

# *MixFishSim*: highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

Paul J. Dolder<sup>a,b,\*</sup>, C  il  n Minto<sup>a</sup>, Jean-Marc Guarini<sup>c</sup>, Jan Jaap Poos<sup>d</sup>

<sup>a</sup>*Galway-Mayo Institute of Technology (GMIT), Dublin Road, Galway, Ireland*

<sup>b</sup>*Centre for Environment, Fisheries and Aquaculture Science (Cefas), Pakefield Road, Lowestoft, UK*

<sup>c</sup>*Sorbonne Universit  , Faculty of Sciences ~~Universit   Pierre-et-Marie-Curie<sup>JM</sup>~~, 4 Place Jussieu, 75005 Paris, France*

<sup>d</sup>*Wageningen Marine Research, Haringkade 1 1976 CP IJmuiden, Netherlands*

---

## Abstract

Most fisheries ~~Fishing~~<sup>JJ</sup> exploits<sup>JJ</sup> spatially and temporally heterogeneous fish populations, using species-unselective gear that can result in unintended, unwanted catch of low quota or protected species. Reducing these unwanted catches is crucial for biological and economic sustainability of ‘mixed fisheries’ and implementation of an ecosystem approach to fishing.

If fisheries are to avoid unwanted catch ~~To implement effective spatial measures to reduce discards~~<sup>PD</sup> a good understanding of spatiotemporal fishery dynamics is required. However, traditional scientific advice is limited by a lack of highly resolved knowledge of population distribution, movement and how fishers interact with different fish populations. This reflects that data on fish location at high temporal and spatial resolutions is expensive and difficult to collect and therefore proxies inferred from either scientific surveys or commercial catch data are often used to model distributions, often with limited spatial and temporal resolution.

To understand how resolution impacts mixed fisheries inference, we develop

---

\*Corresponding author

Email address: `paul.dolder@gmit.ie` (Paul J. Dolder)

a highly resolved spatiotemporal simulation model incorporating: i) delay-difference population dynamics, ii) population movement using Gaussian Random Fields to simulate patchy, heterogeneously distributed populations, and iii) fishery dynamics for multiple fleet characteristics based on targeting via correlated random walk movement and learned behaviour.

We simulate 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, and ii) the true underlying population structures input to the simulation, to establish the potential and limitations of fishery-dependent data - an inherently biased sampling method due to fisher's targeting- to provide a robust picture of spatiotemporal distributions. Finally, we simulate an area closure based on areas defined from commercial the known ("real-population") distribution, commercial catch data and survey data at different temporal and spatial resolutions and assess their effectiveness on reducing catches of a fish population.

We conclude from our simulations that commercial data, while not unbiased, provides a useful tool for managing catches in mixed fisheries if applied at the correct spatiotemporal scale.

[333 words]

*Keywords:* Some, keywords, here. Max 6

*2010 MSC:* 00-01, 99-00

---

## 1. Introduction

Fishers exploit fish populations that are heterogeneously distributed in space and time with varying knowledge of species distributions using species-unselective fishing gear. In doing so<sup>PD</sup> fisheries ~~that~~<sup>PD</sup> catch an assemblage of species

~~and~~<sup>PD</sup>, ~~known as mixed fisheries~~ may, ~~when managed by single-species quotas~~  
~~can end up~~<sup>JJ</sup> ~~discarding~~<sup>JJ</sup> overquota catch when managed by single species  
 quotas,<sup>JJ</sup> leading to overexploitation of fish populations (Ulrich et al., 2011; Bat-  
 sleer et al., 2015)<sup>JJ</sup>. This discarding of fish in excess of quota hampers the abil-  
 ity to limit fishing mortality to within sustainable limits (Alverson et al., 1994;  
 Crowder and Murawski, 1998; Rijnsdorp et al., 2007)<sup>JJ</sup> ~~; reducing discarding~~  
~~is crucial~~<sup>PD</sup> to ensure biological and economic sustainability of fisheries ~~and~~  
~~implementation of an ecosystem approach to fisheries~~<sup>JJ</sup> ~~and. As such~~<sup>PD</sup> there  
 is increasing interest in technical solutions such as gear and spatial closures as  
 ways of ~~reducing unwanted catch~~ ~~avoiding discarding of fish~~<sup>JJPD</sup> (Kennelly and  
 Broadhurst, 2002; Catchpole and Revill, 2008; Bellido et al., 2011).

Changes to spatial fishing patterns ~~have~~ ~~Use of spatial management as a~~  
~~tools~~<sup>PD</sup> been proposed as a method to reduce discards (Holmes et al., 2011;  
 Little et al., 2014; Dunn et al., 2014)<sup>PD</sup>. However, ~~its~~<sup>PD</sup> implementation is  
 hampered by lack of knowledge of fish and fishery spatiotemporal dynamics and  
 understanding of the scale at which processes are important for management.  
 Understanding the correct scale for spatial management is crucial in order to  
 implement measures at a resolution that ensures effective management (Dunn  
 et al., 2016) while minimising economic impact. For example, a scale that  
 promotes species avoidance for vulnerable or low quota species while allowing  
 continuance of sustainable fisheries for available quota species.

~~Identifying~~ ~~Ensuring measures are implemented at~~<sup>PD</sup> an appropriate scale  
 has been a challenge in the past that has led to ineffectual measures with unin-  
 tended consequences such as limited impact towards the management objective  
 or increased benthic impact on previously unexploited areas (e.g. the cod clo-  
 sure in the North Sea (Rijnsdorp et al., 2001; Dinmore et al., 2003)). ~~MSince~~  
~~then in~~<sup>PD</sup> more refined spatial information has ~~since~~<sup>PD</sup> become available through  
 the combination of logbook and Vessel Monitoring System (VMS) data (Lee  
 et al., 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al., 2016)

36 and more real-time spatial management has been possible (e.g. Holmes et al.,  
 37 2011). Such information is, however, patchy and derived from an inherently  
 38 biased sampling programme (i.e. targeted fishing). ~~Further, fishers generally~~  
 39 ~~only recorded landings (not catch) on a daily basis. This leads to questions~~  
 40 ~~about the validity of inference that can be drawn from landings data assigned~~  
 41 ~~to VMS activity pings.~~<sup>PD</sup>

42  
 43 In order to understand ~~the consequences of using~~challenges that face<sup>PD</sup>  
 44 VMS-linked landings to draw inference on the underlying population structure  
 45 we develop a simulation model where population dynamics are highly-resolved  
 46 in space and time. ~~Being and are~~<sup>PD</sup> known ~~directly~~<sup>PD</sup> rather than inferred from  
 47 sampling or commercial catches, we can use the population model to evaluate  
 48 how inference from fisheries-dependent and fisheries independent sampling re-  
 49 lates to the real population structure<sup>PD</sup>. In our model system ~~p~~<sup>PD</sup>opulation  
 50 movement is driven by random (diffusive) and directed (advective) processes and  
 51 we incorporate characterisation of a number of different fisheries ~~dynamics~~<sup>PD</sup>  
 52 exploiting four fish populations with different spatial and population demo-  
 53 graphics.

54  
 55 Using our model we simulate ~~2040~~<sup>PD</sup> years of exploitation of the fish popu-  
 56 lations. ~~We and~~<sup>PD</sup> use the results ~~from the fishing model:~~<sup>PD</sup>

- 57 1. to understand how sampling-derived data reflects the underlying popula-  
 58 tion structures. We compare at different spatial and temporal aggregations  
 59 of data the real population to:
  - 60 (a) the inferred population from a stratified fixed-site sampling survey  
 61 design commonly used for fisheries monitoring purposes, otherwise  
 62 know as a fisheries-independent survey,
  - 63 (b) the inferred population from our fishery-dependent model which in-  
 64 cludes fishery-induced sampling dynamics.

65

This comes as a surprise: I thought this was going to be about discards<sup>JJ</sup> Agree, have removed this to avoid confusion<sup>PD</sup>

2. to understand the impact of data aggregation and source on spatial fisheries management measures we simulate a fishery closure to protect a species based on different spatial and temporal data aggregations:

- (a) as if the real spatial population structure were known,
- (b) the fishery-independent inferred population structure
- (c) the fishery-dependent inferred population structure

We evaluate the theoretical "benefit" to the population of the closure(s), and effect on the other three populations. ~~Further, we extend our analysis to a range of spatial and temporal scales to assess the impact of these processes on the success of the management measure.~~<sup>PD</sup>

## 2. Materials and Methods

~~A~~We developed and implemented a simulation model with a<sup>PD</sup> modular event-based simulation model was developed with~~approach, where sub-~~<sup>PD</sup>modules ~~are~~<sup>PD</sup> implemented on independent time-scales appropriate to capture the characteristic of the ~~different processes~~<sup>PD</sup> (Figure 1). The following sub-modules were included to capture the full system: 1) Population dynamics, 2) Recruitment dynamics, 3) Population movement, 4) fishery dynamics.<sup>PD</sup>

~~The fishing model operated on a tow-by-tow basis, while~~<sup>PD</sup> ~~p-~~<sup>PD</sup> population dynamics (fishing and natural mortality, growth) operate on a daily time-step, while ~~p-~~<sup>PD</sup> population movement occurs on a weekly time-step. ~~R,~~ while ~~r~~<sup>PD</sup> recruitment ~~takes place~~<sup>PD</sup> periodically each year for a set time ~~duration~~<sup>PD</sup> (e.g. 3 weeks)<sup>PD</sup> at a specified point individual to a species.<sup>PD</sup>, while the fishing module operates on a tow-by-tow basis (i.e. multiple events a day)<sup>PD</sup>. The simulation framework is implemented in the statistical software package R (R Core Team, 2017) and<sup>PD</sup> available as an R package from the authors github ([www.github.com/pdolder/MixFishSim](http://www.github.com/pdolder/MixFishSim)).

If the paper has two goals this should be clear from the start, but may be better over 2 MSs<sup>JJ</sup> I would like to keep both parts, but have made clearer in how its set out. The closure scenarios form validation of the data aggregation, rather than effectiveness of the closures themselves - so its a continuation of the same question in my eyes<sup>PD</sup>

95 Here we describe each of the model components; 1) Population dynamics, 2)  
 96 Recruitment dynamics, 3) Population movement dynamics, 4) fishery dynamics.<sup>PD</sup>

## 97 2.1. Population dynamics

98 The basic population level processes are simulated using a modified two-  
 99 stage Deriso-Schnute delay difference model (Deriso, 1980; Schnute, 1985; Dich-  
 100 mont et al., 2003) occurring at a daily time-step. A daily time-step was cho-  
 101 sen as to discretise continuous population processes on a biologically relevant  
 102 and computationally tractable timescale.<sup>PD</sup> Under the population dynamics  
 103 module<sup>PD</sup> Here,<sup>PD</sup> population biomass growth and depletion for pre-recruits and  
 104 fish<sup>PD</sup> recruited fish<sup>PD</sup> to the fishery<sup>PD</sup> are modelled separately as a function  
 105 of previous recruited biomass, intrinsic population growth and recruitment:

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

106 where  $\rho$  is Brody's coefficient, shown to be approximately equal to  $\exp(-K)$ ,  
 107 where  $K$  is the growth rate from a von bertalanffy logistic growth model (Schnute,  
 108 1985).  $Wt_{R-1}$  is the weight of fish prior to recruitment, while  $Wt_R$  is the re-  
 109 cruited weight.  $\alpha_d$  represents the proportion of fish recruited during that day  
 110 for the year, while  $R_{\tilde{c},y}$  is the annual recruits in cell  $c$  for year  $y$ .

111

112 Mortality  $Z_{c,d}$  can be decomposed to natural mortality,  $M_{c,d}$ , and fishing  
 113 mortality,  $F_{c,d}$ , where both  $M_{c,d}$  and  $F_{c,d}$  are instantaneous rates with  $M_{c,d}$   
 114 fixed and  $F_{c,d}$  calculated by solving the Baranov catch equation (Hilborn and  
 115 Walters, 1992) for  $F_{c,d}$ :

$$C_{c,d} = \frac{F_{c,d}}{F_{c,d} + M_{c,d}} * (1 - e^{-(F_{c,d} + M_{c,d})}) * B_{c,d}$$

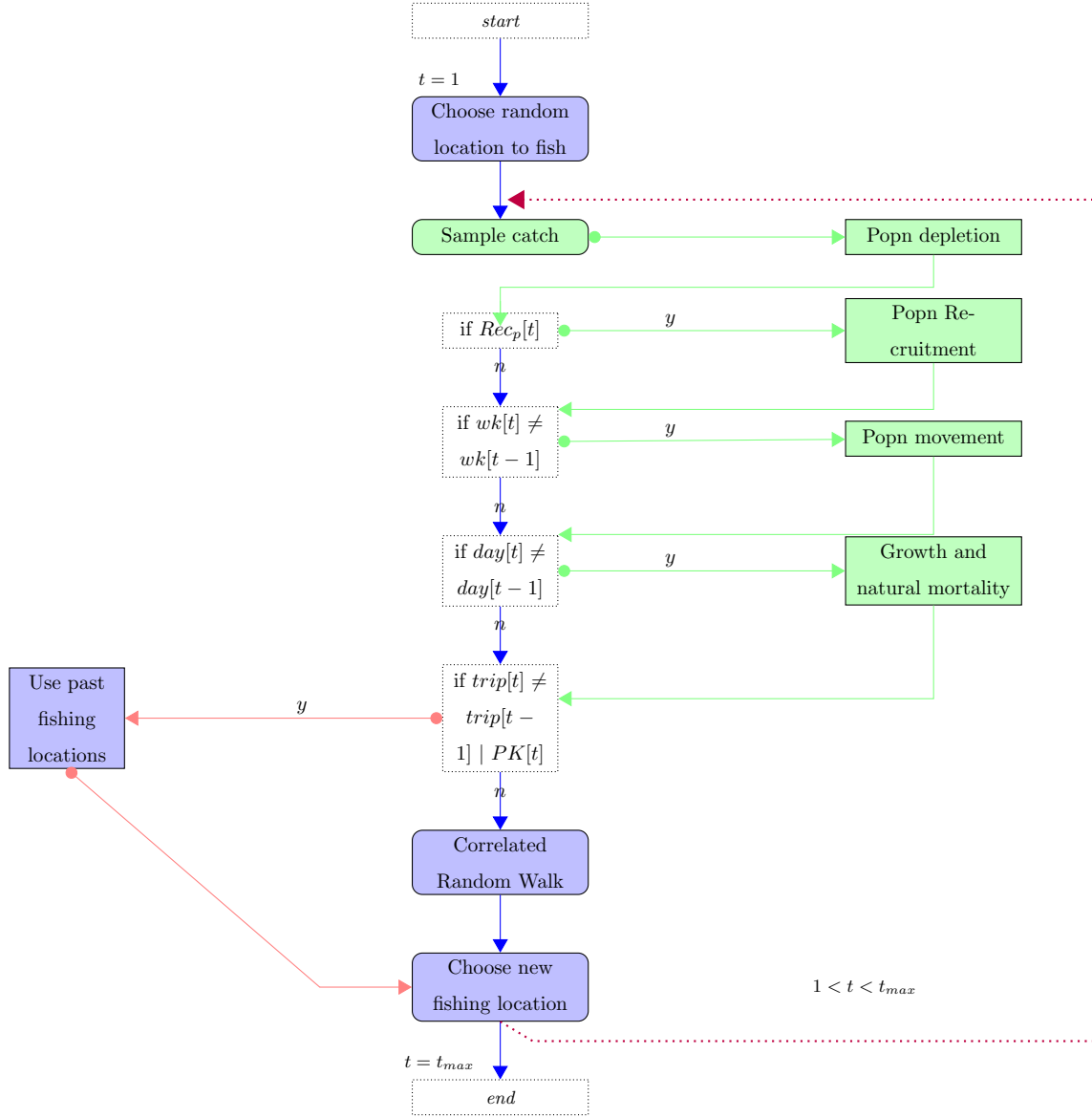


Figure 1: Overview Schematic of simulation model. The blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the timesteps at which processes occur;  $Rec$  is a recruitment period for population  $p$ ,  $t = tow$ ,  $t_{max}$  is the total number of tows,  $wk$  is a weekly timestep,  $day$  is a day timestep,  $trip$  is a trip time step.

116 where  $C_{c,d}$  is the summed catch from the fishing model across all fleets and  
 117 vessels in cell  $c$  for the population during the day  $d$ , and  $B_{c,d}$  the daily biomass  
 118 for the population in the cell.

## 120 2.2. Recruitment dynamics

121 Recruitment is modelled through a function relating the mature biomass to  
 122 recruits at time of recruitment. In *mixfishsim*, it can be modelled either either  
 123 as a stochastic Beverton-Holt stock-recruit form (Beverton and Holt, 1957):

$$\bar{R}_{c,d} = \frac{(\alpha * B_{c,d})}{(\beta + B_{c,d})}$$

$$R_{c,d} \sim \log N[(\log(\bar{R}_{c,d}), \log(\sigma^2))]$$

124 Where  $\alpha$  is the maximum recruitment rate,  $\beta$  the spawning stock biomass (SSB)  
 125 required to produce half the maximum,  $B$  current SSB and  $\sigma^2$  the variability  
 126 in the recruitment due to stochastic processes.

127  
 128 or a stochastic Ricker form (Ricker, 1954):

$$\bar{R}_{c,d} = B_{c,d} * e^{(\alpha - \beta * B_{c,d})}$$

$$R_{c,d} \sim \log N[(\log(\bar{R}_{c,d}), \log(\sigma^2))]$$

129 where  $\alpha$  is the maximum productivity per spawner and  $\beta$  the density depen-  
 130 dent reduction in productivity as the SSB increases.

## 131 2.3. Population movement dynamics

132 To simulate ~~how~~<sup>JJ</sup> fish populations ~~might be~~<sup>JJ</sup> distributioned<sup>JJ</sup> in space and  
 133 time, ~~we employed~~<sup>JJ</sup> a Gaussian spatial process ~~was employed~~<sup>JJ</sup> to model habi-  
 134 tat suitability for each of the populations. ~~An, with an~~<sup>JJ</sup> advection-diffusion  
 135 process ~~to~~<sup>JJ</sup> controlled<sup>JJ</sup> ~~how the~~<sup>JJ</sup> populations<sup>JJ</sup> movement<sup>JJ</sup> over time with  
 136 a moving temperature covariate to capture temporal dependencies. ~~This was~~

[link  $F$  to effort and catchability - as I think we have  $F$  as an emergent property of the fleets rather than something we solve for (I could be wrong though!) - catch for a vessel is a product of catchability and biomass, i.e.  $C = qB$ , but this catch is summed to solve for  $F$ . So its both really]CM

What have a temperature covariate? Could just use time<sup>JJ</sup> Was intended as some biological meaning - species thermal tolerances load onto the temperature



intended to balance realism in population movement, capturing the main directed and random processes, and practicality of modelling the population rather than individual fish.<sup>JJ</sup>

For the<sup>PD</sup> habitat we defined<sup>PD</sup> a Gaussian random field process,  $\{S(c) : c \in \mathbb{R}^2\}$ , that is a stochastic process<sup>PD</sup> where for<sup>PD</sup> any set of cells  $c_1, \dots, c_n$  where for each  $c_i \in \mathbb{R}^{2PD}$ , the joint distribution of  $S = \{S(c_1), \dots, S(c_n)\}$  is multivariate Gaussian. The distribution is specified by its mean function,  $\mu(c) = E[S(c)]$  and its covariance function,  $\gamma(c, c') = Cov\{S(c), S(c')\}$  (Diggle and Ribeiro, 2007).

The covariance structure affects the smoothness of the surfaces which the process generates; and<sup>PD</sup> we used the Matérn family of<sup>PD</sup> covariance structures<sup>PD</sup>, as one where<sup>PD</sup> the correlation strength weakens the further the distance apart (i.e. the correlation between  $S(x)$  and  $S(x')$  decreases as the distance  $u = \|x - x'\|$  increases)<sup>PD</sup>. The Matérn covariance structure models the spatial autocorrelation observed with animal distributions (Tobler, 1970; F. Dormann et al., 2007)<sup>PD</sup> and the Matérn correlation<sup>PD</sup> is a two-parameter family where:

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

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

In the simulation model, the habitat for each of the populations was<sup>PD</sup> generated with<sup>PD</sup> the *RFSimulate* function of the *RandomFields* R package (Schlatter et al., 2015), implementing different parameter settings to affect the patchiness of the populations. Each population was<sup>PD</sup> initialised at a single location, and subsequently moved<sup>PD</sup> according to a probabilistic distribution based on habitat suitability, temperature and distance from current

Not clear how habitat/GRF affect local abundances, only have  $B_{y,d}$ <sup>JJ</sup> Have included cell reference,  $c$  to make spatial link explicit<sup>PD</sup>

Introduce the gamma function, and why this covariance structure? Why correlate values in the random field?<sup>JM</sup> to allow populations to have different aggregation densities; have tried to clarify<sup>PD</sup>

167 cell:<sup>PD</sup>

$$Pr(J|I) = \frac{e^{-\lambda * d_{IJ}} \cdot (Hab_{J,p}^2 \cdot Tol_{J,p,wk})}{\sum_{c=1}^C e^{-\lambda * d} \cdot (Hab_{c,p}^2 \cdot Tol_{c,p,wk})} \quad (1)$$

168 Where  $d_{IJ}$  is the euclidean distance between cell  $I$  and cell  $J$ ,  $\lambda$  is a given  
 169 rate of decay,  $Hab_{J,p}^2$  is the squared index of habitat suitability for cell  $J$  and  
 170 population  $p$ , with  $Tol_{J,p,wk}$  the temperature tolerance for cell  $J$  by population  
 171  $p$  in week  $wk$ .

172

173 During specified weeks of the year, the habitat quality <sup>was</sup>is<sup>PD</sup> modified for  
 174 user-defined<sup>PD</sup> spawning habitats<sup>PD</sup>, resulting in ~~meaning~~<sup>PD</sup> each population  
 175 ~~had~~has<sup>PD</sup> a concentrated area where spawning takes place and the population  
 176 moved<sup>PD</sup> towards these cell~~s~~his<sup>PD</sup> in the weeks prior to spawning.

177

178 The temperature field <sup>was</sup>is<sup>PD</sup> simulated to be on a gradient from a South-  
 179 Westerly to North-Easterly direction, with temperature in each cell changing  
 180 gradually on a week-by-week basis so that initially high temperature areas cy-  
 181 cled<sup>PD</sup> to lower temperatures and low temperature areas vice versa. Each pop-  
 182 ulation  $p$  ~~wa~~i<sup>PD</sup>s assigned a thermal tolerance with mean,  $\mu_p^{\text{PD}}$  and variance,  
 183  $\sigma_p^2^{\text{PD}}$  so that each cell and population temperature suitability is defined that:

$$Tol_{c,p,wk}^{\text{PD}} = \frac{1}{\sqrt{(2\pi \cdot \sigma_p^2)}} \cdot \exp\left(-\frac{(T_{c,wk}^{\text{PD}} - \mu_p^{\text{PD}})^2}{2 \cdot \sigma_p^2}\right) \quad (2)$$

184 Where  $Tol_{c,p,wk}^{\text{PD}}$  is the tolerance of population  $p$  in cell  $c$  in week  $wk^{\text{PD}}$ ,  
 185  $T_{c,wk}^{\text{PD}}$  is the temperature in the cell given the week<sup>PD</sup> and  $\mu_p^{\text{PD}}$  and  $\sigma_p^2^{\text{PD}}$   
 186 the mean and standard deviation of the population temperature tolerance.

187

188 The final process resulted in independent populations structure and move-  
 189 ment patterns, with population movement occuring on a weekly basis. This  
 190 process approximated the demographic shifts in fish populations throughout a  
 191 year while maintaining seasonal patterns for spawning.<sup>PD</sup>

What does  
it mean con-  
cisely? Areas  
are assigned?<sup>JM</sup>  
Yes, the ar-  
eas are pre-  
defined - I have  
amended to re-  
flect and tried  
to clarify.<sup>PD</sup>

## 192 2.4. Fleet dynamics

193 The fleet dynamics can be broadly categorised into three components; fleet  
194 targeting - which determined<sup>PD</sup> the fleet catch efficiency and preference towards  
195 a particular species; trip-level decisions, which determined<sup>PD</sup> the initial location  
196 to be fished at the beginning of a trip; and within-trip decisions, determining  
197 movement from one fishing spot to another within a trip.

### 198 2.4.1. Fleet targeting

199 Each fleet of  $n$  vessels was<sup>PD</sup> characterised by both a general efficiency,  $Q$ ,  
200 and a population specific efficiency,  $Q_p$ . Thus, the product of these parameters  
201 affected<sup>PD</sup> the overall catch rates for the fleet and the preferential targeting of  
202 one population over another. This, in combination with the parameter choice  
203 for the step-function defined below<sup>PD</sup> (as well as some randomness from the  
204 exploratory fishing process) determined<sup>PD</sup> the preference of fishing locations for  
205 the fleet. All species prices were<sup>PD</sup> kept the same, across fleets and seasons;  
206 ~~though can be made to vary seasonally<sup>PD</sup>.~~

### 207 2.4.2. Trip-level decisions

208 NOTE: THIS IS EXPLORE-EXPLOIT STRATEGY VIZ. BAILEY ET AL  
209 POSEIDON MODEL.

210 Several studies (e.g. Hutton et al., 2004; Tidd et al., 2012; Girardin et al.,  
211 2015) have confirmed past activity and past catch rates are strong predictors  
212 of fishing location choice. For this reason, the fleet dynamics sub-model in-  
213 cluded<sup>PD</sup> a learning component, where a vessel's initial fishing location in a  
214 trip was<sup>PD</sup> based on selecting from previously successful fishing locations. This  
215 was<sup>PD</sup> achieved by calculating expected profit from locations fished during<sup>PD</sup>  
216 previous fishing events in the previous trip as well as the previous time periods  
217 in past years, and choosing randomly from the top 75 % of fishing events as de-  
218 fined by the expected profit<sup>PD</sup>. Expected profit was estimated from the  
219 revenue from previous times fished at a location minus the fuel cost of travelling  
220 to the location.<sup>PD</sup> Simulation testing indicated that this learning increased the

mean value of catches for the vessels, over just relying on the correlated random walk function as described for the 'within trip' decisions below<sup>PD</sup>.

Correlated random walk of what<sup>JJ</sup>

### 2.4.3. Within-trip decisions

Fishing locations within a trip are initially<sup>PD</sup> determined by a modified random walk process. As the simulation progresses, the within-trip decision become gradually more influenced by past locations fished, based on the same process as the initial location, influenced by expected profit at a fishing location.<sup>PD</sup> A random walk was chosen for the exploratory fishing process as it is the simplest assumption commonly used in ecology to describe optimal<sup>PD</sup> animal movement which<sup>PD</sup> search strategizing<sup>PD</sup> for exploiting<sup>PD</sup> homogeneously distributed prey about which there is uncertain knowledge (Viswanathan et al., 1999). In a random walk, movement is a stochastic process through a series of steps. These steps have a length, and a direction<sup>JJ</sup> that can either be equal in length or take some other functional form. The direction of the random walk can be correlated, (known as 'persistence'), providing some overall location-of<sup>PD</sup> directional movement (Codling et al., 2008) or uncorrelated<sup>PD</sup>.

A Lévy flight<sup>JJ</sup> is a particular form of random walk characterised by a heavy-tailed distribution of step-length. The Lévy flight<sup>JJ</sup> has received a lot of attention in ecological theory in recent years as having shown to have very similar characteristics as those observed by animals in nature, and being a near optimum searching strategy for predators pursuing patchily distributed prey (Viswanathan et al., 1999; Bartumeus et al., 2005; Sims et al., 2008). Bertrand et al. (2007) showed that Peruvian anchovy fishermen have a stochastic search pattern similar to that observed with a Lévy walk. However, it remains a subject of debate (e.g. see Edwards, 2011; Reynolds, 2015)<sup>PD</sup>, with the contention that search patterns may be more simply characterised as random walks (Sakiyama and Gunji, 2013) with specific patterns related to the characteristics of the prey field (Sims et al., 2012).

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<sup>JJ</sup> recent fishing success, measured as the summed value of fish caught (revenue,  $Rev$ ),

$$Rev = \sum_{p=1}^P \underline{LC}^{PD}_p \cdot Pr_p$$

251 where  $\underline{LC}^{PD}_p$  is ~~landingscatch~~<sup>PD</sup> of a population  $p$ , and  $Pr_p$  price of a popula-  
 252 tion, to step distance. Here, when fishing is successful vessels remain in a similar  
 253 location and continue to exploit the local fishing grounds. When unsuccessful,  
 254 they move some distance away from the current fishing location. The movement  
 255 distance retains some degree of stochasticity, which can be controlled separately.

256 The step function takes the form:

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

257  
 258 So that, a step from (x1,y1) to (x2, y2) is defined by:

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

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

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

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

259 with  $k$  the concentration parameter from the von ~~Mm~~<sup>JJ</sup>ises distribution  
 260 which we correlate with the revenue so that  $k = (Rev + 1/RefRev) * max_k$ ,  
 261 where  $max_k$  is the maximum concentration value,  $k$ , and RefRev is parame-  
 262 terised as for  $\beta_3$  in the step length function.

So step length increases with increasingly gross revenue?<sup>JJ</sup> No, the opposite<sup>PD</sup>

#### 263 2.4.4. Local population depletion

264 Where several fishing vessels are exploiting the same fish population compe-  
265 tition is known to play an important role in local distribution of fishing effort  
266 (Gillis and Peterman, 1998). If several vessels are fishing on the same patch of  
267 fish, local depletion and interference ~~competition~~<sup>JJ</sup> will affect fishing location  
268 choice of the fleet as a whole (Rijnsdorp, 2000; Poos and Rijnsdorp, 2007). In  
269 order to account for this behaviour, the fishing sub-model operates spatially on  
270 a daily time-step so that for future days the biomass available to the fishery  
271 is reduced in the areas fished. The cumulative effect is to make heavily fished  
272 areas less attractive as future fishing opportunities.

#### 273 2.5. Fisheries independent survey

274 A fisheries-independent survey is simulated where fishing on a regular grid  
275 begins each year at the same time for a given number of stations (a fixed station  
276 survey design). Catches of the populations ~~at each station~~<sup>JJ</sup> are recorded  
277 but not removed from the population. This provides a fishery independent  
278 snapshot of the populations at a regular spatial ~~intervals~~<sup>JJ</sup> each  
279 year, similar to scientific surveys undertaken by fisheries research agencies.

### 280 3. Calculation

#### 281 3.1. Population parameterisation

282 We parameterised the simulation model for four populations with differing  
283 habitat preference, ~~and~~ temperature tolerances (Figures S1, S3, S4, S5, S6, S7),  
284 population demographic, ~~and~~ recruitment functions. In addition, each of the  
285 populations has two defined spawning areas which result in the populations  
286 moving towards these areas in given weeks (Figure S2) and population-specific  
287 movement rates (Table 4). The realised movement of the populations for a num-  
288 ber of weeks is shown in Figure S9 while the realised daily fishing mortality are  
289 shown in Figure S10.

290

291 *3.2. Fleet parameterisation*

292 The fleets were parameterised to reflect five different characteristics based  
293 on targeting preference and exploitation dynamics (Table 5). ~~Setting a tar-~~  
294 ~~geting parameter ( $Q$ ) that differed across fleets ensured different spatial dy-~~  
295 ~~namics, due to preferential targeting of populations that differ in their spatial~~  
296 ~~distributions. This ensures that different fleets have different spatial dynamics,~~  
297 ~~preferentially targeted different fish populations~~<sup>PD</sup>. The stochasticity in the  
298 random walk process ensures that different vessels within a fleet have slightly  
299 different spatial distributions based on individual experience, while the step  
300 function was parameterised dynamically so that vessels take smaller steps where  
301 the fishing location yields in a top quartile of the value available in that year  
302 (as defined per fleet in Table 5).

303

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

308 An example of the realised fleet movements for a single vessel during a single  
309 trip are given in Figure S11, while Figure S12 shows multiple trips for a single  
310 vessel, ~~Figure~~<sup>PD</sup> S13 the vessel movements for some trips overlaid on the value  
311 field, ~~Figure~~<sup>PD</sup> S14 shows fishing locations for an entire fleet of 20 vessels for  
312 a single trip, ~~and Figure~~<sup>PD</sup> S15 shows an example of the step function  
313 realisation and turning angles from the correlated random walk.

314 *3.3. Survey settings*

315 The survey simulation was set up with follow a fixed gridded station design  
316 with 100 stations fished each year, starting on day 92 ~~and ending on day 112~~  
317 ~~(5 stations per day)~~<sup>PD</sup> with same catchability parameters for all populations  
318 ( $Q_p = 1$ ).

Move some of  
the supple-  
mentary fig-  
ures to the  
manuscript<sup>JJ</sup>

### 3.4. Simulation settings

To illustrate the capabilities on *MixFishSim*, we investigate the influence of the temporal and spatial resolution of different data sources on the reduction in catches of a population given spatial closures. To do so, we first set up with simulation to run for 10 years based on a 100 X 100 square grid, with five fleets of 20 vessels each and four fish populations. Fishing takes place four times a day per vessel and five days a week, while population movement is every week.

We allow the simulation to run unrestricted for 5 years, and subsequently close areas for the last 5 years of the simulation based on data (either derived from the commercial catches, fisheries-independent survey or the 'real population' - the underlying populations assumed to be known perfectly) used at different spatial and temporal scales.

The following steps are undertaken to determine closures:

1. Extract data source
2. Aggregate according to resolution
3. Interpolate across entire area at desired resolution
4. Close top 5 % of areas

In total 56 closure scenarios were run which represent combinations of

- **data types:** commercial logbook data, survey data and 'real population',
- **temporal resolutions:** weekly, monthly and yearly closures,
- **spatial resolutions:** 1 x 1 grid, 5 x 5 grid, 10 x 10 grid and 20 x 20 grid.

Survey closures were on an annual basis only, as this was the most temporally resolved survey data available.

move to start of methods section<sup>JJ</sup> I think ecological modelling wants the 'calculations' section here..will check<sup>PD</sup>

Is there equilibrium after 5 years or still some trend in B<sup>JJ</sup> Not at equilibrium yet...I need to rerun until steady state, looks 20 years. Will update<sup>PD</sup>

Procedure unclear. Refer to symbols in methods section or switch order starting with description of data type etc..<sup>JJ</sup> Yes, will redo<sup>PD</sup>



## 344 4. Results

345 The species distribution themselves

346 The consequences of different spatial aggregations of the data are shown in  
347 Figure 2, which represents the aggregation of catch from each of the data sources  
348 over a year at different spatial resolutions.

349  
350 The finer spatial grid for the the real population (top left) and commercial  
351 data (top middle) show similar patterns, though there are unsampled gaps in  
352 the commercial data from a lack of fishing activity (particularly in the lower left  
353 part of the sampling domain). The survey data at this spatial resolution shows  
354 very sparse and uninformative information about the spatial distributions of the  
355 populations. The slightly aggregated data on a 5 x 5 grid shows similar patterns,  
356 and while losing some of the spatial detail there remains good consistency be-  
357 tween the 'real population' and the commercial data. Survey data starts to pick  
358 out some of the similar patterns as the other data sources, but lacks coverage.  
359 The spatial catch information on a 10 x 10 and 20 x 20 grid loses a signifi-  
360 cant amount of information about the spatial resolutions for all data sources,  
361 and some differences between the commercial and 'real population' data emerge.

362  
363 Figure 3 shows the consequences of different temporal aggregations of the  
364 data, with 156 weekly (top), 36 monthly (middle) and 3 yearly (bottom) catch  
365 compositions across a 20 x 20 area.

366  
367 As can be seen from the 'real population', the monthly aggregation captures  
368 the major patterns seen in the weekly data, albeit missing more subtle differ-  
369 ences. The yearly data results in a constant catch pattern due to the aggregation  
370 process (sometimes known as an aggregation bias). The commercial data on a  
371 weekly basis shows some of the same patterns as the 'real population', though  
372 the first species (in red) is less well represented and some weeks are missing  
373 catches from the area. The monthly data. The monthly data shows some con-

374 sistency between the 'real population' and commercial data for species 2 - 4,  
375 though species 1 remains underrepresented. On an annual basis, interestingly  
376 the commercial data underrepresents the first species (in red) while the survey  
377 overrepresents species 1. This is likely due to the biases in commercial sampling,  
378 with the fisheries not targeting the areas where species 1 are present, and the  
379 biases in the survey sampling from overrepresentation of the spatial distribution.

380  
381 We implemented a spatial closure using the different data sources and spatial  
382 and temporal aggregations as outlined in the protocol in Section 3.4. We used  
383 this to assess the efficacy of a closure in reducing fishing mortality on species 1,  
384 given availability of data and its use at different resolutions in order to evaluate  
385 the trade-offs in data sources. Figure 4 shows the trend in fishing mortality  
386 for each species simulated (columns) given the data sources (rows), temporal  
387 aggregations (colour lines) and spatial aggregations (linestyles), while Figure 5  
388 shows the change in fishing mortality from before the closure (average F years  
389 2 - 4) to after the closure (average F years 8 - 10).

390  
391 For the closures based on 'real population' (bottom row), the most disag-  
392 gregated data (a weekly timescale and 1 x 1 resolution) was most effective,  
393 reducing fishing mortality on species 1 (left) by  $\sim 60\%$ . Next was the monthly  
394 closures ( $< \sim 30\%$ ). The least effective were the yearly closures (blue lines)  
395 at all spatial resolutions, which resulted in increased fishing mortalities ( $> 30$   
396  $\%$  - N.B. Note though, this is consistent with the increasing trends in F, which  
397 is probably more related to the fact that Fs hadn't stabilised in the simulation  
398 from the fishing vessels "learning" the best locations - I will rerun the sims for  
399 a longer time (20 - 30 years).

400  
401 For the survey data, which can only be implemented on a yearly timescale,  
402 the closures had no effect at any data resolution. The results are identical for  
403 the different data resolutions except 20 x 20, which is why you can't see more  
404 than 2 points. This is because of the sparsity of the sampling locations.

405

406 For the commercial data, the most effective closure scenario was based on 1  
407 x 1 data at a monthly temporal resolution. This results in  $\sim 10\%$  reduction  
408 in  $F$  for species 1. This was the only closure scenario to have positive effect  
409 according to Figure 5, though looking at the trend in Figure 4 this looks more  
410 related to the continued increased in  $F$  trend, as other scenarios had an initial  
411 effect. Interestingly the monthly data scenario was more effective than weekly  
412 data, which I'd posit is due to the increase amount of data available from the  
413 commercial sampling across a month compared to a week. Commercial data  
414 used at an annual timestep was ineffective in bringing fishing mortality down  
415 for species 1.

416

417 Given the scenarios above, it seems clear that spatial disaggregation is more  
418 important than the temporal disaggregation of the commercial data, except  
419 when its used at an annual timeframe, which is the scenario that gave the worst  
420 results.

421 For the other species in the simulation (population 2 - 4) there was little  
422 difference in fishing mortalities across scenarios.

423 Note: The monthly commercial data scenario is the most effective of the  
424 realistic scenarios, as the 'real population' can only be seen as a baseline com-  
425 parison.

## 426 5. Discussion

## 427 6. Conclusions

## 428 Appendices

## 429 Abbreviations

430 Detail any unusual ones used.

Table 1: Description of variables for population dynamics sub-module

| Variable                      | Meaning  | Units            |
|-------------------------------|--|------------------|
| <b>Population dynamics</b>    |  |                  |
| <i>Delay-difference model</i> |  |                  |
| $B_{c,d}$                     | Biomass in cell $c$ and day $d$                                      | kg               |
| $Z_{c,d}$                     | Total mortality in cell $c$ for day $d$                              | -                |
| $R_{c,\bar{y}}$               | Annually recruited fish in cell                                      | yr <sup>-1</sup> |
| $\rho$                        | Brody's growth coefficient   | yr <sup>-1</sup> |
| $Wt_R$                        | Weight of a fully recruited fish                                     | kg               |
| $Wt_{R-1}$                    | Weight of a pre-recruit fish   | kg               |
| $\alpha_d$                    | Proportion of annually recruited fish recruited during day $d$       | -                |
| <i>Baranov catch equation</i> |  |                  |
| $C_{c,d}$                     | Catch from cell $c$ for day $d$                                      | kg               |
| $F_{c,d}$                     | Instantaneous rate of fishing mortality in cell $c$ on day $d$       | -                |
| $M_{c,d}$                     | Instantaneous rate of natural mortality in cell $c$ on day $d$       | -                |
| $B_{c,d}$                     | Biomass in cell $c$ on day $d$                                       | kg               |
| <b>Recruitment dynamics</b>   |  |                  |
| $\tilde{R}_{c,d}$             | is the recruitment in cell $c$ for day $d$                           | $d^{-1}$         |
| $B_{c,d}$                     | is the Biomass in cell $c$ for day $d$                               | $d^{-1}$         |
| $\alpha$                      | the maximum recruitment rate   | kg               |
| $\beta$                       | the biomass required to produce half the maximum rate of recruitment | kg               |

## Acknowledgements

those providing help during the research..

Table 2: Description of variables for population movement sub-module

| Variable                            | Meaning   | Units |
|-------------------------------------|---|-------|
| <b>Population movement dynamics</b> |   |       |
| <i>Habitat model</i>                |   |       |
| a                                   | b   | c     |
| <i>Thermal tolerance</i>            |   |       |
| $T_{c,wk}$                          | Temperature for cell in week                                  | °C    |
| $\mu_p$                             | Mean of the thermal tolerance for population                  | °C    |
| $\sigma_p^2$                        | Standard deviation of thermal tolerance for the population    | °C    |
| <i>Population movement model</i>    |   |       |
| $\lambda$                           | decay rate for population movement                            | -     |
| $Hab_{c,p}^2$                       | Square of habitat suitability for cell $c$ and population $p$ | -     |
| $Tol_{c,p,wk}$                      | Thermal tolerance for population $p$ in cell $c$ at week $wk$ | -     |
| $d_{IJ}$                            | euclidean distance between cell $I$ and cell $J$              | -     |

### 433 Funding

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

Table 3: Description of variables for fleet dynamics sub-module

| Variable                         | Meaning  | Units                 |
|----------------------------------|--|-----------------------|
| <b>Short-term fleet dynamics</b> |  |                       |
| $Rev$                            | Revenue from fishing tow                           | €                     |
| $L_p$                            | Landings of population $p$                         | kg                    |
| $Pr_p$                           | Average price of population $p$                    | € kg <sup>-1</sup>    |
| StepL                            | Step length for vessel                             | euclidean<br>distance |
| Br                               | Bearing  | degrees               |
| $k$                              | Concentration parameter for Von mises distribution | -                     |
| $\beta_1$                        | shape parameter for step function                  | -                     |
| $\beta_2$                        | shape parameter for step function                  | -                     |
| $\beta_3$                        | shape parameter for step function                  | -                     |

Table 4: Population dynamics and movement parameter setting

| Parameter                        | Pop 1                       | Pop 2                       | Pop 3                       | Pop 4                       |
|----------------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| Habitat quality                  |                             |                             |                             |                             |
| Matérn $\nu$                     | 1/0.15                      | 1/0.05                      | 1/0.55                      | 1/0.05                      |
| Matérn $\kappa$                  | 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;<br>80,90,60,70 | 50,60,30,40;<br>80,90,90,90 | 30,34,10,20;<br>60,70,20,30 | 50,55,80,85;<br>30,40,30,40 |
| Spawning multiplier              | 10                          | 10                          | 10                          | 10                          |
| Movement $\lambda$               | 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 $\sigma^2$ | 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 5: Fleet dynamics parameter setting

| Parameter               | Fleet<br>1 | Fleet<br>2 | Fleet<br>3 | Fleet<br>4 | Fleet<br>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 $\beta_1$ | 1          | 2          | 1          | 2          | 3          |
| step function $\beta_2$ | 10         | 10         | 8          | 12         | 7          |
| step function $\beta_3$ | Q90        | Q90        | Q85        | Q90        | Q80        |
| step function $rate$    | 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       |



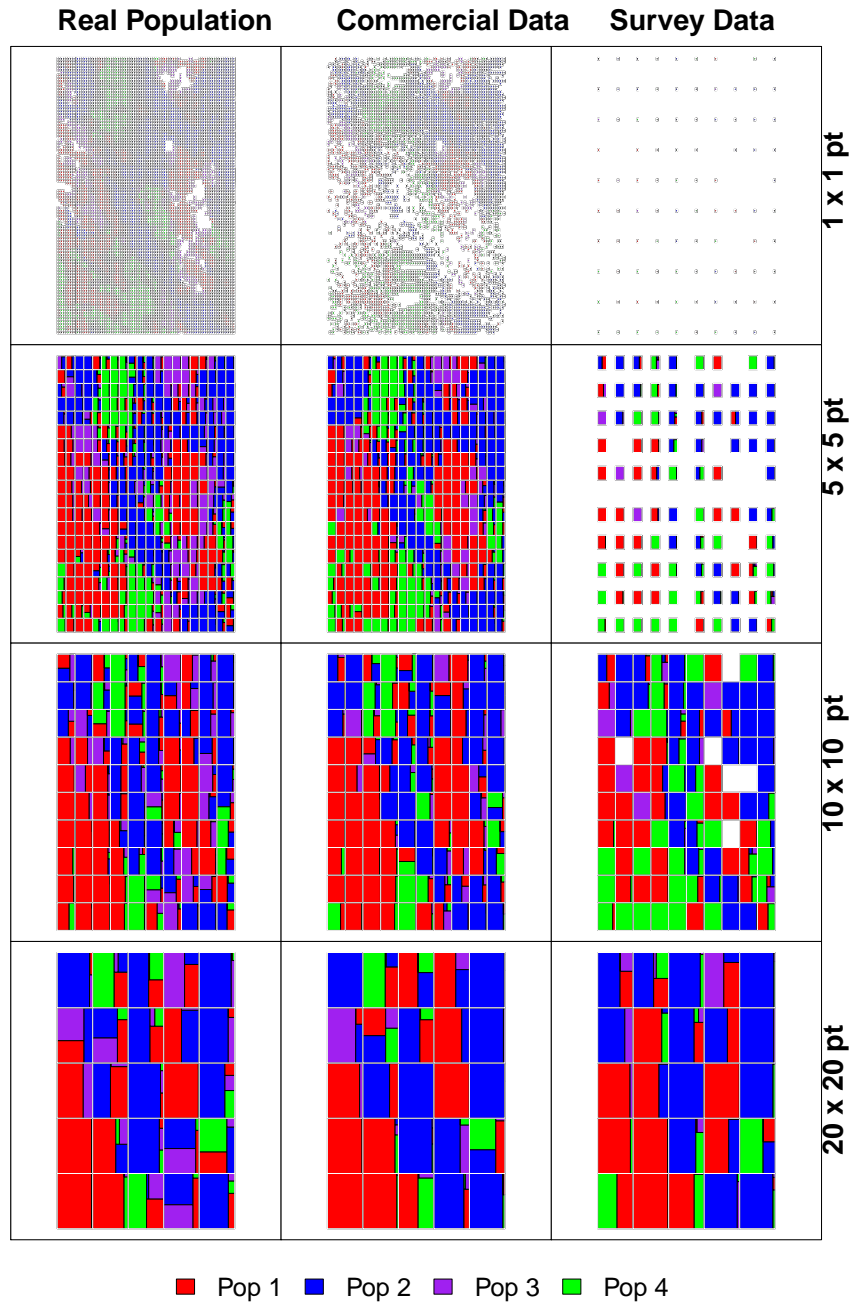


Figure 2: Data aggregation at different spatial resolutions

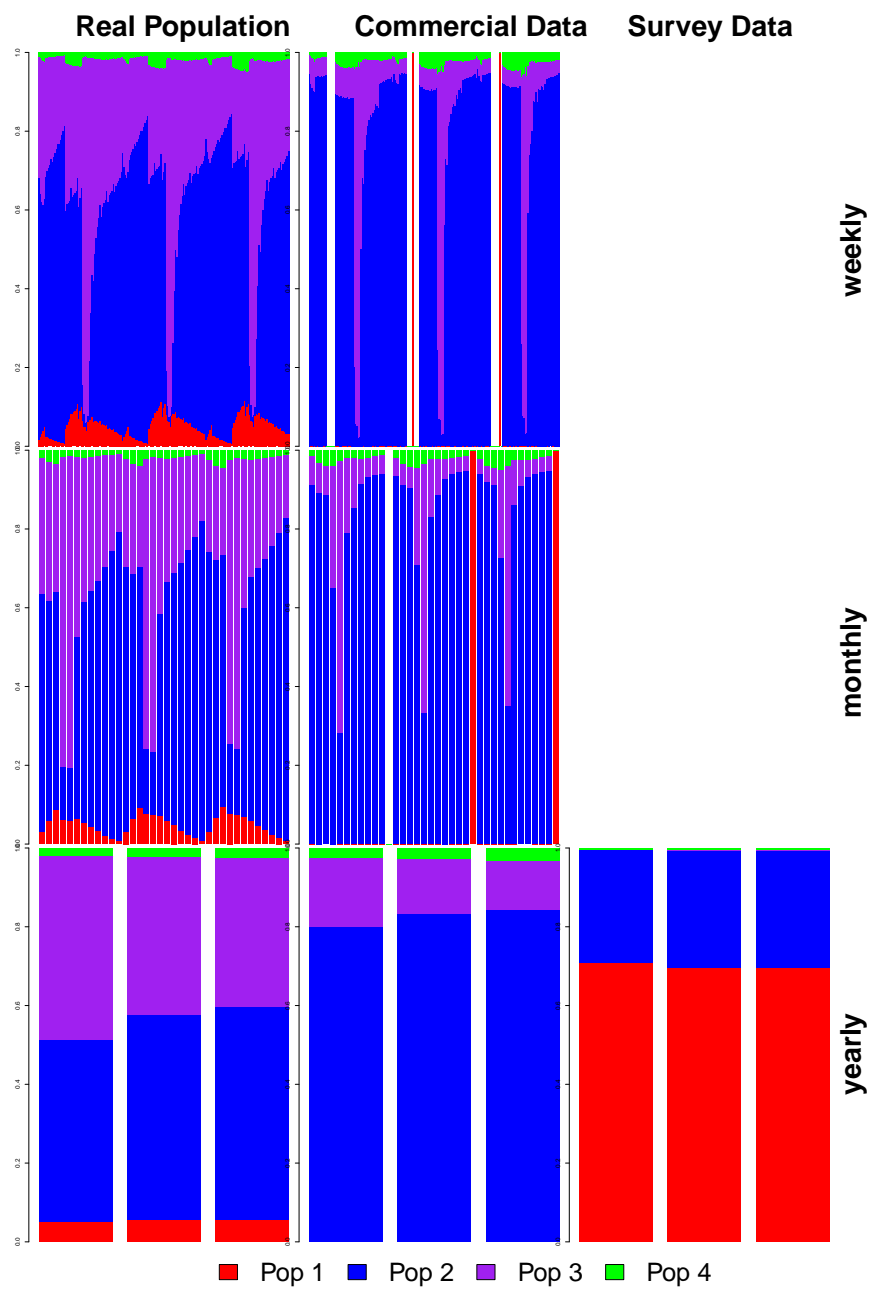


Figure 3: Data aggregation at different temporal resolutions

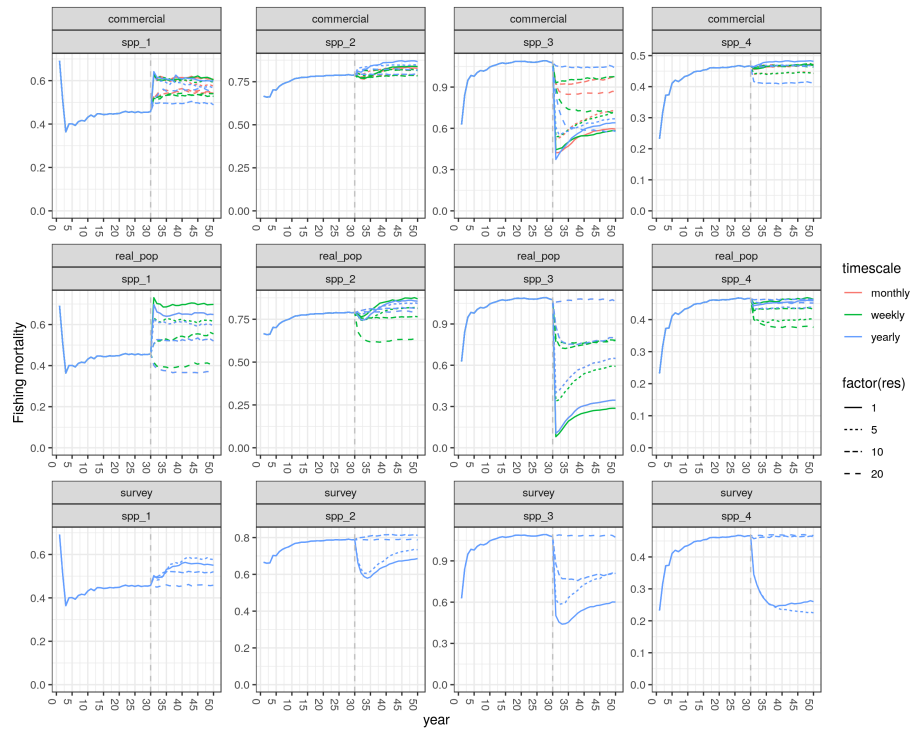


Figure 4: Comparison of closure scenarios - F trends

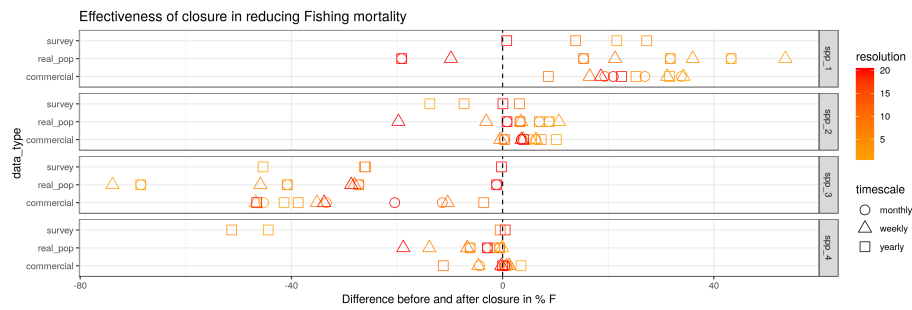


Figure 5: Comparison of closure scenarios

## 436 **References**

- 437 Alverson, D.L., Freeberg, M.H., Murawski, S.A., Pope, J., 1994. A global as-  
438 sessment of fisheries bycatch and discards.
- 439 Bartumeus, F., Da Luz, M.G.E., Viswanatham, G.M., Catalan, J., 2005. Animal  
440 Search Strategies: A Quantitative Random Walk Analysis. *Ecological Society  
441 of America* 86, 3078–3087.
- 442 Bastardie, F., Nielsen, J.R., Ulrich, C., Egekvist, J., Degel, H., 2010. De-  
443 tailed mapping of fishing effort and landings by coupling fishing logbooks  
444 with satellite-recorded vessel geo-location. *Fisheries Research* 106, 41–53.
- 445 Batsleer, J., Hamon, K.G., Overzee, H.M.J., Rijnsdorp, A.D., Poos, J.J., 2015.  
446 High-grading and over-quota discarding in mixed fisheries. *Reviews in Fish  
447 Biology and Fisheries* 25, 715–736.
- 448 Bellido, J.M., Santos, M.B., Pennino, M.G., Valeiras, X., Pierce, G.J., 2011.  
449 Fishery discards and bycatch: Solutions for an ecosystem approach to fisheries  
450 management?
- 451 Bertrand, S., Bertrand, A., Guevara-Carrasco, R., Gerlotto, F., 2007. Scale-  
452 invariant movements of fishermen: The same foraging strategy as natural  
453 predators. *Ecological Applications* 17, 331–337.
- 454 Beverton, R.J., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations  
455 , 533.
- 456 Catchpole, T.L., Revill, A.S., 2008. Gear technology in Nephrops trawl fisheries.  
457 *Reviews in Fish Biology and Fisheries* 18, 17–31.
- 458 Codling, E.A., Plank, M.J., Benhamou, S., Interface, J.R.S., 2008. Random  
459 walk models in biology. *Journal of the Royal Society, Interface / the Royal  
460 Society* 5, 813–34.
- 461 Crowder, L.B., Murawski, S.A., 1998. Fisheries Bycatch: Implications for Man-  
462 agement. *Fisheries* 23, 8–17.

463 Deriso, R.B., 1980. Harvesting Strategies and Parameter Estimation for an Age-  
464 Structured Model. *Canadian Journal of Fisheries and Aquatic Sciences* 37,  
465 268–282. [arXiv:1410.7455v3](#).

466 Dichmont, C.M., Punt, A.E., Deng, A., Dell, Q., Venables, W., 2003. Applica-  
467 tion of a weekly delay-difference model to commercial catch and effort data  
468 for tiger prawns in Australia ’ s Northern Prawn Fishery. *Fisheries Research*  
469 65, 335–350.

470 Diggle, P.J., Ribeiro, P.J., 2007. *Model-based Geostatistics* (Springer Series in  
471 Statistics). volume 1.

472 Dinmore, T.A., Duplisea, D.E., Rackham, B.D., Maxwell, D.L., Jennings, S.,  
473 2003. Impact of a large-scale area closure on patterns of fishing disturbance  
474 and the consequences for benthic communities. *ICES Journal of Marine Sci-*  
475 *ence* 60, 371–380.

476 Dunn, D.C., Boustany, A.M., Roberts, J.J., Brazer, E., Sanderson, M., Gardner,  
477 B., Halpin, P.N., 2014. Empirical move-on rules to inform fishing strategies:  
478 A New England case study. *Fish and Fisheries* 15, 359–375.

479 Dunn, D.C., Maxwell, S.M., Boustany, A.M., Halpin, P.N., 2016. Dynamic  
480 ocean management increases the efficiency and efficacy of fisheries manage-  
481 ment. *Proceedings of the National Academy of Sciences* , 201513626.

482 Edwards, A.M., 2011. Overturning conclusions of Lévy flight movement patterns  
483 by fishing boats and foraging animals. *Ecology* 92, 1247–1257.

484 F. Dormann, C., M. McPherson, J., B. Araújo, M., Bivand, R., Bolliger, J.,  
485 Carl, G., G. Davies, R., Hirzel, A., Jetz, W., Daniel Kissling, W., Kühn, I.,  
486 Ohlemüller, R., R. Peres-Neto, P., Reineking, B., Schröder, B., M. Schurr,  
487 F., Wilson, R., 2007. Methods to account for spatial autocorrelation in the  
488 analysis of species distributional data: A review. *Ecography* 30, 609–628.

489 Gerritsen, H.D., Lordan, C., Minto, C., Kraak, S.B.M., 2012. Spatial patterns  
490 in the retained catch composition of Irish demersal otter trawlers: High-

491 resolution fisheries data as a management tool. *Fisheries Research* 129-130,  
492 127–136.

493 Gillis, D.M., Peterman, R.M., 1998. Implications of interference among fishing  
494 vessels and the ideal free distribution to the interpretation of CPUE. *Canadian*  
495 *Journal of Fisheries and Aquatic Sciences* 55, 37–46.

496 Girardin, R., Vermard, Y., Thébaud, O., Tidd, A., Marchal, P., 2015. Predicting  
497 fisher response to competition for space and resources in a mixed demersal  
498 fishery. *Ocean & Coastal Management* 106, 124–135.

499 Hilborn, R., Walters, C., 1992. Quantitative fisheries stock assessment: Choice,  
500 dynamics and uncertainty. volume 2. [arXiv:1011.1669v3](#).

501 Holmes, S.J., Bailey, N., Campbell, N., Catarino, R., Barratt, K., Gibb, A., Fer-  
502 nandes, P.G., 2011. Using fishery-dependent data to inform the development  
503 and operation of a co-management initiative to reduce cod mortality and cut  
504 discards. *ICES Journal of Marine Science* 68, 1679–1688.

505 Hutton, T., Mardle, S., Pascoe, S., Clark, R.a., 2004. Modelling fishing location  
506 choice within mixed fisheries: English North Sea beam trawlers in 2000 and  
507 2001. *ICES Journal of Marine Science* 61, 1443–1452.

508 Kennelly, S.J., Broadhurst, M.K., 2002. By-catch begone: Changes in the phi-  
509 losophy of fishing technology. *Fish and Fisheries* 3, 340–355.

510 Lee, J., South, A.B., Jennings, S., 2010. Developing reliable, repeatable, and  
511 accessible methods to provide high-resolution estimates of fishing-effort distri-  
512 butions from vessel monitoring system (VMS) data. *ICES Journal of Marine*  
513 *Science* 67, 1260–1271.

514 Little, A.S., Needle, C.L., Hilborn, R., Holland, D.S., Marshall, C.T., 2014.  
515 Real-time spatial management approaches to reduce bycatch and discards:  
516 experiences from Europe and the United States. *Fish and Fisheries* , n/a–  
517 n/a.

518 Mateo, M., Pawlowski, L., Robert, M., 2016. Highly mixed fisheries: fine-scale  
519 spatial patterns in retained catches of French fisheries in the Celtic Sea. ICES  
520 Journal of Marine Science: Journal du Conseil , fsw129.

521 Poos, J.J., Rijnsdorp, A.D., 2007. An "experiment" on effort allocation of fishing  
522 vessels: the role of interference competition and area specialization. Canadian  
523 Journal of Fisheries and Aquatic Sciences 64, 304–313.

524 R Core Team, 2017. R Core Team (2017). R: A language and environment for  
525 statistical computing. R Foundation for Statistical Computing, Vienna, Aus-  
526 tria. URL <http://www.R-project.org/> , R Foundation for Statistical Com-  
527 puting.

528 Reynolds, A., 2015. Liberating Lévy walk research from the shackles of optimal  
529 foraging.

530 Ricker, W.E., 1954. Stock and recruitment. Journal of the Fisheries Research  
531 Board of Canada 11, 559 – 623.

532 Rijnsdorp, A., 2000. Competitive interactions among beam trawlers exploiting  
533 local patches of flatfish in the North Sea. ICES Journal of Marine Science 57,  
534 894–902.

535 Rijnsdorp, a.D., Daan, N., Dekker, W., Poos, J.J., Van Densen, W.L.T., 2007.  
536 Sustainable use of flatfish resources: Addressing the credibility crisis in mixed  
537 fisheries management. Journal of Sea Research 57, 114–125.

538 Rijnsdorp, A.D., Piet, G.J., Poos, J.J., 2001. Effort allocation of the Dutch  
539 beam trawl fleet in response to a temporarily closed area in the North Sea.  
540 Ices Cm 2001/N: 01 , 1–17.

541 Sakiyama, T., Gunji, Y.P., 2013. Emergence of an optimal search strategy from  
542 a simple random walk. Journal of the Royal Society, Interface 10, 20130486.

543 Schlater, M., Malinowski, A., Menck, P.J., 2015. Analysis, Simulation and Pre-  
544 diction of Multivariate Random Fields with Package RandomFields. Journal  
545 of Statistical Software 63, 1–25. [arXiv:1501.0228](https://arxiv.org/abs/1501.0228).

- 546 Schnute, J., 1985. A general theory for analysis of catch and effort data. Canadian  
547 Journal of Fisheries and Aquatic Sciences 42, 414–429.
- 548 Sims, D.W., Humphries, N.E., Bradford, R.W., Bruce, B.D., 2012. Lévy flight  
549 and Brownian search patterns of a free-ranging predator reflect different prey  
550 field characteristics. Journal of Animal Ecology 81, 432–442.
- 551 Sims, D.W., Southall, E.J., Humphries, N.E., Hays, G.C., Bradshaw, C.J.A.,  
552 Pitchford, J.W., James, A., Ahmed, M.Z., Brierley, A.S., Hindell, M.A., Mor-  
553 ritt, D., Musyl, M.K., Righton, D., Shepard, E.L.C., Wearmouth, V.J., Wil-  
554 son, R.P., Witt, M.J., Metcalfe, J.D., 2008. Scaling laws of marine predator  
555 search behaviour. Nature 451, 1098–U5.
- 556 Tidd, A.N., Hutton, T., Kell, L.T., Blanchard, J.L., 2012. Dynamic prediction  
557 of effort reallocation in mixed fisheries. Fisheries Research 125–126, 243–253.
- 558 Tobler, W.R., 1970. A Computer Movie Simulating Urban Growth in the Detroit  
559 Region. Economic Geography 46, 234. [arXiv:1011.1669v3](https://arxiv.org/abs/1011.1669v3).
- 560 Ulrich, C., Reeves, S.a., Vermard, Y., Holmes, S.J., Vanhee, W., 2011. Re-  
561 conciling single-species TACs in the North Sea demersal fisheries using the  
562 Fcube mixed-fisheries advice framework. ICES Journal of Marine Science 68,  
563 1535–1547.
- 564 Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Da Luz, M.G.E., Raposo, E.P.,  
565 Stanley, H.E., 1999. Optimizing the success of random searches. Nature 401,  
566 911–914.