

# *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, 4 Place Jussieu, 75005 Paris, France*

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

---

## Abstract

Most fisheries exploit a variety of 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 a good understanding of spatiotemporal fishery dynamics is required. However, traditional scientific advice is limited by a lack of highly resolved knowledge of population distributions, population movement and how fishers interact with different fish populations. This reflects the fact that data on fish location at high temporal and spatial resolutions is expensive and difficult to collect. Proxies inferred from either scientific surveys or commercial catch data are often used to model distributions, often with sparse data at limited spatial and temporal resolution.

To understand how data resolution impacts inference on mixed fisheries interactions, we develop a highly resolved spatiotemporal simulation model incorporating: i) delay-difference population dynamics, ii) population movement

---

\*Corresponding author

Email address: [paul.dolder@gmit.ie](mailto:paul.dolder@gmit.ie) (Paul J. Dolder)

using Gaussian Random Fields to simulate patchy, heterogeneously distributed populations, and iii) fishery dynamics for multiple fleet characteristics based on species targeting via a mix of correlated random walk movement (for exploration) and learned behaviour (for exploitation) phases of the fisheries.

We simulate 50 years of fishing and use the results from the fisheries catch 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. We use the results to establish the potential and limitations of fishery-dependent data in providing a robust picture of spatiotemporal distributions. Finally, we simulate an area closure based on areas defined from 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 containing bias, 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 a variety of fish populations that are heterogeneously distributed in space and time with varying knowledge of species distributions using species non-selective fishing gear. In doing so fisheries catch an assemblage of species and may discard over-quota catch when managed by single species quotas and fishers exhaust or more quota, may lead to overexploitation of fish

7 populations (Ulrich et al., 2011; Batsleer et al., 2015). This discarding of fish in  
8 excess of quota hampers the ability to limit fishing mortality to within sustain-  
9 able limits (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp et al., 2007)  
10 and the ability to manage for the biological and economic sustainability of fish-  
11 eries. As such, there is increasing interest in technical solutions such as gear and  
12 spatial closures as ways of reducing unwanted catch (Kennelly and Broadhurst,  
13 2002; Catchpole and Reville, 2008; Bellido et al., 2011).

14  
15 Changes to spatial fishing patterns have been proposed as a method to reduce  
16 discards (Holmes et al., 2011; Little et al., 2014; Dunn et al., 2014). However,  
17 implementation of avoidance measures is hampered by lack of knowledge of fish  
18 and fishery spatiotemporal dynamics and understanding of the scale at which  
19 processes are important for management. Understanding the correct scale for  
20 spatial measures is crucial in order to implement measures at a resolution that  
21 ensures effective management (Dunn et al., 2016) while minimising economic  
22 impact. For example, a scale that promotes species avoidance for vulnerable or  
23 low quota species while allowing continuance of sustainable fisheries for avail-  
24 able quota species.

25  
26 Identifying an appropriate scale has been a challenge in the past that has  
27 led to ineffectual measures with unintended consequences such as limited impact  
28 towards the management objective or increased benthic impact on previously  
29 unexploited areas (e.g. the cod closure in the North Sea (Rijnsdorp et al., 2001;  
30 Dinmore et al., 2003)). More refined spatial information has since become avail-  
31 able through the combination of logbook and Vessel Monitoring System (VMS)  
32 data (Lee et al., 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al.,  
33 2016) and more real-time spatial management has been possible (e.g. Holmes  
34 et al., 2011). However, such information is derived from an inherently biased  
35 sampling programme, targeted fishing.

36  
37 In order to understand the consequences of using VMS-linked landings to

This comes as a surprise: I thought this was going to be about discards. Agree, have removed this to avoid confusion

draw inference on the underlying population structure we develop a simulation model where population dynamics are highly-resolved in space and time. Being known directly rather than inferred from sampling or commercial catch, we can use the population model to evaluate how inference from fisheries-dependent and fisheries independent sampling relates to the real population structure. In our model system population movement is driven by random (diffusive) and directed (advective) processes and we incorporate characterisation of a number of different fishing fleet dynamics exploiting four fish populations with different spatial and population demographics.

Using our model we simulate 50 years of exploitation of the fish populations. We use the results

1. to understand how sampling-derived data reflects the underlying population structures. We compare at different spatial and temporal aggregations of the simulated population distributions to:
  - (a) the inferred population from a stratified fixed-site sampling survey design commonly used for fisheries monitoring purposes, otherwise known as a fisheries-independent survey,
  - (b) the inferred population from our fishery-dependent model which includes fishery-induced sampling dynamics.
2. to understand the impact of data aggregation and data 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), the effect on the other three populations and fishery catch.

If the paper has two goals this should be clear from the start, but may be better over 2 MSsI would like to keep both parts, but have made clearer in how its set out. The closure scenarios form valida-

## 68 2. Materials and Methods

69 A modular event-based simulation model was developed with sub-modules  
70 implemented on independent time-scales appropriate to capture the character-  
71 istic of the different processes (Figure 1). The following sub-modules were in-  
72 cluded to capture the full system: 1) Population dynamics, 2) Recruitment  
73 dynamics, 3) Population movement, 4) fishery dynamics.

74  
75 Population dynamics (fishing and natural mortality, growth) operate on a  
76 daily time-step, while population movement occurs on a weekly time-step. Re-  
77 cruitment takes place periodically each year for a set time duration specified for  
78 each population, while the fishing module operates on a tow-by-tow basis (i.e.  
79 multiple events a day). The simulation framework is implemented in the sta-  
80 tistical software package R (R Core Team, 2017) and available as an R package  
81 from the authors github site ([www.github.com/pdolder/MixFishSim](https://www.github.com/pdolder/MixFishSim)).

82



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 time steps at which processes occur;  $t = \text{tow}$ ,  $t_{max}$  is the total number of tows; (Rec), (Pop Movement), (Pop Dynamics) logic gates for recruitment periods, population movement and population dynamics for each of the populations, (Past Knowledge) a switch whether to use a random (exploratory) or past knowledge (exploitation) fishing strategy.

83 *2.1. Population dynamics*

The basic population level processes are simulated using a modified two-stage Deriso-Schnute delay difference model (Deriso, 1980; Schnute, 1985; Dichmont et al., 2003) occurring at a daily time-step. A daily time-step was chosen as to discretise continuous population processes on a biologically relevant and computationally tractable timescale. Under the population dynamics module population biomass growth and depletion for pre-recruits and recruited fish are modelled separately as a function of previous recruited biomass, intrinsic population growth and recruitment. Biomass for each cell is incremented each day as follows (the full parameter list is detailed in Table 1):

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

84 where  $\rho$  is Brody's coefficient, shown to be approximately equal to  $e^{-K}$  when  
 85  $K$  is the growth rate from a von Bertalanffy logistic growth model (Schnute,  
 86 1985).  $Wt_{R-1}$  is the weight of fish prior to recruitment, while  $Wt_R$  is the re-  
 87 cruited weight.  $\alpha_d$  represents the proportion of fish recruited during that day  
 88 for the year, while  $R_{c,\tilde{y}}$  is the annual recruits in cell  $c$  for year  $y$ .

89

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

$$C_{c,d} = \frac{F_{c,d}}{F_{c,d} + M_{c,d}} * (1 - e^{-(F_{c,d} + M_{c,d})}) * B_{c,d} \tag{2}$$

90 where  $C_{c,d}$  is the summed catch from the fishing model across all fleets and  
 91 vessels in cell  $c$  for the population during the day  $d$ , and  $B_{c,d}$  the daily biomass  
 92 for the population in the cell. Here, catch and fishing mortality are the sum of

those across all fleets and vessels, where  $F_{fl,v,c,d,p} = E_{fl,v,c,d} \cdot Q_{fl,p} \cdot B_{c,d,p}$  with  $fl$ ,  $v$  and  $p$  the fleet, vessel and population respectively and  $E$  and  $Q$  fishing effort and catchability.

## 2.2. Recruitment dynamics

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

$$\begin{aligned}\bar{R}_{c,d} &= \frac{(\alpha * B_{c,d})}{(\beta + B_{c,d})} \\ R_{c,d} &\sim \log N[(\log(\bar{R}_{c,d}), \log(\sigma^2))]\end{aligned}\tag{3}$$

Where  $\alpha$  is the maximum recruitment rate,  $\beta$  the spawning stock biomass (SSB) required to produce half the maximum,  $B$  current SSB and  $\sigma^2$  the variability in the recruitment due to stochastic processes, or a stochastic Ricker form (Ricker, 1954):

$$\begin{aligned}\bar{R}_{c,d} &= B_{c,d} * e^{(\alpha - \beta * B_{c,d})} \\ R_{c,d} &\sim \log N[(\log(\bar{R}_{c,d}), \log(\sigma^2))]\end{aligned}\tag{4}$$

where  $\alpha$  is the maximum productivity per spawner and  $\beta$  the density dependent reduction in productivity as the SSB increases. In this study, the Beverton-Holt form of stock recruit relationship was used for all populations.

## 2.3. Population movement dynamics

To simulate fish population distribution in space and time a Gaussian spatial process was employed to model habitat suitability for each of the populations on a 2d grid. An advection-diffusion process controlled population movement, with a time-varying temperature covariate used to change the spatial bounds of suitable habitat on a weekly time-step.

For habitat we first defined a Gaussian random field process,  $\{S(c) : c \in \mathbb{R}^2\}$ , where for any set of cells  $c_1, \dots, c_n$ , the joint distribution of  $S =$

[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]

What have a temperature covariate? Could just use time- Was intended as some biological meaning - species thermal tolerances load onto the temperature effect - so could be different per species

Not clear how



110  $\{S(c_1), \dots S(c_n)\}$  is multivariate Gaussian. The distribution is specified by its  
 111 mean function,  $\mu(c) = E[S(c)]$  and its covariance function,  $\gamma(c, c') = Cov\{S(c), S(c')$   
 112 (Diggle and Ribeiro, 2007).

113

114 The covariance structure affects the smoothness of the surfaces which the  
 115 process generates; we used the *Matérn* covariance structure, where the corre-  
 116 lation strength weakens with distance. This enables us to model the spatial  
 117 autocorrelation observed in animal populations where density is more similar  
 118 in nearby locations (Tobler, 1970; F. Dormann et al., 2007) and we change the  
 119 parameters to implement different spatial structures for the populations. The  
 120 *Matérn* correlation is a two-parameter family where:

$$121 \quad \rho(u) = \{2^{\kappa-1}\Gamma\kappa\}^{-1}(u/\phi)^{\kappa}K_{\kappa}(u/\phi)$$

122  $K_{\kappa}(\cdot)$  is a modified Bessel function of order  $\kappa$ ,  $\phi > 0$  is a scale parameter with  
 123 the dimensions of distance, and  $\kappa > 0$ , called the order, is a shape parameter  
 124 which determines the smoothness of the underlying process (Figure S16).

125

The habitat for each of the populations was generated with the *RFSimulate*  
 function of the *RandomFields* R package (Schlatter et al., 2015). Each popu-  
 lation was initialised at a single location, and subsequently moved according  
 to a probabilistic distribution based on habitat suitability (represented by the  
 normalised values from the GRFs), temperature and distance from current cell:

$$Pr(J|I) = \frac{e^{-\lambda*d_{IJ}} \cdot (Hab_{J,p}^2 \cdot Tol_{J,p,wk})}{\sum_{c=1}^C e^{-\lambda*d} \cdot (Hab_{c,p}^2 \cdot Tol_{c,p,wk})} \quad (5)$$

126 Where  $d_{IJ}$  is the euclidean distance between cell  $I$  and cell  $J$ ,  $\lambda$  is a given rate  
 127 of decay,  $Hab_{J,p}^2$  is the squared index of habitat suitability for cell  $J$  and popu-  
 128 lation  $p$ , with  $Tol_{J,p,wk}$  the temperature tolerance for cell  $J$  by population  $p$  in  
 129 week  $wk$ .

130

131 During pre-defined weeks of the year the habitat quality is modified with

Introduce the gamma function, and why this covariance structure? Why correlate values in the random field? to allow populations to have different aggregation densities: have tried to clarify

132 user-defined spawning habitat locations, resulting in each population having  
133 concentrated areas where spawning takes place. In the simulations the popu-  
134 lations moved towards these cells in the weeks prior to spawning, resulting in  
135 directional movement towards the spawning grounds.

136  
The temperature field was defined on a gradient from a South-Westerly to  
North-Easterly direction, with temperature in each cell changing gradually on  
a week-by-week basis so that initially high temperature areas cycled to lower  
temperatures and low temperature areas *vice versa*. Each population  $p$  was  
assigned a thermal tolerance with mean,  $\mu_p$  and variance,  $\sigma_p^2$  so that each cell  
and population temperature suitability is defined that:

$$Tol_{c,p,wk} = \frac{1}{\sqrt{2\pi \cdot \sigma_p^2}} \cdot \exp\left(-\frac{(T_{c,wk} - \mu_p)^2}{2 \cdot \sigma_p^2}\right) \quad (6)$$

137 Where  $Tol_{c,p,wk}$  is the tolerance of population  $p$  for cell  $c$  in week  $wk$ ,  $T_{c,wk}$  is  
138 the temperature in the cell given the week and  $\mu_p$  and  $\sigma_p^2$  the mean and standard  
139 deviation of the population temperature tolerance.

140

141 The final process resulted in independent populations structure and move-  
142 ment patterns, with population movement occurring on a weekly basis. This  
143 process approximated the demographic shifts in fish populations throughout a  
144 year with seasonal spawning patterns (e.g. Figure S5).

#### 145 2.4. Fleet dynamics

146 The fleet dynamics can be broadly categorised into three components; fleet  
147 targeting - which determined the fleet catch efficiency and preference towards a  
148 particular species; trip-level decisions, which determined the initial location to  
149 be fished at the beginning of a trip; and within-trip decisions, determining move-  
150 ment from one fishing spot to another within a trip. Together, these element  
151 implement an explore-exploit type strategy for individual vessels to maximise  
152 their catch from an unknown resource distribution (Bailey et al. (2018)).

What does it mean concisely?  
Areas are assigned? Yes, the areas are pre-defined - I have amended to reflect and tried to clarify

153 *2.4.1. Fleet targeting*

154 Each fleet of  $n$  vessels was characterised by both a general efficiency,  $Q_{fl}$ ,  
155 and a population specific efficiency,  $Q_{fl,p}$ . Thus, the product of these parameters  $[Q_{fl} \cdot Q_{fl,p}]$  affects the overall catch rates for the fleet and the preferential  
156 targeting of one population over another. This, in combination with the parameter choice for the step-function defined below (as well as some randomness from  
157 the exploratory fishing process) determined the preference of fishing locations  
158 for the fleet. All species prices were kept the same across fleets and seasons.  
159  
160

161 *2.4.2. Trip-level decisions*

162 Several studies (e.g. Hutton et al., 2004; Tidd et al., 2012; Girardin et al.,  
163 2015) have confirmed past activity and past catch rates are strong predictors of  
164 fishing location choice. For this reason, the fleet dynamics sub-model included a  
165 learning component, where a vessel's initial fishing location in a trip was based  
166 on selecting from previously successful fishing locations. This was achieved by  
167 calculating an expected revenue based on the catches from locations fished in  
168 the preceding trip as well as the same month periods in previous years and the  
169 travel costs from the port to the fishing grounds, and choosing randomly from  
170 the top 75 % of fishing events as defined by the expected profit. Simulation  
171 testing indicated that this learning increased the mean value of catches for the  
172 vessels, over just relying on the correlated random walk function as described  
173 for the 'within trip' decisions below (MIGHT NEED TO INCLUDE IN SUPPLEMENTARY).  
174

Correlated random walk of what

175 *2.4.3. Within-trip decisions*

176 Fishing locations within a trip are initially determined by a modified random walk process. As the simulation progresses the within-trip decision become  
177 gradually more influenced by experience gained from past fishing locations (as  
178 per the initial trip-level location choice), moving location choice towards areas  
179 of higher perceived profit. A random walk was chosen for the exploratory fishing  
180 process as it is the simplest assumption commonly used in ecology to describe  
181

182 optimal animal search strategy for exploiting homogeneously distributed prey  
183 about which there is uncertain knowledge (Viswanathan et al., 1999). In a ran-  
184 dom walk, movement is a stochastic process through a series of steps. These  
185 steps have a length, and a direction that can either be equal in length or take  
186 some other functional form. The direction of the random walk was also cor-  
187 related (known as ‘persistence’) providing some overall directional movement  
188 (Codling et al., 2008) .

189

190 We use a *Lévy flight* which is a particular form of random walk charac-  
191 terised by a heavy-tailed distribution of step-length. The Lévy flight has re-  
192 ceived a lot of attention in ecological theory in recent years as having shown to  
193 have very similar characteristics as those observed by animals in nature, and  
194 being a near optimum searching strategy for predators pursuing patchily dis-  
195 tributed prey (Viswanathan et al., 1999; Bartumeus et al., 2005; Sims et al.,  
196 2008). Bertrand et al. (2007) showed that Peruvian anchovy fishermen have a  
197 stochastic search pattern similar to that observed with a lévy flight. However,  
198 it remains a subject of debate (e.g. see Edwards et al., 2011; Reynolds, 2015),  
199 with the contention that search patterns may be more simply characterised as  
200 random walks (Sakiyama and Gunji, 2013) with specific patterns related to the  
201 characteristics of the prey field (Sims et al., 2012).

202

For our implementation of a random walk directional change is based on  
a negatively 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. The step length (i.e. the distance travelled from the current to the  
next fishing location) is determined by recent fishing success, measured as the  
summed value of fish caught (revenue,  $Rev$ ),

$$Rev = \sum_{p=1}^P L_p \cdot Pr_p \quad (7)$$

where  $L_p$  is landings of a population  $p$ , and  $Pr_p$  price of a population. Here,  
when fishing is successful vessels remain in a similar location and continue to

exploit the local fishing grounds. When unsuccessful, they move some distance away from the current fishing location. The movement distance retains some degree of stochasticity, which can be controlled separately, but is determined by the relationship:

$$StepL = e^{\log(\beta_1) + \log(\beta_2) - (\log(\frac{\beta_1}{\beta_3}))} * Rev \quad (8)$$

Where  $\beta_1$ ,  $\beta_2$  and  $\beta_3$  are parameters determining the shape of the step function in its relation to revenue, so that, a step from (x1,y1) to (x2, y2) is defined by:

$$\begin{aligned} (x2, y2) = & x1 + StepL \cdot \cos\left(\frac{\pi \cdot Br}{180}\right), \\ & y1 + StepL \cdot \sin\left(\frac{\pi \cdot Br}{180}\right) \end{aligned} \quad (9)$$

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

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

So step length increases with increasingly gross revenue? No, the opposite

where  $k$  the concentration parameter from the von Mises distribution which we correlate with the revenue so that  $k = (Rev + 1/RefRev) * max_k$ , where  $max_k$  is the maximum concentration value,  $k$ , and  $RefRev$  is parametrised as for  $\beta_3$  in the step length function. A realised example of the step length and turning angle relationships to revenue can be seen at Figure S15.

#### 2.4.4. Local population depletion

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

## 218 2.5. Fisheries independent survey

219 A fisheries-independent survey is simulated where fishing on a regular grid  
220 begins each year at the same time for a given number of stations (a fixed station  
221 survey design). Catches of the populations at each station are recorded but not  
222 removed from the population. This provides a fishery independent snapshot  
223 of the populations at a regular spatial intervals each year, similar to scientific  
224 surveys undertaken by fisheries research agencies.

## 225 3. Calculation

### 226 3.1. Population parametrisation

227 We parametrised the simulation model for four populations with different  
228 population demographics; growth rates, natural mortality and recruitment func-  
229 tions (Table 4). Habitat preference (Figure S1) and temperature tolerances  
230 (Figures S3, S4) were unique to each population resulting in differently weekly  
231 distribution patterns (Figures S5-S7). In addition, each of the populations has  
232 two defined spawning areas which result in the populations moving towards  
233 these areas in pre-defined weeks (Figure S2) with population-specific movement  
234 rates (Table 4). The realised movement of the populations for a number of  
235 weeks is shown in Figure S9 while the realised daily fishing mortality are shown  
236 in Figure S10.

### 237 3.2. Fleet parametrisation

238 The fleets were parametrised to reflect five different characteristic fisheries  
239 with unique exploitation dynamics (Table 5). By setting different catchability  
240 parameters ( $Q_{fl,p}$ ) we create different targeting preferences between the fleets  
241 and hence spatial dynamics. The stochasticity in the random walk process  
242 ensures that within a fleet different vessels have slightly different spatial dis-  
243 tributions based on individual experience. The step function was parametrised  
244 dynamically within the simulations as the maximum revenue obtainable was  
245 not known beforehand. This was implemented so that vessels take smaller steps

when fishing at a location yields landings value which is in the top 90th percentile of the value experienced in that year (as defined per fleet in Table 5).

With increasing probability throughout the simulation, fishing locations were chosen based on experience of profitable catches built up in the same month from previous years and from the previous trip. 'Profitable' in this context was defined as the locations where the top 70 % of expected profit would be found given previous trips revenue and cost of movement to the new fishing location. This probability was based on a logistic sigmoid function with a lower asymptote of 0 and upper asymptote of 0.95, and a growth rate which ensures the upper asymptote (where decisions are mainly based on past knowledge) is reached  $\sim$  halfway through the simulation.

An example of the realised fleet movements for a single vessel during a single trip are given in Figure S11, while Figure S12 shows multiple trips for a single vessel, Figure S13 the vessel movements for several trips overlaid on the value field (sum of the population densities  $\times$  price), Figure S14 shows fishing locations for an entire fleet of 20 vessels for a single trip, and Figure S15 shows an example of the step function realisation and turning angles from the correlated random walk.

### 3.3. Survey settings

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

### 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 set up a simulation

Move some of the supplementary figures to the manuscript

275 to run for 50 years based on a  $100 \times 100$  square grid, with five fleets of 20 vessels  
276 each and four fish populations. Fishing takes place four times a day per vessel  
277 and five days a week, while population movement is every week.

278  
279 We allow the simulation to run unrestricted for 30 years, then implement  
280 spatial closed areas for the last 20 years of the simulation based on data (either  
281 derived from the commercial catches, fisheries-independent survey or the 'real  
282 population') used at different spatial and temporal scales.

283  
284 The following steps are undertaken to determine closures:

- 285 1. Extract data source
- 286 2. Aggregate according to desired spatial and temporal resolution
- 287 3. Interpolate across entire area at desired resolution
- 288 4. Close area covering top 5 % of catch

289 In total 56 closure scenarios were run which represent combinations of:

- 290 • **data types:** commercial logbook data, survey data and 'real population',
- 291 • **temporal resolutions:** weekly, monthly and yearly closures,
- 292 • **spatial resolutions:** 1 x 1 grid, 5 x 5 grid, 10 x 10 grid and 20 x 20 grid,
- 293 • **closure basis:** high catch rates of protected species, or high ratio of  
294 protected species v secondary species.

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

## 297 4. Results

298 The consequences of different spatial aggregations of the data are shown  
299 in Figure 2, which represents the aggregation of catch from each of the data  
300 sources over a ten year period (to average seasonal patterns) at different spatial

move to start  
of methods  
section I think  
ecological mod-  
elling wants  
the 'calcula-  
tions' section  
here. will check

Is there equi-  
librium after  
5 years or still  
some trend in  
B? I have rerun  
to ensure some  
steady state dy-  
namics

Procedure un-  
clear. Refer  
to symbols in  
methods sec-  
tion or switch  
order starting  
with description  
of data type  
etc. Yes, will  
redo



301 resolutions.

302

303 The finer spatial grid for the real population (top left) and commercial data  
304 (top middle) show visually similar patterns, though there are unsampled gaps in  
305 the commercial data from a lack of fishing activity (particularly in the lower left  
306 part of the sampling domain). The survey data at this spatial resolution shows  
307 very sparse information about the spatial distributions of the populations. The  
308 slightly aggregated data on a 5 x 5 grid shows similar patterns and, while los-  
309 ing some of the spatial detail, there remains good consistency between the 'real  
310 population' and the commercial data. Survey data starts to pick out some of  
311 the similar patterns as the other data sources, but lacks coverage. The spatial  
312 catch information on a 10 x 10 and 20 x 20 grid loses a significant amount of  
313 information about the spatial resolutions for all data sources, and some differ-  
314 ences between the survey, commercial and 'real population' data emerge.

315

316 Figure 3 shows the consequences of different temporal aggregations of the  
317 data over a three year period, with 156 weekly (top), 36 monthly (middle) and  
318 3 yearly (bottom) catch compositions from across an aggregated 20 x 20 area.

319

320 As can be seen by comparison to the 'real population', the monthly aggre-  
321 gation captures the major patterns seen in the weekly data, albeit missing more  
322 subtle differences. The yearly data results in a constant catch pattern due to  
323 the aggregation process (sometimes known as an aggregation bias). The com-  
324 mercial data on a weekly basis shows some of the same patterns as the 'real  
325 population', though the first species (in red) is less well represented and some  
326 weeks are missing catches from the area. The monthly data. The monthly data  
327 shows some consistency between the 'real population' and commercial data for  
328 species 2 - 4, though species 1 remains under-represented. On an annual ba-  
329 sis, interestingly the commercial data under represents the first species (in red)  
330 while the survey over represents species 1. This is likely due to the biases in  
331 commercial sampling, with the fisheries not targeting the areas where species 1

are present, and the biases in the survey sampling from over representation of the spatial distribution.

We implemented a spatial closure using the different data sources and spatial and temporal aggregations as outlined in the protocol in Section 3.4. We used this to assess the efficacy of a closure in reducing fishing mortality on species 1, given availability of data and its use at different resolutions in order to evaluate the trade-offs in data sources. Figure 4 shows the trend in fishing mortality for each species simulated (columns) given the data sources (rows), temporal aggregations (colour lines) and spatial aggregations (line-styles), while Figure 5 shows the change in fishing mortality from before the closure (year 29) to after the closure (year 50).

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

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

For the commercial data, the most effective closure scenario was based on 1 x 1 data at a monthly temporal resolution. This results in  $\sim 10\%$  reduction in  $F$  for species 1. This was the only closure scenario to have positive effect accord-

ing to Figure 5, though looking at the trend in Figure 4 this looks more related to the continued increased in F trend, as other scenarios had an initial effect. Interestingly the monthly data scenario was more effective than weekly data, which I'd posit is due to the increase amount of data available from the commercial sampling across a month compared to a week. Commercial data used at an annual time-step was ineffective in bringing fishing mortality down for species 1.

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

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

Note: The monthly commercial data scenario is the most effective of the realistic scenarios, as the 'real population' can only be seen as a baseline comparison.

## 5. Discussion

Our study evaluates the importance of data scaling and considers potential biases introduced through data aggregation when using commercial fisheries logbooks and Vessel Monitoring Systems for inference on spatio-temporal dynamics in fisheries. Understanding how fishers exploit multiple heterogeneously distributed fish populations with different catch limits or conservation status requires detailed understanding of the overlap of resources; this is difficult to achieve using conventional modelling approaches due to the patchy and irregular nature of fisheries resulting in preferential sampling Martínez-Minaya et al. (2018). Often data is aggregated or extrapolated which requires assumptions about the spatial and temporal scale of processes. Our study explores the assumptions behind such aggregation and preferential sampling to identify potential impacts on management advice. With modern management approaches

392 increasingly employing more nuanced spatio-temporal approaches in order to  
393 maximise productivity while taking account of both the biological and human  
394 processes operating on different time-frames Dunn et al. (2016), understanding  
395 assumptions behind the data used is vital to ensure measures are effective.

396

397 We employ a simulation approach to model each of the population and fish-  
398 ery processes in a hypothetical 'mixed fishery', allowing us to i) evaluate the  
399 consequences of different aggregation assumptions on our understanding of the  
400 spatio-temporal distribution of the underlying fish populations, and ii) evaluate  
401 the effectiveness of a spatial closure given those assumptions. Our approach  
402 captures fine scale population and fishery dynamics not usually considered (al-  
403 though see Bastardie et al. (2010); Bailey et al. (2018)) which offers the ad-  
404 vantage that larger scale fishery patterns are emergent properties of the system  
405 rather than the result of a statistical modelling framework.

406

407 Our results show commercial data can provide at right scale and resolution  
408 - depends on scale of process: pop movement etc... Important to consider how  
409 fishers interact / adapt to changes with the resource and mgmt.

410

411 Closure scenarios demonstrate potential to reduce  $F$  - not as high as with  
412 real pop, but good. Make link to other studies – read up on these.

413

414 The what next:

415

416 Real world spatiotemp closures rarely been able to consider these issues / de-  
417 signed with these issues fully in mind - NS cod closures, plaice and trevose box...

418

419 Use of commercial data increasing - likely to become more important in  
420 future. Also collaborative approach with industry, e.g. hotspot mapping, spa-  
421 tiotemp advice...

422

423 Other potential uses of the model

424

425 Survey design

426

427 commercial index standardization methods

428

429 Sampling scheme design

430

431 Testing fleet dynamics models at an aggregated level

432

433 Bigger picture stuff:: LO, increasing desire for more nuanced spatiotemp  
434 mgmt... Wider applicability: birds, wildlife ??

## 435 **6. Conclusions**

436 Study shows ....

437

438 This is important because ....

439

440 How we might apply this in future ....

441

## 442 **Abbreviations**

443 Detail any unusual ones used.

## 444 **Acknowledgements**

445 those providing help during the research..

## 446 **Funding**

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

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 $d$	-
$R_{c,\tilde{y}}$	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

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 $J$	-

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 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 $\nu$	1/0.015	1/0.05	1/0.01	1/0.005
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; 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 $\lambda$	0.1	0.1	0.1	0.1
Population dynamics				
Starting Biomass	1e5	2e5	1e5	1e4
Beverton-Holt Recruit 'a'	6	27	18	0.3
Beverton-Holt Recruit 'b'	4	4	11	0.5
Beverton-Holt Recruit $\sigma^2$	0.7	0.6	0.7	0.6
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	0.1	0.2	0.1
Movement dynamics				
$\mu$	12	15	17	14
$\sigma^2$	8	9	7	10

Table 5: 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	350	350	350	350	350
Price Pop4	600	600	600	600	600
$Q$ 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	15	8	12	7
step function $\beta_3$	Q90	Q90	Q85	Q90	Q80
step function $rate$	20	30	25	35	20
Past Knowledge	T	T	T	T	T
Past Year & Month	T	T	T	T	T
Past Trip	T	T	T	T	T
Threshold	0.7	0.7	0.7	0.7	0.7
Fuel Cost	3	2	5	2	1

Table 6: Fishing mortality effects of the closure scenarios (ordered by most effective first)

scenario	metric	pop	before	after	diff	timescale	basis	data_type	resolution
9	F	spp_3	1.08	0.29	-73.47	weekly	high_pop	real_pop	1.00
10	F	spp_3	1.08	0.29	-72.94	monthly	high_pop	real_pop	1.00
11	F	spp_3	1.08	0.35	-68.04	yearly	high_pop	real_pop	1.00
45	F	spp_3	1.08	0.58	-46.70	yearly	high_pop	commercial	20.00
1	F	spp_3	1.08	0.58	-46.21	weekly	high_pop	commercial	1.00
23	F	spp_3	1.08	0.59	-45.27	weekly	high_pop	real_pop	5.00
2	F	spp_3	1.08	0.59	-45.06	monthly	high_pop	commercial	1.00
7	F	spp_3	1.08	0.60	-44.48	yearly	high_pop	survey	1.00
24	F	spp_3	1.08	0.61	-43.20	monthly	high_pop	real_pop	5.00
3	F	spp_3	1.08	0.64	-40.82	yearly	high_pop	commercial	1.00
25	F	spp_3	1.08	0.65	-39.94	yearly	high_pop	real_pop	5.00
17	F	spp_3	1.08	0.67	-38.11	yearly	high_pop	commercial	5.00
15	F	spp_3	1.08	0.71	-34.38	weekly	high_pop	commercial	5.00
43	F	spp_3	1.08	0.71	-34.31	weekly	high_pop	commercial	20.00
16	F	spp_3	1.08	0.73	-32.58	monthly	high_pop	commercial	5.00
51	F	spp_3	1.08	0.78	-27.92	weekly	high_pop	real_pop	20.00
37	F	spp_3	1.08	0.78	-27.76	weekly	high_pop	real_pop	10.00
39	F	spp_3	1.08	0.79	-26.98	yearly	high_pop	real_pop	10.00
38	F	spp_3	1.08	0.81	-25.47	monthly	high_pop	real_pop	10.00
21	F	spp_3	1.08	0.81	-25.21	yearly	high_pop	survey	5.00
35	F	spp_3	1.08	0.81	-25.05	yearly	high_pop	survey	10.00
44	F	spp_3	1.08	0.87	-19.91	monthly	high_pop	commercial	20.00
52	F	spp_3	1.08	0.88	-18.39	monthly	high_pop	real_pop	20.00
30	F	spp_3	1.08	0.96	-11.06	monthly	high_pop	commercial	10.00
29	F	spp_3	1.08	0.98	-9.80	weekly	high_pop	commercial	10.00
31	F	spp_3	1.08	1.03	-4.36	yearly	high_pop	commercial	10.00
53	F	spp_3	1.08	1.06	-1.64	yearly	high_pop	real_pop	20.00
49	F	spp_3	1.08	1.07	-1.01	yearly	high_pop	survey	20.00

Table 7: Fishing mortality effects of the closure scenarios (based on highest ratio, ordered by most effective first)

scenario	metric	pop	before	after	diff	timescale	basis	data_type	resolution
6	F	spp_3	1.08	0.52	-52.27	yearly	high_ratio	commercial	1.00
48	F	spp_3	1.08	0.57	-47.06	yearly	high_ratio	commercial	20.00
50	F	spp_3	1.08	0.63	-41.53	yearly	high_ratio	survey	20.00
18	F	spp_3	1.08	0.71	-34.23	weekly	high_ratio	commercial	5.00
19	F	spp_3	1.08	0.72	-33.42	monthly	high_ratio	commercial	5.00
34	F	spp_3	1.08	0.78	-27.75	yearly	high_ratio	commercial	10.00
5	F	spp_3	1.08	0.80	-25.99	monthly	high_ratio	commercial	1.00
20	F	spp_3	1.08	0.81	-25.27	yearly	high_ratio	commercial	5.00
4	F	spp_3	1.08	0.85	-21.52	weekly	high_ratio	commercial	1.00
54	F	spp_3	1.08	0.89	-17.46	weekly	high_ratio	real_pop	20.00
55	F	spp_3	1.08	0.89	-17.46	monthly	high_ratio	real_pop	20.00
56	F	spp_3	1.08	0.89	-17.46	yearly	high_ratio	real_pop	20.00
26	F	spp_3	1.08	0.92	-14.73	weekly	high_ratio	real_pop	5.00
27	F	spp_3	1.08	0.92	-14.73	monthly	high_ratio	real_pop	5.00
28	F	spp_3	1.08	0.92	-14.73	yearly	high_ratio	real_pop	5.00
13	F	spp_3	1.08	0.96	-11.53	monthly	high_ratio	real_pop	1.00
14	F	spp_3	1.08	0.96	-11.01	yearly	high_ratio	real_pop	1.00
12	F	spp_3	1.08	0.97	-10.66	weekly	high_ratio	real_pop	1.00
32	F	spp_3	1.08	1.02	-5.94	weekly	high_ratio	commercial	10.00
22	F	spp_3	1.08	1.02	-5.64	yearly	high_ratio	survey	5.00
33	F	spp_3	1.08	1.02	-5.29	monthly	high_ratio	commercial	10.00
36	F	spp_3	1.08	1.03	-4.52	yearly	high_ratio	survey	10.00
40	F	spp_3	1.08	1.03	-4.52	weekly	high_ratio	real_pop	10.00
41	F	spp_3	1.08	1.03	-4.52	monthly	high_ratio	real_pop	10.00
42	F	spp_3	1.08	1.03	-4.52	yearly	high_ratio	real_pop	10.00
46	F	spp_3	1.08	1.04	-3.50	weekly	high_ratio	commercial	20.00
8	F	spp_3	1.08	1.06	-2.42	yearly	high_ratio	survey	1.00
47	F	spp_3	1.08	1.09	0.52	monthly	high_ratio	commercial	20.00

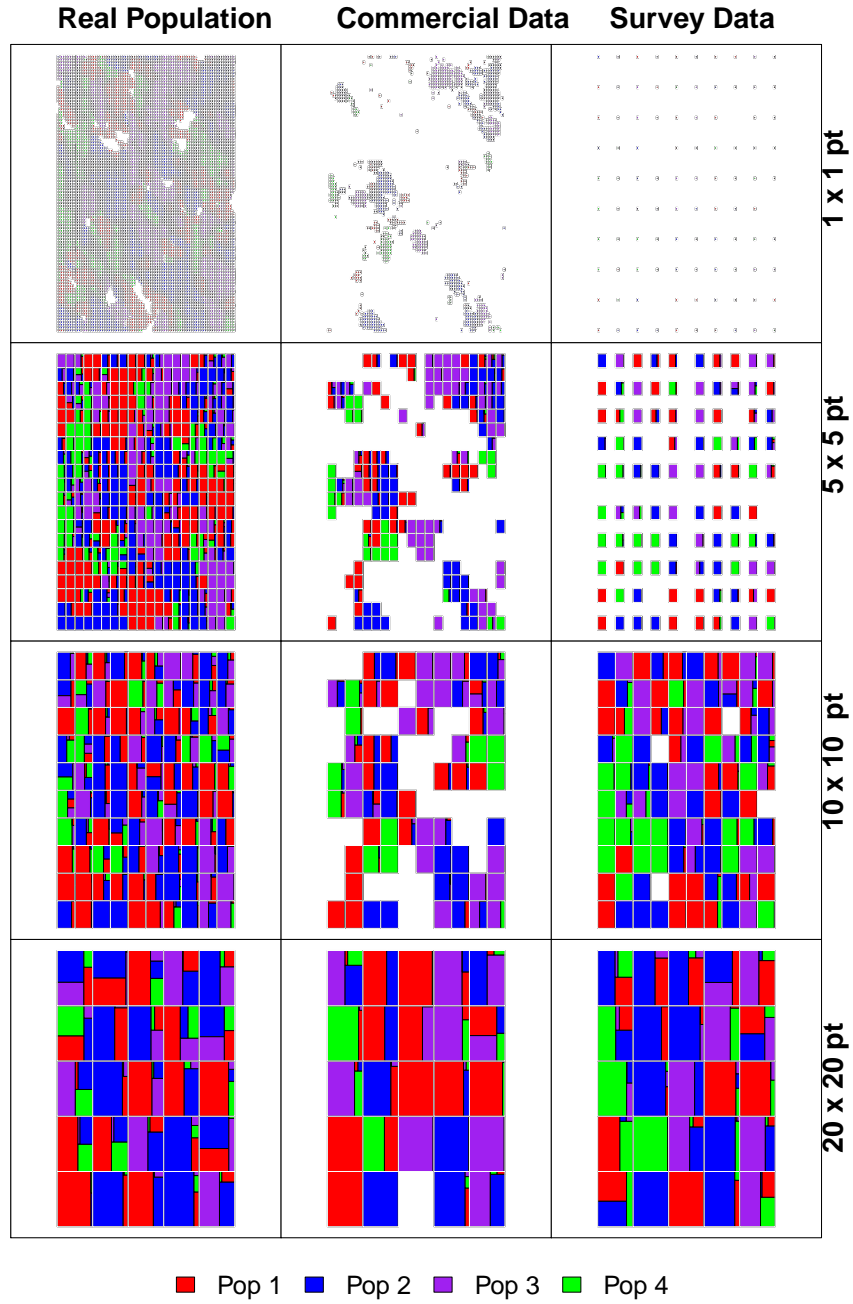


Figure 2: Data aggregation at different spatial resolutions over a ten year period

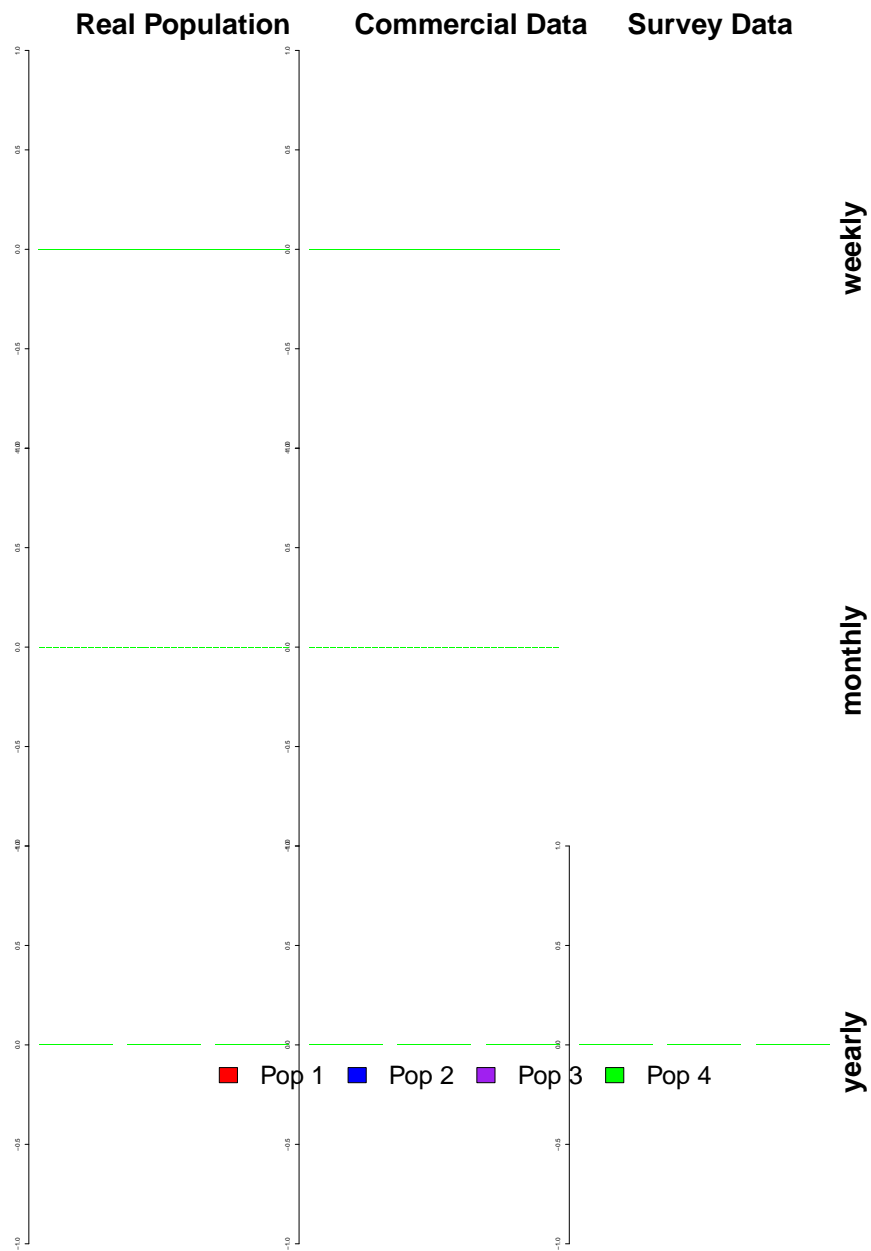


Figure 3: Data aggregation at different temporal resolutions over a three year period

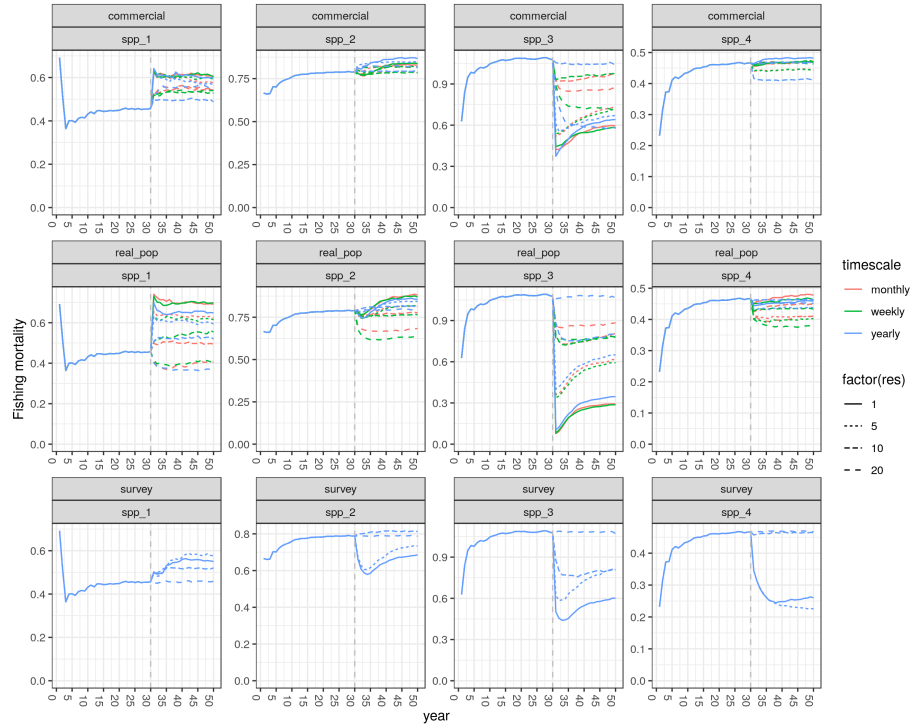


Figure 4: Comparison of closure scenarios - Fishing mortality trends. Only the scenarios based on high catch rates of population 3 are shown.

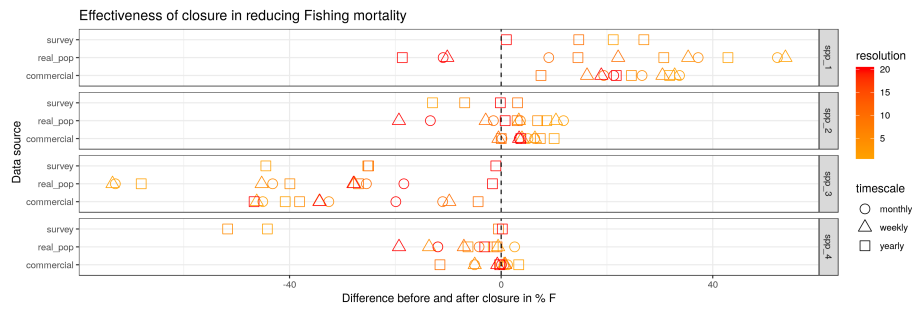


Figure 5: Comparison of closure scenarios. Points indicate the difference between the fishing mortality pre-closure (year 29) and post-closure (year 50) for population 3. Only the scenarios based on high catch rates of population 3 are shown.

## 450 References

- 451 Alverson, D.L., Freeberg, M.H., Murawski, S.A., Pope, J., 1994. A global assessment of  
452 fisheries bycatch and discards.
- 453 Bailey, R.M., Carrella, E., Axtell, R., Burgess, M.G., Cabral, R.B., Drexler, M., Dorsett, C.,  
454 Madsen, J.K., Merkl, A., Saul, S., 2018. A computational approach to managing coupled  
455 human–environmental systems: the POSEIDON model of ocean fisheries.
- 456 Bartumeus, F., Da Luz, M.G.E., Viswanatham, G.M., Catalan, J., 2005. Animal Search  
457 Strategies: A Quantitative Random Walk Analysis. *Ecological Society of America* 86,  
458 3078–3087.
- 459 Bastardie, F., Nielsen, J.R., Ulrich, C., Egekvist, J., Degel, H., 2010. Detailed mapping  
460 of fishing effort and landings by coupling fishing logbooks with satellite-recorded vessel  
461 geo-location. *Fisheries Research* 106, 41–53.
- 462 Batsleer, J., Hamon, K.G., Overzee, H.M.J., Rijnsdorp, A.D., Poos, J.J., 2015. High-grading  
463 and over-quota discarding in mixed fisheries. *Reviews in Fish Biology and Fisheries* 25,  
464 715–736.
- 465 Bellido, J.M., Santos, M.B., Pennino, M.G., Valeiras, X., Pierce, G.J., 2011. Fishery discards  
466 and bycatch: Solutions for an ecosystem approach to fisheries management? *Hydrobiologia*  
467 670, 317–333.
- 468 Bertrand, S., Bertrand, A., Guevara-Carrasco, R., Gerlotto, F., 2007. Scale-invariant move-  
469 ments of fishermen: The same foraging strategy as natural predators. *Ecological Applica-*  
470 *tions* 17, 331–337.
- 471 Beverton, R.J., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations , 533.
- 472 Catchpole, T.L., Revill, A.S., 2008. Gear technology in Nephrops trawl fisheries. *Reviews in*  
473 *Fish Biology and Fisheries* 18, 17–31.
- 474 Codling, E.A., Plank, M.J., Benhamou, S., Interface, J.R.S., 2008. Random walk models in  
475 biology. *Journal of the Royal Society, Interface / the Royal Society* 5, 813–34.
- 476 Crowder, B.L.B., Murawski, S.a., Crowder, L.B., Murawski, S.a., 1998. Fisheries Bycatch:  
477 Implications for Management. *Fisheries* 23, 8–17.
- 478 Deriso, R.B., 1980. Harvesting Strategies and Parameter Estimation for an Age-Structured  
479 Model. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 268–282. **arXiv:1410.**  
480 **7455v3.**



481 Dichmont, C.M., Punt, A.E., Deng, A., Dell, Q., Venables, W., 2003. Application of a weekly  
482 delay-difference model to commercial catch and effort data for tiger prawns in Australia 's  
483 Northern Prawn Fishery. *Fisheries Research* 65, 335–350.

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

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

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

492 Dunn, D.C., Maxwell, S.M., Boustany, A.M., Halpin, P.N., 2016. Dynamic ocean management  
493 increases the efficiency and efficacy of fisheries management. *Proceedings of the National*  
494 *Academy of Sciences* , 201513626.

495 Edwards, A.M., Station, P.B., Canada, O., 2011. Overturning conclusions of Lévy flight  
496 movement patterns by fishing boats and foraging animals. *Ecology* 92, 1247–1257.

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

502 Gerritsen, H.D., Lordan, C., Minto, C., Kraak, S.B.M., 2012. Spatial patterns in the re-  
503 tained catch composition of Irish demersal otter trawlers: High-resolution fisheries data as  
504 a management tool. *Fisheries Research* 129-130, 127–136.

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

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

511 Hilborn, R., Walters, C., 1992. Quantitative fisheries stock assessment: Choice, dynamics and  
512 uncertainty. volume 2. [arXiv:1011.1669v3](https://arxiv.org/abs/1011.1669v3).

513 Holmes, S.J., Bailey, N., Campbell, N., Catarino, R., Barratt, K., Gibb, A., Fernandes, P.G.,  
514 2011. Using fishery-dependent data to inform the development and operation of a co-  
515 management initiative to reduce cod mortality and cut discards. *ICES Journal of Marine*  
516 *Science* 68, 1679–1688.

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

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

522 Lee, J., South, A.B., Jennings, S., 2010. Developing reliable, repeatable, and accessible meth-  
523 ods to provide high-resolution estimates of fishing-effort distributions from vessel monitor-  
524 ing system (VMS) data. *ICES Journal of Marine Science* 67, 1260–1271.

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

528 Martínez-Minaya, J., Cameletti, M., Conesa, D., Pennino, M.G., 2018. Species distribution  
529 modeling: a statistical review with focus in spatio-temporal issues.

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

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

536 R Core Team, 2017. R Core Team (2017). R: A language and environment for statistical  
537 computing. R Foundation for Statistical Computing, Vienna, Austria. URL [http://www.R-](http://www.R-project.org/)  
538 [project.org/](http://www.R-project.org/). , R Foundation for Statistical Computing.

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

540 Ricker, W.E., 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*  
541 11, 559 – 623.

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

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

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

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

551 Schlater, M., Malinowski, A., Menck, P.J., 2015. Analysis, Simulation and Prediction of  
552 Multivariate Random Fields with Package RandomFields. *Journal of Statistical Software*  
553 63, 1–25. [arXiv:1501.0228](#).

554 Schnute, J., 1985. A genera theory for analysis of catch and effort data. *Canadian Journal of*  
555 *Fisheries and Aquatic Sciences* 42, 414–429.

556 Sims, D.W., Humphries, N.E., Bradford, R.W., Bruce, B.D., 2012. Lévy flight and Brownian  
557 search patterns of a free-ranging predator reflect different prey field characteristics. *Journal*  
558 *of Animal Ecology* 81, 432–442.

559 Sims, D.W., Southall, E.J., Humphries, N.E., Hays, G.C., Bradshaw, C.J.A., Pitchford, J.W.,  
560 James, A., Ahmed, M.Z., Brierley, A.S., Hindell, M.A., Morritt, D., Musyl, M.K., Righton,  
561 D., Shepard, E.L.C., Wearmouth, V.J., Wilson, R.P., Witt, M.J., Metcalfe, J.D., 2008.  
562 Scaling laws of marine predator search behaviour. *Nature* 451, 1098–U5.

563 Tidd, A.N., Hutton, T., Kell, L.T., Blanchard, J.L., 2012. Dynamic prediction of effort  
564 reallocation in mixed fisheries. *Fisheries Research* 125–126, 243–253.

565 Tobler, W.R., 1970. A Computer Movie Simulating Urban Growth in the Detroit Region.  
566 *Economic Geography* 46, 234. [arXiv:1011.1669v3](#).

567 Ulrich, C., Reeves, S.a., Vermard, Y., Holmes, S.J., Vanhee, W., 2011. Reconciling single-  
568 species TACs in the North Sea demersal fisheries using the Fcube mixed-fisheries advice  
569 framework. *ICES Journal of Marine Science* 68, 1535–1547.

570 Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Da Luz, M.G.E., Raposo, E.P., Stanley, H.E.,  
571 1999. Optimizing the success of random searches. *Nature* 401, 911–914.