on experience built up in the same month from previous years and from
249 past trip fishing success. 'Success' in this context was defined as the locations
250 where the top 75 % of revenue from was found in previous trips.

251 *3.4. Survey settings*

252 The survey simulation was set up with follow a fixed gridded station design
253 with 49 stations fished each year, starting on day 92 with same catchability
254 parameters for all populations ($Q = 1$).

255 **4. Results**

256 Need to consider what best to present here as 4 / 5 figures:

- Spatial dynamics: e.g. Figure 14. showing the population movement across weeks, including a spawning period.
- Overall population trends: e.g. Figure 3, showing the population dynamics at play.
- Realised step function: e.g. Figure 13, showing how the movement and turning angle responds. This could be combined with Figure 7 for a more complete visualisaiton.
- Catch composition and spatial clustering: e.g. Figure 10, showing the importance of spatial resolution.
- Some measure of temporal trends/changes in spatial composition - could pick a certain cell and show how the proportions change over time ? An example is Figure 15, though there is little variation here. I think this is because the static habitat with population movement is far more stable than the previous directly affected population distributions (where there was an advective-diffusive process from the SPDE). Might need to consider how to change this? Could include a spatio-temporally changing habitat suitability covariate, e.g. temperature ??
- Comparison of population structure from i) commercial sampling, ii) fisheries independent survey, iii) real population. This should be some statistical measure...not sure best approach here.

ether this is also a seasonal~~z~~closure.

- Present simulated closures in terms of % change in population biomass and fishery.
- [Guidance: Results should be clear and concise.]

5. Discussion

- [Guidance: This should explore the significance of the results of the work, not repeat them. A combined Results and Discussion section is often appropriate.]

²⁸⁴ Avoid extensive citations and discussion of published literature.]

²⁸⁵ **6. Conclusions**

²⁸⁶ [Guidance: The main conclusions of the study may be presented in a short
²⁸⁷ Conclusions section, which may stand alone or form a subsection of a Discussion
²⁸⁸ or Results and Discussion section.]

²⁸⁹ **Appendices**

²⁹⁰ [Guidance: If there is more than one appendix, they should be identified
²⁹¹ as A, B, etc. Formulae and equations in appendices should be given separate
²⁹² numbering: Eq. (A.1), Eq. (A.2), etc.; in a subsequent appendix, Eq. (B.1)
²⁹³ and so on. Similarly for tables and figures: Table A.1; Fig. A.1, etc.]

²⁹⁴ **Abbreviations**

²⁹⁵ Detail any unusual ones used.

²⁹⁶ **Acknowledgements**

²⁹⁷ those providing help during the research..

²⁹⁸ **Funding**

²⁹⁹ This work was supported by the MARES doctoral training program; and the
³⁰⁰ Centre for Environment, Fisheries and Aquaculture Science seedcorn program.

Table 1: Population dynamics and movement parameter setting

Parameter	Pop 1	Pop 2	Pop 3	Pop 4
Habitat quality				
Matérn ν	1/0.15	1/0.05	1/0.55	1/0.05
Matérn κ	1	2	1	1
Anisotropy	1.5,3,-3,4	1,2,-1,2	2.5,1,-1,2	0.1,2,-1,0.2
Spawning areas (bound box)	40,50,40,50; 80,90,60,70	50,60,30,40; 80,90,90,90	30,34,10,20; 60,70,20,30	50,55,80,85; 30,40,30,40
Spawning multiplier	10	10	10	10
Movement λ	0.3	0.3	0.3	0.3
Population dynamics				
Starting Biomass	1e5	2e5	1e5	1e4
Beverton-Holt Recruit 'a'	60	100	80	2
Beverton-Holt Recruit 'b'	250	250	200	50
Beverton-Holt Recruit σ^2	0.4	0.3	0.4	0.3
Recruit week	13-16	12-16	14-16	16-20
Spawn week	16-18	16-19	16-18	18-20
K	0.3	0.3	0.3	0.3
wt	1	1	1	1
wt_{d-1}	0.1	0.1	0.1	0.1
M (annual)	0.2	0.2	0.2	0.1

Table 2: Fleet dynamics parameter setting

Parameter	Fleet	Fleet	Fleet	Fleet	Fleet
	1	2	3	4	5
Targeting preferences					
Price Pop1	100	100	100	100	100
Price Pop2	200	200	200	200	200
Price Pop3	600	600	600	600	600
Price Pop4	1600	1600	1600	1600	1600
Q Pop1	0.01	0.02	0.02	0.01	0.01
Q Pop2	0.02	0.01	0.02	0.01	0.03
Q Pop3	0.01	0.02	0.02	0.01	0.02
Q Pop4	0.02	0.01	0.02	0.05	0.01
Exploitation dynamics					
step function β_1	1	2	1	2	3
step function β_2	10	10	8	12	7
step function β_3	Q90	Q90	Q85	Q90	Q80
step function <i>rate</i>	10	20	15	25	10
Past Knowledge	T	T	T	T	T
Past Year & Month	T	T	T	T	T
Past Trip	T	T	T	T	T
Threshold	0.75	0.75	0.75	0.75	0.75

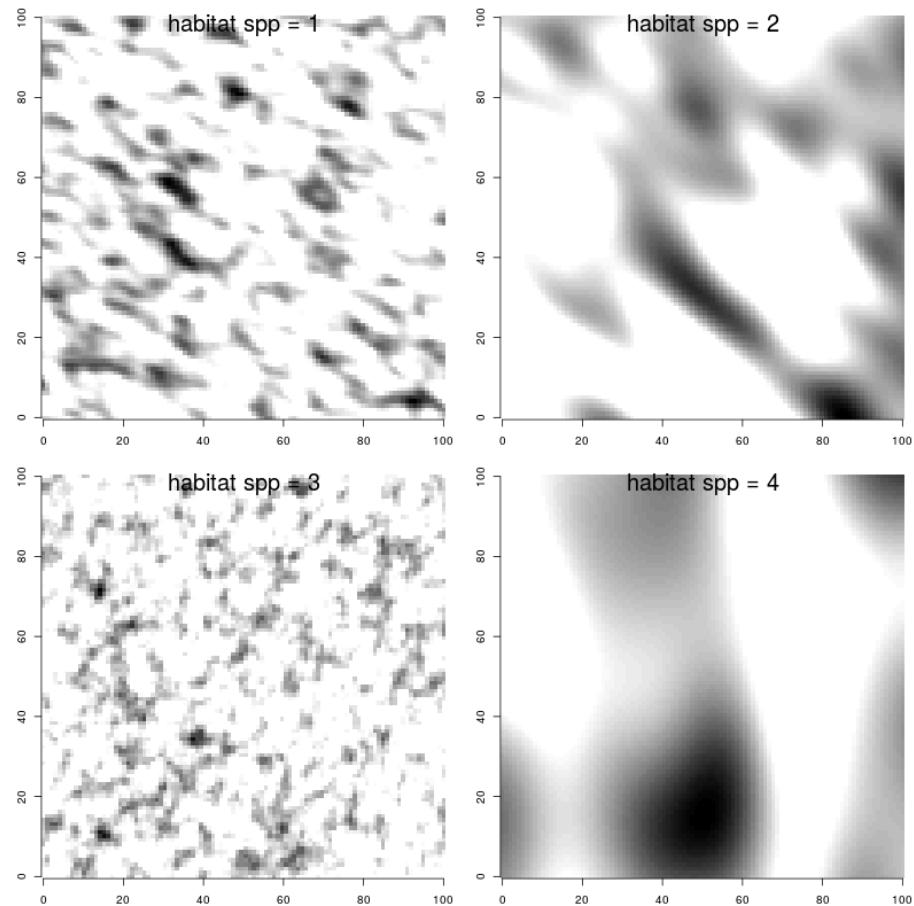


Figure 2: habitat preference

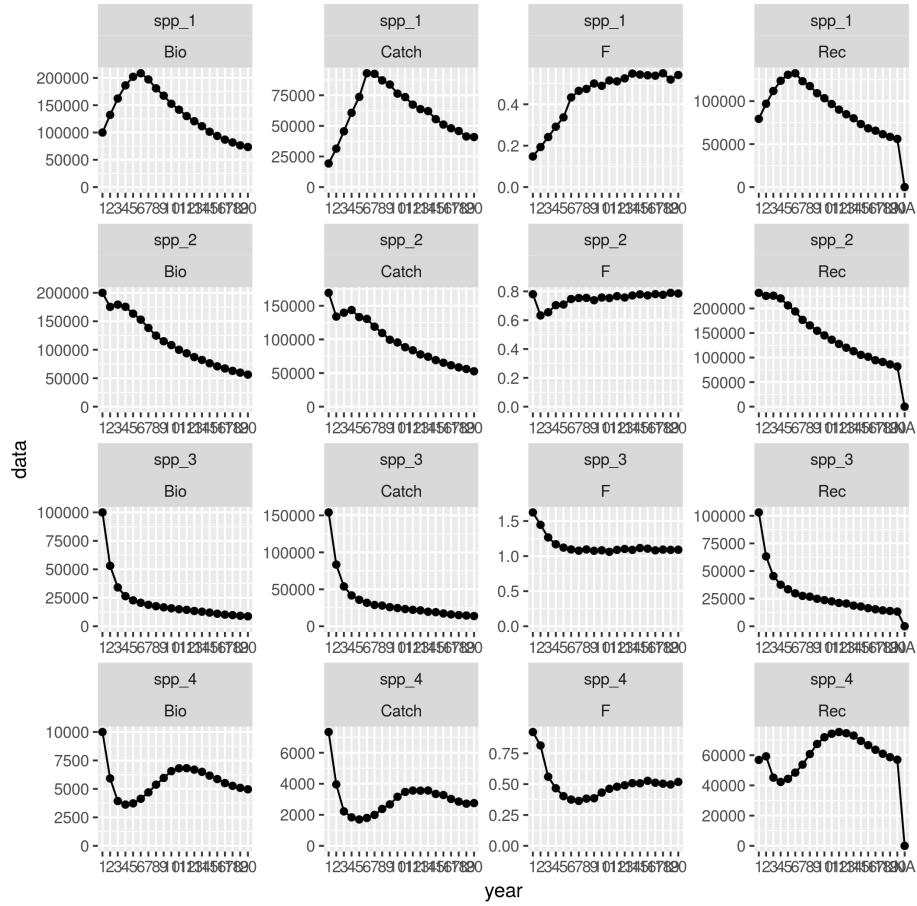


Figure 3: Summary of annualised metrics: biomass, catch, fishing mortality and recruitment. x-axis is the year, y the value

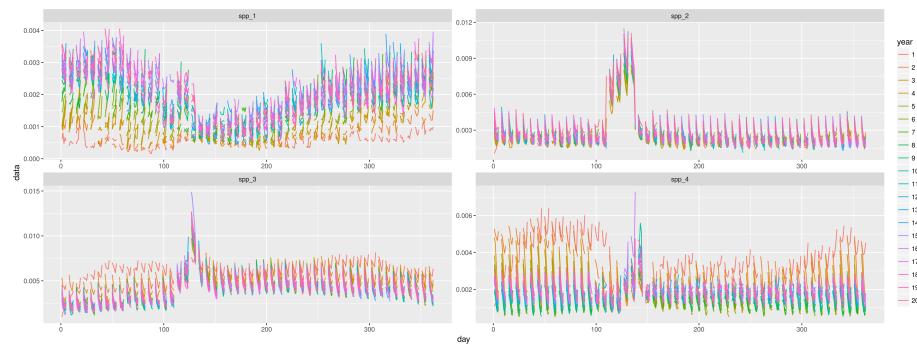


Figure 4: f dynamics - the daily fishing mortalities, each year is a different colour

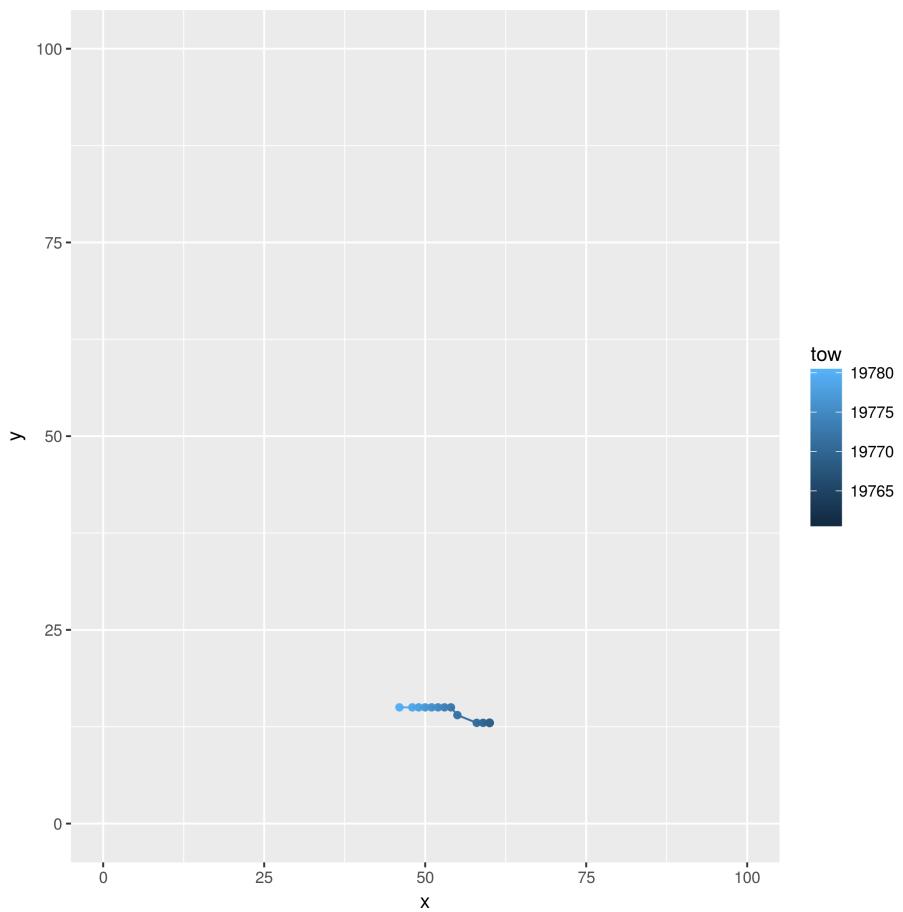


Figure 5: vessel movement - a single trip movement for one vessel

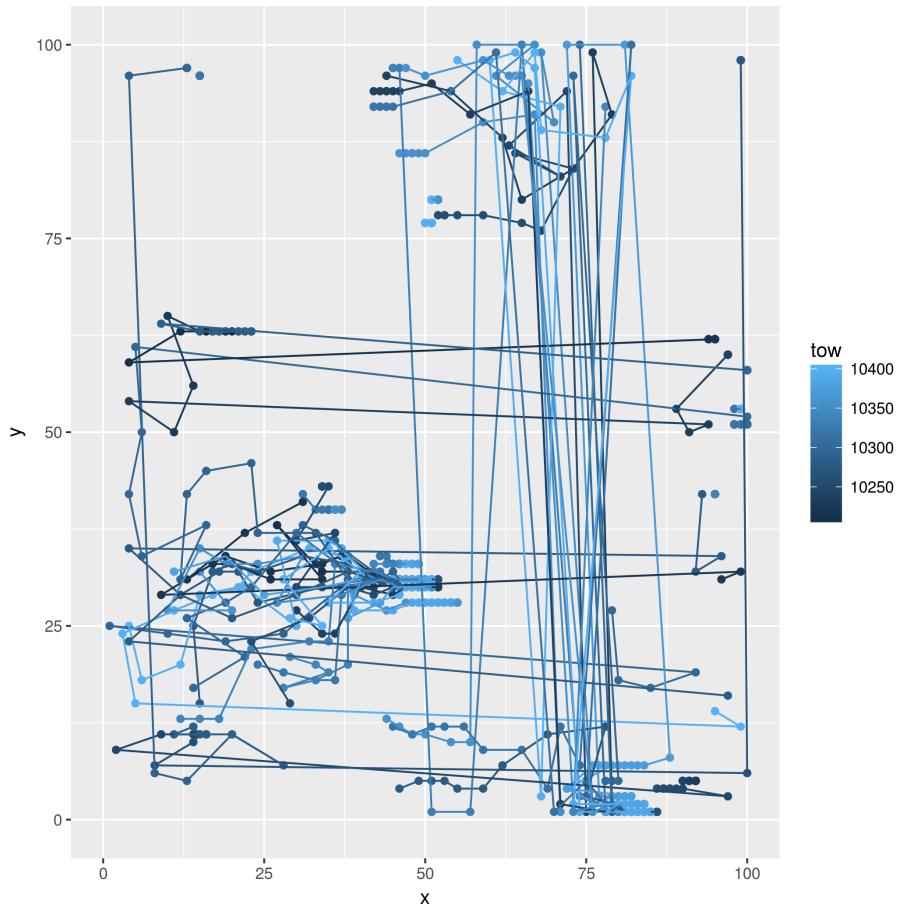


Figure 6: vessel movement for multiple trips from a single vessel. Note the movement off the side pops up the other side, but is joined by a line across the grid. This is from the torus approach rather than the edges being barriers

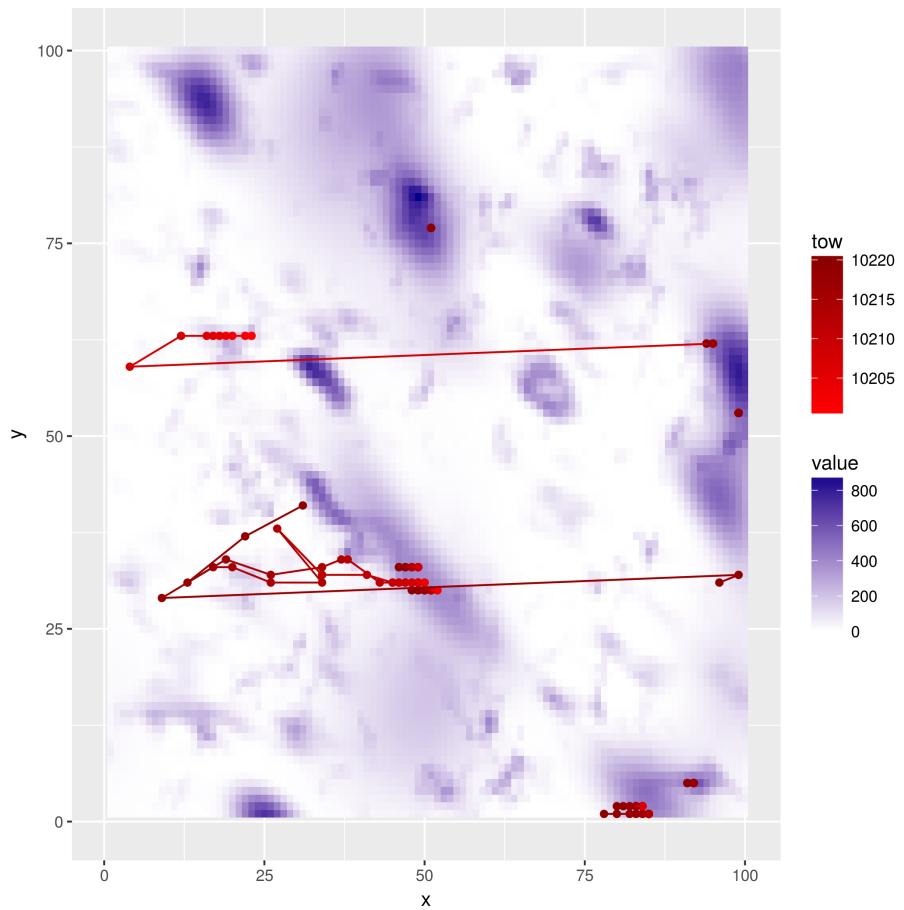


Figure 7: movement of a single vessel over a few trips overlaid on the value field (i.e. sum of the population abundance x catchability x value)

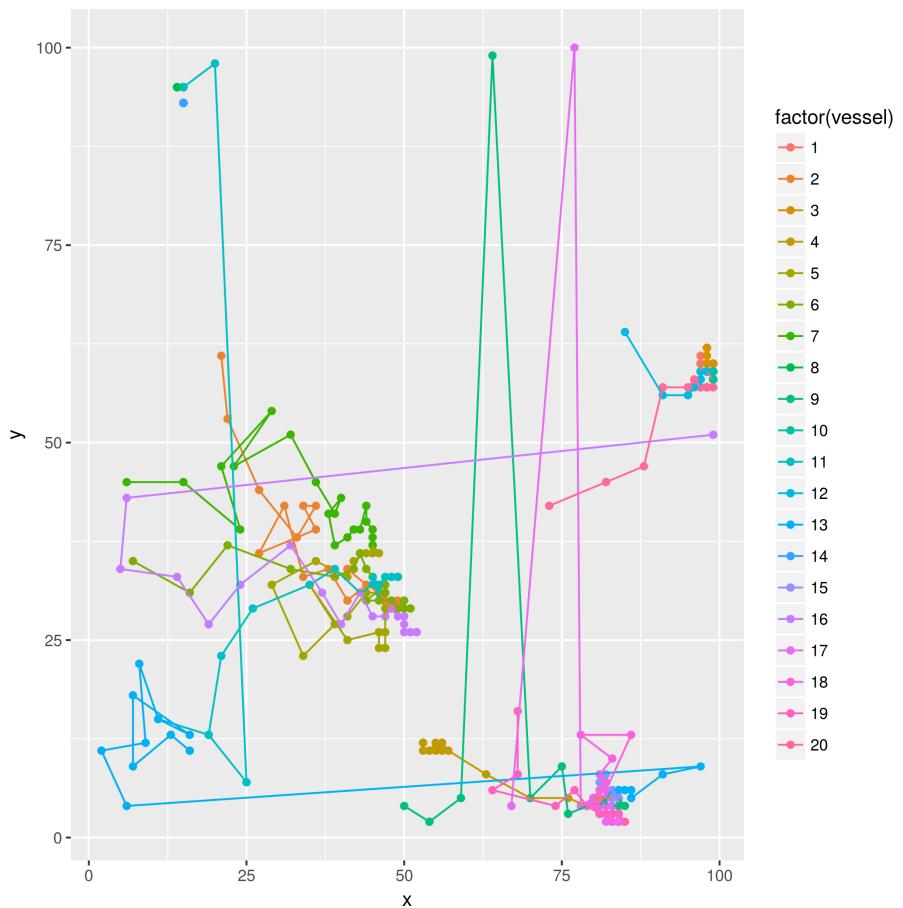


Figure 8: An entire fleets (20 vessels) movement for a single trip

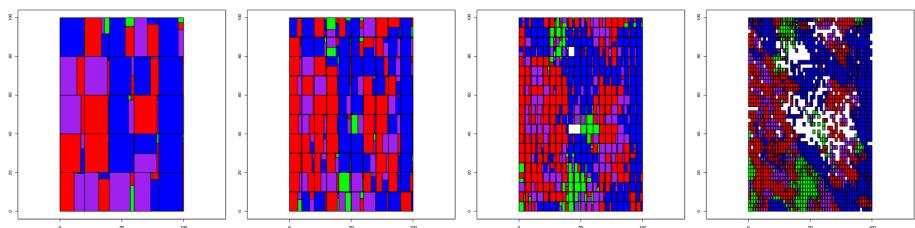


Figure 9: spatial catch composition - the raw catches per cell at 4 different spatial resolutions.
Sorry, its a bit small at the moment!

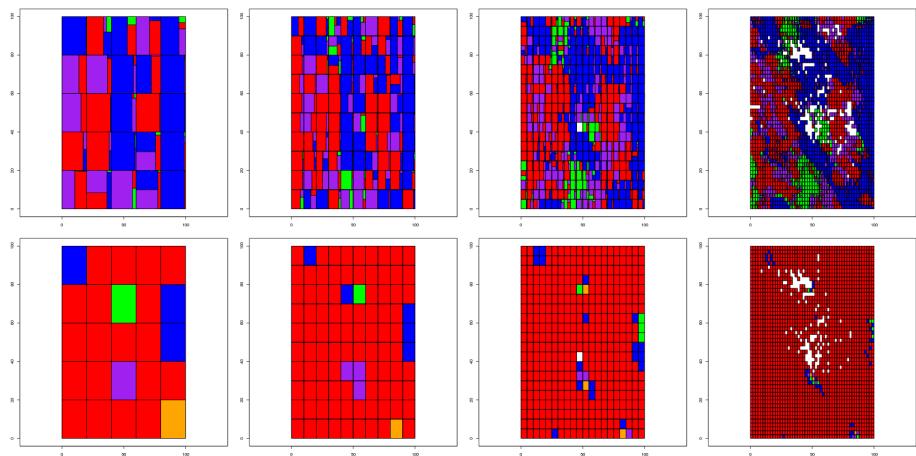


Figure 10: spatial catch composition (as above) but with clustering of cells performs on the bottom row. I'm confused as to why some entirely blue cells in the raw catch composition get allocated to the same cluster as some entirely red cells - needs investigating, it may be the clustering is not optimal

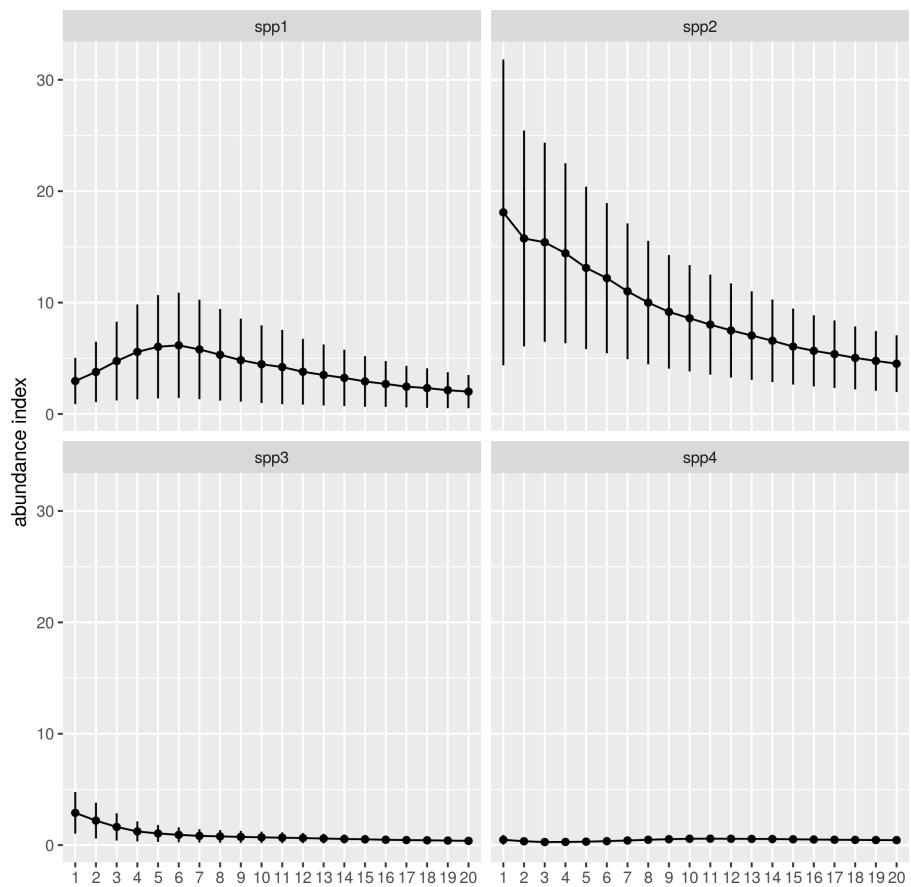


Figure 11: survey index - a non-spatial index generated from the fishery independent survey

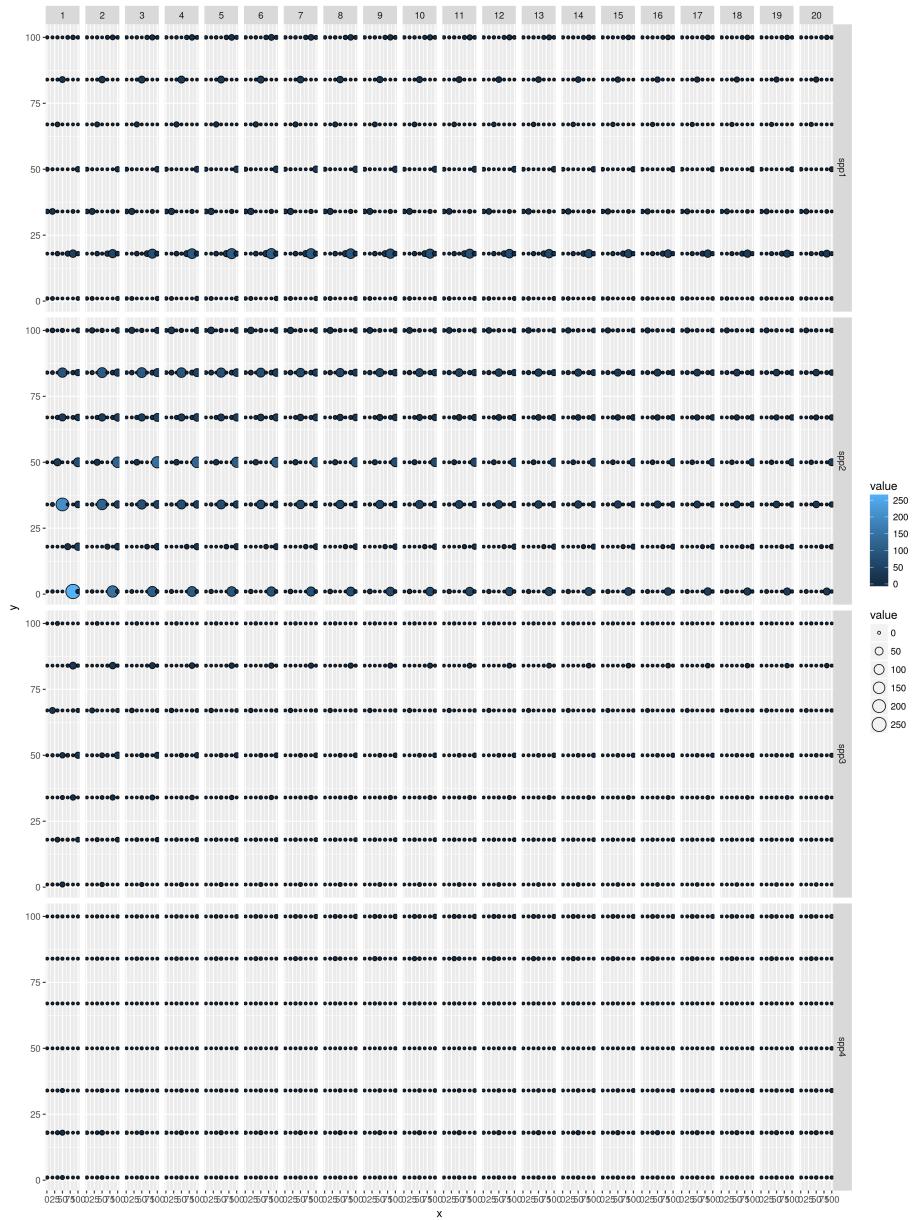


Figure 12: survey spatial abundance - a bubble plot of the survey abundances, not really useful for the paper

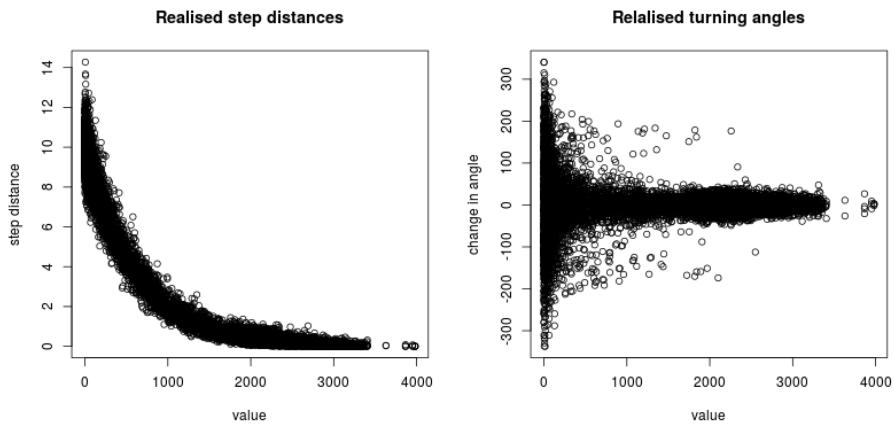


Figure 13: Realised step function - the step function as realised for a single fleet. For turning angles, it can be seen that at higher values, the turning range is less

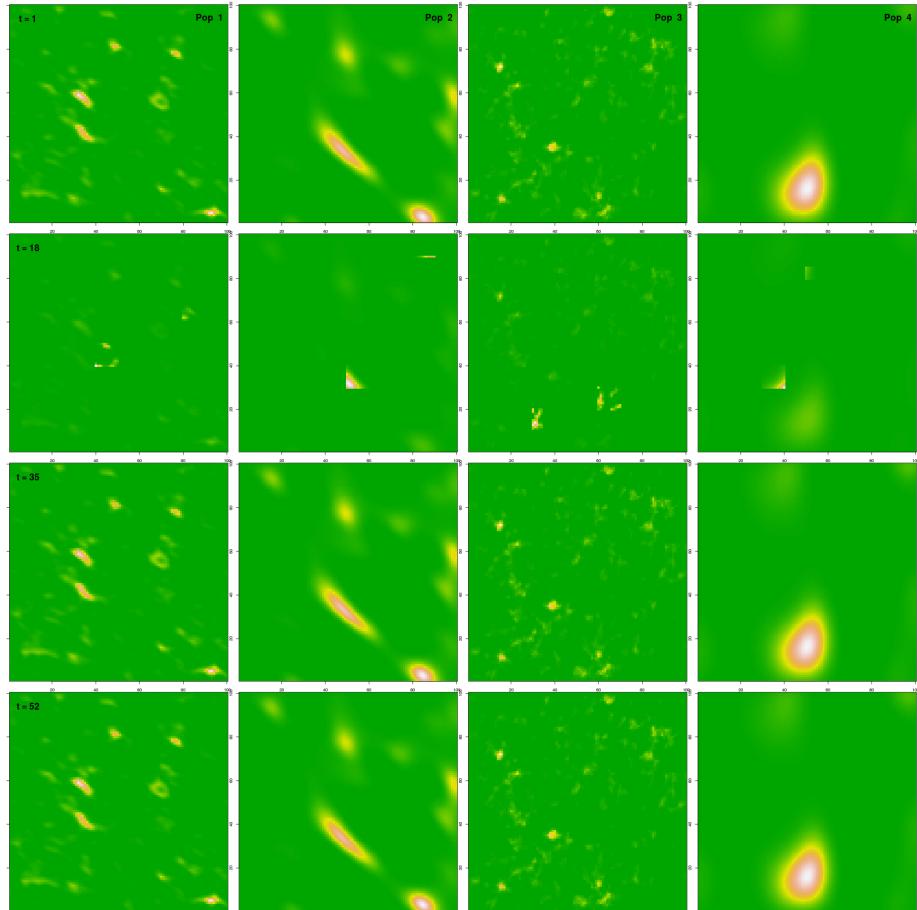


Figure 14: Spatial dynamics - the four populations at four time steps. Not really happy about the lack of dynamics here - mainly down to the static habitat leading to the populations settle in same cells over most time steps (exception: during the spawning period). Could include a temperature covariate or something to force some more temporal changes?

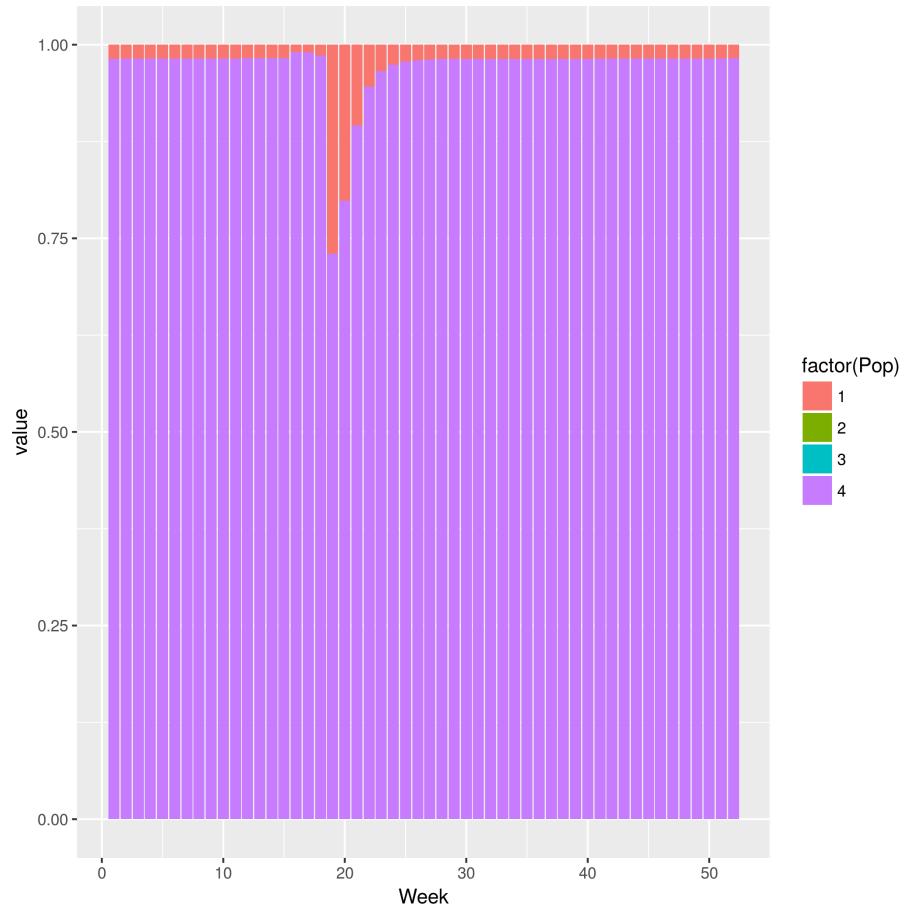


Figure 15: Temporal dynamics - the proportion of each population in a randomly chosen cell.
Similar criticism as above

³⁰¹ **References**