

# *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, usually 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 under an explore-exploit strategy 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 a simulated fixed-site sampling design commonly used for fisheries monitoring purposes and the true underlying population structures. We i) use the results to establish the potential and limitations of fishery-dependent data in providing a robust picture of spatiotemporal distributions; and ii) simulate an area closure based on areas defined from the different data sources at a range of 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 and 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 one or more quota. This may lead to overexploita-

tion of fish populations (Ulrich et al., 2011; Batsleer et al., 2015). Discarding of fish in excess of quota limits the ability to maintain fishing mortality within sustainable limits (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp et al., 2007) and the ability to manage for the biological and economic sustainability of fisheries. As such, there is increasing interest in technical solutions such as gear and spatial closures as measures to reduce unwanted catch (Kennelly and Broadhurst, 2002; Catchpole and Revell, 2008; Bellido et al., 2011)(ADD COS-GROVE REFERENCE HERE).

Changes to spatial fishing patterns have been proposed as a method to reduce discards (Holmes et al., 2011; Little et al., 2014; Dunn et al., 2014). Implementation of avoidance measures is, however, restricted by lack of knowledge of fish and fishery spatiotemporal dynamics and understanding of the scale at which processes become important for management. Understanding the correct scale for spatial measures is crucial for implementation 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 an appropriate scale has been a challenge in the past that has led to ineffectual measures with unintended consequences such as limited impact towards the management objective or increased benthic impact on previously unexploited areas (e.g. the cod closure in the North Sea (Rijnsdorp et al., 2001; Dinmore et al., 2003)). More refined spatial information has since 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) and more real-time spatial management has been possible (e.g. Holmes et al., 2011). Such information is, however, derived from an inherently biased sampling programme, targeted fishing, where fishers establish favoured fishing grounds through an explore-exploit strategy (Bailey et al., 2018) where they

38 search for areas with high catches and then use experience to return to areas  
39 where they've experienced high catch in the past.

40  
41 We ask two fundamental questions regarding spatiotemporal inference de-  
42 rived from observational data:

- 43 1. How does sampling-derived data reflects the underlying population struc-  
44 tures?
- 45 2. How does data aggregation and source impact on spatial fisheries man-  
46 agement measures?

47 To answer these questions we i) develop a simulation model where population  
48 dynamics are highly-resolved in space and time. Being known directly rather  
49 than inferred from sampling or commercial catch, we can use the population  
50 model to validate how inference from fisheries-dependent and fisheries indepen-  
51 dent sampling relates to the real population structure in a way we could not  
52 with real data. We ii) compare, at different spatial and temporal aggregations,  
53 the simulated population distributions to samples from fisheries-dependent and  
54 fisheries independent catches to test if these are a true reflection of the relative  
55 density of the populations. We then iii) simulate a fishery closure to protect a  
56 species based on different spatial and temporal data aggregations. We use these  
57 evaluations to draw inference on the utility of commercial data in supporting  
58 management decisions.

59  
60 [We find..]

## 61 2. Materials and Methods

62 A simulation model that is modular and discrete-event based was developed.  
63 This approach enables efficient computation by allowing for sub-modules imple-  
64 mented on time-scales appropriate to capture the characteristic of the different  
65 processes (Figure 1). The following sub-modules were included to capture the

This comes as a surprise: I thought this was going to be about discard-sAgree, have removed this to avoid confusion

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 validation of the data aggregation, rather than effectiveness of the closures themselves - so its a continuation of the same question in my eyes

66 full system: 1) Population dynamics, 2) Recruitment dynamics, 3) Population  
67 movement, 4) fishery dynamics.

68

69     Population dynamics (fishing and natural mortality, growth) operate on a  
70 daily time-step, while population movement occurs on a weekly time-step. Re-  
71 cruitment takes place periodically each year for a set time duration specified for  
72 each population, while the fishing module operates on a tow-by-tow basis (i.e.  
73 multiple events a day).

74     In the model system population movement is driven by random (diffusive)  
75 and directed (advective) processes and we incorporate characterisation of a num-  
76 ber of different fishing fleet dynamics exploiting four fish populations with dif-  
77 ferent spatial and population demographics. The following describes the imple-  
78 mentation of each of the sub-modules.



Figure 1: Schematic overview of the simulation model. 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.

79 *2.1. Population dynamics*

80 The basic population level processes are simulated using a modified two-stage  
 81 Deriso-Schnute delay difference model (Deriso, 1980; Schnute, 1985; Dichmont  
 82 et al., 2003) occurring at a daily time-step. A daily time-step was chosen to  
 83 discretise continuous population processes on a biologically relevant and com-  
 84 putationally tractable timescale. Under the population dynamics module pop-  
 85 ulation biomass growth and depletion for pre-recruits and recruited fish are  
 86 modelled separately as a function of previous recruited biomass, intrinsic popu-  
 87 lation growth and recruitment functionally linked to the adult population size.  
 88 Biomass for each cell  $c$  is incremented each day  $d$  as follows (the full parameter  
 89 list is detailed in Table 1):

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

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

95

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

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

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

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 adult biomass to recruits at time of recruitment. In *MixFishSim*, it can be modelled either either as a stochastic Beverton-Holt stock-recruit form (Beverton and Holt, 1957):

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

Where  $\alpha$  is the maximum recruitment rate,  $\beta$  the spawning stock biomass (SSB) required to produce half the maximum stock size,  $S$  current stock size 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 our example application the Beverton-Holt form of stock recruit relationship was used for all populations though either functional form can be chosen.

## 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.

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  $S = \{S(c_1), \dots, S(c_n)\}$

[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]

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



is multivariate Gaussian with a *Matérn* covariance structure, where the correlation strength weakens with distance. This enables us to model the spatial autocorrelation observed in animal populations where density is more similar in nearby locations (Tobler, 1970; F. Dormann et al., 2007) and we change the parameters to implement different spatial structures for the populations.

The habitat for each of the populations was generated with the *RFSimulate* function of the *RandomFields* R package (Schlatter et al., 2015), which simulates a Gaussian Random Field process given a user defined error model and correlation structure. We define a stationary habitat field and combine with a temporally dynamic thermal tolerance field to imitate two key drivers of population dynamics. Each population 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:

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

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

During pre-defined weeks of the year the habitat quality is modified with user-defined spawning habitat locations, resulting in each population having concentrated areas where spawning takes place. In the simulations the populations move towards these cells in the weeks prior to spawning, resulting in directional movement towards the spawning grounds.

An advection-diffusion process controls population movement, with a time-varying temperature covariate used to change the interaction between time and

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

154 suitable habitat on a weekly time-step. Each population  $p$  was assigned a ther-  
 155 mal tolerance with mean,  $\mu_p$  and variance,  $\sigma_p^2$  so that each cell and population  
 156 temperature suitability is defined that:

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

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

160

161 The final process results in a population structure and movement pattern  
 162 unique to each species, with population movement occurring on a weekly basis.  
 163 The decision to model population movement on a weekly timescale was to reflect  
 164 that fish tend to aggregate in species specific locations and range within a week  
 165 is fairly limited [REF!!]. Therefore this process approximated the demographic  
 166 shifts in fish populations throughout a year with seasonal spawning patterns  
 167 (e.g. Figure ??).

#### 168 2.4. Fleet dynamics

169 The fleet dynamics can be broadly categorised into three components; fleet  
 170 targeting - which determined the fleet catch efficiency and preference towards a  
 171 particular species; trip-level decisions, which determined the initial location to  
 172 be fished at the beginning of a trip; and within-trip decisions, determining move-  
 173 ment from one fishing spot to another within a trip. Together, these elements  
 174 implement an explore-exploit type strategy for individual vessels to maximise  
 175 their catch from an unknown resource distribution (Bailey et al. (2018)). The  
 176 decision to use an individual based model for fishing vessels was taken because  
 177 fishers as a group tend to show heterogeneity and individual rather than group  
 178 dynamics [REF!]. Therefore in the simulations fleet dynamics are the productive  
 179 of individual experiences rather than pre-defined group dynamics.

What have a  
 temperature co-  
 variate? Could  
 just use time-  
 Was intended  
 as some biolog-  
 ical meaning  
 - species ther-  
 mal tolerances  
 load onto the  
 temperature ef-  
 fect - so could  
 be different per  
 species

#### 180 2.4.1. Fleet targeting

181 Each fleet of  $n$  vessels was characterised by both a general efficiency,  $Q_{fl}$ ,  
182 and a population specific efficiency,  $Q_{fl,p}$ . Thus, the product of these param-  
183 eters  $[Q_{fl} \cdot Q_{fl,p}]$  affects the overall catch rates for the fleet and the preferential  
184 targeting of one population over another. This, in combination with the param-  
185 eter choice for the step-function defined below (as well as some randomness from  
186 the exploratory fishing process) determined the preference of fishing locations  
187 for the fleet. All species prices were kept the same across fleets and seasons.

#### 188 2.4.2. Trip-level decisions

189 Several studies (e.g. Hutton et al., 2004; Tidd et al., 2012; Girardin et al.,  
190 2015) have confirmed past activity and past catch rates are strong predictors of  
191 fishing location choice. For this reason, the fleet dynamics sub-model included a  
192 learning component, where a vessel's initial fishing location in a trip was based  
193 on selecting from previously successful fishing locations. This was achieved by  
194 calculating an expected revenue based on the catches from locations fished in  
195 the preceding trip as well as the same month periods in previous years and the  
196 travel costs from the port to the fishing grounds, and choosing randomly from  
197 the top 75 % of fishing events as defined by the expected profit, which has a  
198 seasonal component.

#### 199 2.4.3. Within-trip decisions

200 Fishing locations within a trip are initially determined by a modified ran-  
201 dom walk process. As the simulation progresses the within-trip decision become  
202 gradually more influenced by experience gained from past fishing locations (as  
203 per the initial trip-level location choice), moving location choice towards areas  
204 of higher perceived profit. A random walk was chosen for the exploratory fishing  
205 process as it is the simplest assumption commonly used in ecology to describe  
206 optimal animal search strategy for exploiting homogeneously distributed prey  
207 about which there is uncertain knowledge (Viswanathan et al., 1999). In a ran-  
208 dom walk, movement is a stochastic process through a series of steps. These

209 steps have a length, and a direction that can either be equal in length or take  
 210 some other functional form. The direction of the random walk was also cor-  
 211 related (known as ‘persistence’) providing some overall directional movement  
 212 (Codling et al., 2008).

213

214 We use a *Lévy flight* which is a particular form of random walk charac-  
 215 terised by a heavy-tailed distribution of step-length. The Lévy flight has re-  
 216 ceived a lot of attention in ecological theory in recent years as having shown to  
 217 have very similar characteristics as those observed by animals in nature, and  
 218 being a near optimum searching strategy for predators pursuing patchily dis-  
 219 tributed prey (Viswanathan et al., 1999; Bartumeus et al., 2005; Sims et al.,  
 220 2008). Bertrand et al. (2007) showed that Peruvian anchovy fishermen have a  
 221 stochastic search pattern similar to that observed with a lévy flight. However,  
 222 it remains a subject of debate (e.g. see Edwards et al., 2011; Reynolds, 2015),  
 223 with the contention that search patterns may be more simply characterised as  
 224 random walks (Sakiyama and Gunji, 2013) with specific patterns related to the  
 225 characteristics of the prey field (Sims et al., 2012).

226

227 For our implementation of a random walk directional change is based on  
 228 a negatively correlated circular distribution where a favourable fishing ground  
 229 is likely to be “fished back over” by the vessel returning in the direction it  
 230 came from. The step length (i.e. the distance travelled from the current to the  
 231 next fishing location) is determined by recent fishing success, measured as the  
 232 summed value of fish caught (revenue,  $Rev$ ),

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

233 where  $L_p$  is landings of a population  $p$ , and  $Pr_p$  price of a population. Here,  
 234 when fishing is successful vessels remain in a similar location and continue to  
 235 exploit the local fishing grounds. When unsuccessful, they move some distance  
 236 away from the current fishing location. The movement distance retains some  
 237 degree of stochasticity, which can be controlled separately, but is determined by

238 the relationship:

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

239 Where  $\beta_1$ ,  $\beta_2$  and  $\beta_3$  are parameters determining the shape of the step function  
240 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  $Br_{t-1} < 180, Br_t = 180 + \sim vm[(0, 360), k]$

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

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

#### 246 2.4.4. Local population depletion

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

#### 257 2.5. Fisheries independent survey

258 A fisheries-independent survey is simulated where fishing on a regular grid  
259 begins each year at the same time for a given number of stations (a fixed station

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

survey design). Catches of the populations at each station are recorded but not removed from the population. This provides a fishery independent snapshot of the populations at a regular spatial intervals each year, similar to scientific surveys undertaken by fisheries research agencies.

## 2.6. Software

The simulation framework is implemented in the statistical software package R (R Core Team, 2017) and available as an R package from the authors github site ([www.github.com/pdolder/MixFishSim](https://www.github.com/pdolder/MixFishSim)).

## 3. Parameterisation

### 3.1. Population models

We parametrised the simulation model for four populations with different demographics; growth rates, natural mortality and recruitment functions (Table 4). Habitat preference (Figure ??) and temperature tolerances (Figures ??, ??) were unique to each population resulting in differently weekly distribution patterns (Figures ??-??). In addition, each of the populations has two defined spawning areas which result in the populations moving towards these areas in pre-defined weeks (Figure ??) with population-specific movement rates (Table 4). The individual habitat preferences and thermal tolerances result in different spatial habitat use for each population (Figure ??) and consequently different seasonal exploitation patterns (Fishing mortality in Figure ??).

### 3.2. Fleet parametrisation

The fleets were parametrised to reflect five different characteristic fisheries with unique exploitation dynamics (Table 5). By setting different catchability parameters ( $Q_{fl,p}$ ) we create different targeting preferences between the fleets and hence spatial dynamics. The stochasticity in the random walk process

ensures that within a fleet different vessels have slightly different spatial distributions based on individual experience. The step function was parametrised dynamically within the simulations as the maximum revenue obtainable was not known beforehand. This was implemented so that vessels take smaller steps when fishing at a location that yields landings value in the top 90th percentile of the value experienced in that year so far (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 approximately halfway through the simulation.

### 3.3. Survey settings

The survey simulation was set up with 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 ( $Q_p = 1$ ). This approximates a real world survey design with limited seasonal and spatial coverage.

### 3.4. Example research question

To illustrate the capabilities of *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 to run for 50 years based on a  $100 \times 100$  square grid (undetermined units), with five fleets of 20 vessels each and four fish populations. Fishing takes place four

316 times a day per vessel and five days a week, while population movement is every  
317 week.

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

322  
323 The following steps are undertaken to determine closures:

- 324 1. Extract data source
- 325 2. Aggregate according to desired spatial and temporal resolution
- 326 3. Interpolate across entire area at desired resolution using simple kriging  
327 using the *interp* function from the R package akima [REF!].
- 328 4. Close area covering top 5 % of catch rates

329 In total 28 closure scenarios were run which represent combinations of:

- 330 • **data types:** commercial logbook data, survey data and 'real population',
- 331 • **temporal resolutions:** weekly, monthly and yearly closures,
- 332 • **spatial resolutions:** 1 x 1 grid, 5 x 5 grid, 10 x 10 grid and 20 x 20 grid,
- 333 • **closure basis:** highest 5 % of catch rates for the protected species

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

## 336 4. Results

### 337 4.1. Simulation dynamics

It can be seen from a single vessels movements during a trip that the vessel exploits four different fishing grounds, three of them multiple times (Figure ??), while across several trips fishing grounds that are further apart are fished (Figure

Is there equilibrium after 5 years or still some trend in B? I have rerun to ensure some steady state dynamics

Procedure unclear. Refer to symbols in methods section or switch order starting with description of data type etc..Yes, will redo



??). These different locations relate to areas where the highest revenue were experienced, as shown by Figure ??, where several trips for the vessel overlaid on the revenue field, i.e.

$$\sum_{c=1}^c \sum_{s=1}^s B_{s,c} \cdot Q_{s,c}$$

Vessels from the same fleet (and therefore targeting preference) exploit similar but slightly different fishing grounds depending on their own personal experience during the explore phase of the fishery (Figure ??), which is the result of the randomness in the correlated random walk step function, with distance moved during the exploitation phase and the direction stochastically related to the revenue experienced on the fishing ground (Figure ??).

#### 4.2. How does sampling-derived data reflect the underlying population structure?

In order to answer this question we compare different spatial and temporal aggregations of the simulated population distributions to:

- a) **fisheries-independent data:** the inferred population from a fixed-site sampling survey design as commonly used for fisheries monitoring purposes;
- b) **fisheries-dependent data:** the inferred population from our fleet model which includes fishery-induced sampling dynamics.

Figure 2 shows the aggregated catch composition from each of the data sources over a ten-year period (to average seasonal patterns) at different spatial resolutions. The finer spatial grid for the real population (top left) and commercial data (top middle) show visually similar patterns, though there are large unsampled areas in the commercial data from a lack of fishing activity (particularly in the lower left part of the sampling domain). The survey data at this spatial resolution displays very sparse information about the spatial distributions of the populations. The slightly aggregated data on a 5 x 5 grid shows similar patterns and, while losing some of the spatial detail, there remains good consistency between the ‘real population’ and the commercial data. Survey

Move some of the supplementary figures to the manuscript

362 data starts to pick out some of the similar patterns as the other data sources,  
363 but lacks coverage. The spatial catch information on a 10 x 10 and 20 x 20  
364 grid lose a significant amount of information about the spatial resolutions for  
365 all data sources, and some differences between the survey, commercial and 'real  
366 population' data emerge.

367

368 Figure 3 shows the consequences of different temporal aggregations of the  
369 data over a ten-year period, with weekly (top), monthly (middle) and yearly  
370 (bottom) catch compositions from across an aggregated 20 x 20 area. As can be  
371 seen by comparison to the 'real population', the monthly aggregation captures  
372 the major patterns seen in the weekly data, albeit missing more subtle differ-  
373 ences. The yearly data results in a constant catch pattern due to the aggregation  
374 process (sometimes known as an aggregation bias). The commercial data on a  
375 weekly basis shows some of the same patterns as the 'real population', though  
376 the first species (in red) is less well represented and some weeks are missing  
377 catches from the area. The monthly data shows some consistency between the  
378 'real population' and commercial data for species 2 - 4, though species 1 remains  
379 under-represented. On an annual basis, interestingly the commercial data under-  
380 represents the first species (in red) while the survey over represents species 1.  
381 This is likely due to the biases in commercial sampling, with the fisheries not  
382 targeting the areas where species 1 are present, and the biases in the survey  
383 sampling from over representation of the spatial distribution.

#### 384 4.3. *How does data aggregation and source impact on spatial fisheries manage-* 385 *ment measures?*

386 We implemented a spatial closure using the different data sources and spatial  
387 and temporal aggregations as outlined in the protocol in Section 3.4. We used  
388 this to assess the efficacy of a closure in reducing fishing mortality on species 3,  
389 given availability of data and its use at different resolutions in order to evaluate  
390 the trade-offs in data sources.

391 The trend in fishing mortality for each species show that in most cases the

fishery closure was successful in reducing fishing mortality on the species of interest (species 3; Figure 4), though interestingly the largest reductions in fishing mortality happened immediately after the closures, following which the fisheries "adapted" to the closures and fishing mortality increased again somewhat. The exception to the success was the closures implemented based on the coarsest spatial (20 x 20) and temporal resolution (yearly) which were ineffective with all data sources. As expected, closures based on the "known" population distribution were most effective, with differing degrees of success using the commercial data. Fishing mortality rates on the other species changed in different proportions, depending on whether the displaced fishing effort moved to areas where the populations were found in greater or lesser density.

A regression tree (using the R package REEMtree [ref]) highlights that the factor most contributing to differences in fishing mortality before and after the closure was the population (72 % showing that the closures were effective for population 3), followed by data resolution (21 %), data type (7 %) with the least important factor the timescale (< 1 %). In general the finer the spatial resolution of the data used the greater reduction in fishing mortality for population 3 after the closures (Figure 5). The notable outliers are the commercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly timescale, where closures were nearly as effective as the fine-scale resolution. In this case the closures were sufficiently large to protect the population (and was as effective as when the closure was based on the "real population"; CHECK THIS, COULD PLOT ACTUAL CLOSURE LOCATIONS??) but this may have consequences in terms of restricting a much larger area than necessary.

417

## 418 5. Discussion

Our study evaluates the importance of data scaling and considers potential bias introduced through data aggregation when using fisheries data to infer

421 spatio-temporal dynamics of fish populations. Understanding how fishers ex-  
422 ploit multiple heterogeneously distributed fish populations with different catch  
423 limits or conservation status requires detailed understanding of the overlap of  
424 resources; this is difficult to achieve using conventional modelling approaches  
425 due to species targeting in fisheries resulting in preferential sampling (Martínez-  
426 Minaya et al., 2018). Often data are aggregated or extrapolated which requires  
427 assumptions about the spatial and temporal scale of processes. Our study ex-  
428 plores the assumptions behind such aggregation and preferential sampling to  
429 identify potential impacts on management advice. With modern management  
430 approaches increasingly employing more nuanced spatio-temporal approaches  
431 in order to maximise productivity while taking account of both the biological  
432 and human processes operating on different time-frames (Dunn et al., 2016),  
433 understanding assumptions behind the data used - increasingly a combination  
434 of logbook and positional information from vessel monitoring systems - is vital  
435 to ensure measures are effective.

436

437 We employ a simulation approach to model each of the population and fish-  
438 ery processes in a hypothetical 'mixed fishery', allowing us to i) evaluate the  
439 consequences of different aggregation assumptions on our understanding of the  
440 spatio-temporal distribution of the underlying fish populations, and ii) evaluate  
441 the effectiveness of a spatial closure given those assumptions.

442

443 Our approach captures fine scale population and fishery dynamics and their  
444 interaction in a way not usually possible with real data and thus not usually  
445 considered in fisheries simulations. While other simulation frameworks seek to  
446 model individual vessel dynamics based on inferred dynamics from VMS and  
447 logbook records (Bastardie et al., 2010), or as a system to identify measures to  
448 meet particular management goals (Bailey et al., 2018), our framework allows  
449 users to explore the assumptions in modelling observational data and evaluate  
450 the underlying dynamics of such approaches at a fine spatial and temporal scale.  
451 This offers the advantage that larger scale fishery patterns are emergent prop-

452 erties of the system rather and results can be compared to those obtained under  
453 a statistical modelling framework.

454

455 Our results demonstrate the importance of data scale and resolution when  
456 using observational data to support management measures. In doing so it high-  
457 lights depends on scale of process: pop movement etc... Important to consider  
458 how fishers interact / adapt to changes with the resource and mgmt.

459

460 It seems clear that spatial disaggregation is more important than the tem-  
461 poral disaggregation of the commercial data... WHY

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

464

465 The what next:

466

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

469

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

473

474 Other potential uses of the model

475

476 Survey design

477

478 commercial index standardization methods

479

480 Sampling scheme design

481

482 Testing fleet dynamics models at an aggregated level

483

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

## 486 **6. Conclusions**

487       Study shows ....

488

489       This is important because ....

490

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

492

## 493 **Abbreviations**

494       Detail any unusual ones used.

## 495 **Acknowledgements**

496       those providing help during the research..

## 497 **Funding**

498       This work was supported by the MARES doctoral training program (MARES\_14\_15)  
499 and the Centre for Environment, Fisheries and Aquaculture Science seedcorn  
500 program (DP227AC).

## 501 **Appendices**

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

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 1	Fleet 2	Fleet 3	Fleet 4	Fleet 5
Targeting preferences	pop 2/4	pop 1/3	-	pop 4	pop 2/3
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. Results show the fishing mortality before the closure (f.before) and after the closure (f.after) and the percentage change in f (f.change). The results are ordered by most effective scenario first, least effective last.)

scenario	metric	pop	f.before	f.after	f.change	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

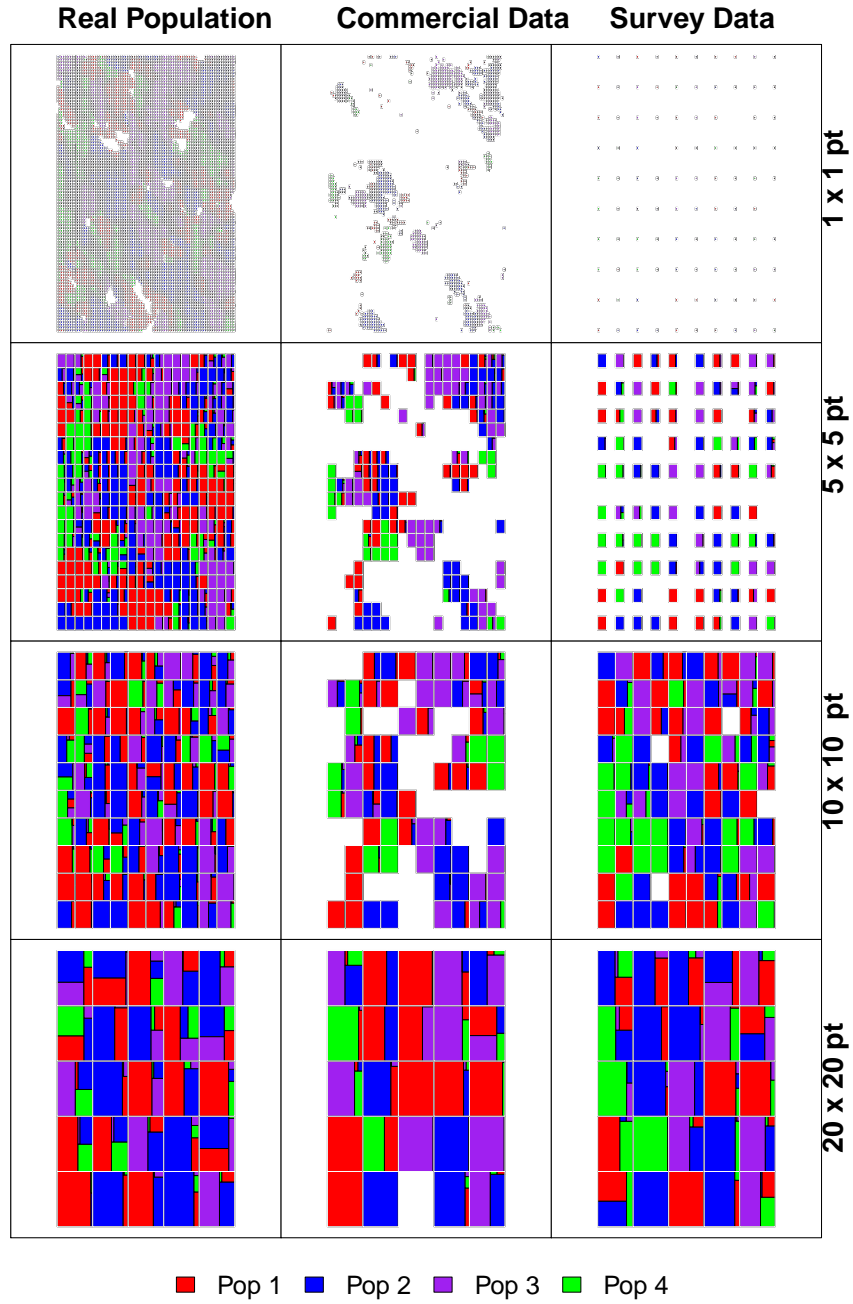


Figure 2: Data aggregation at different spatial resolutions over a ten year period

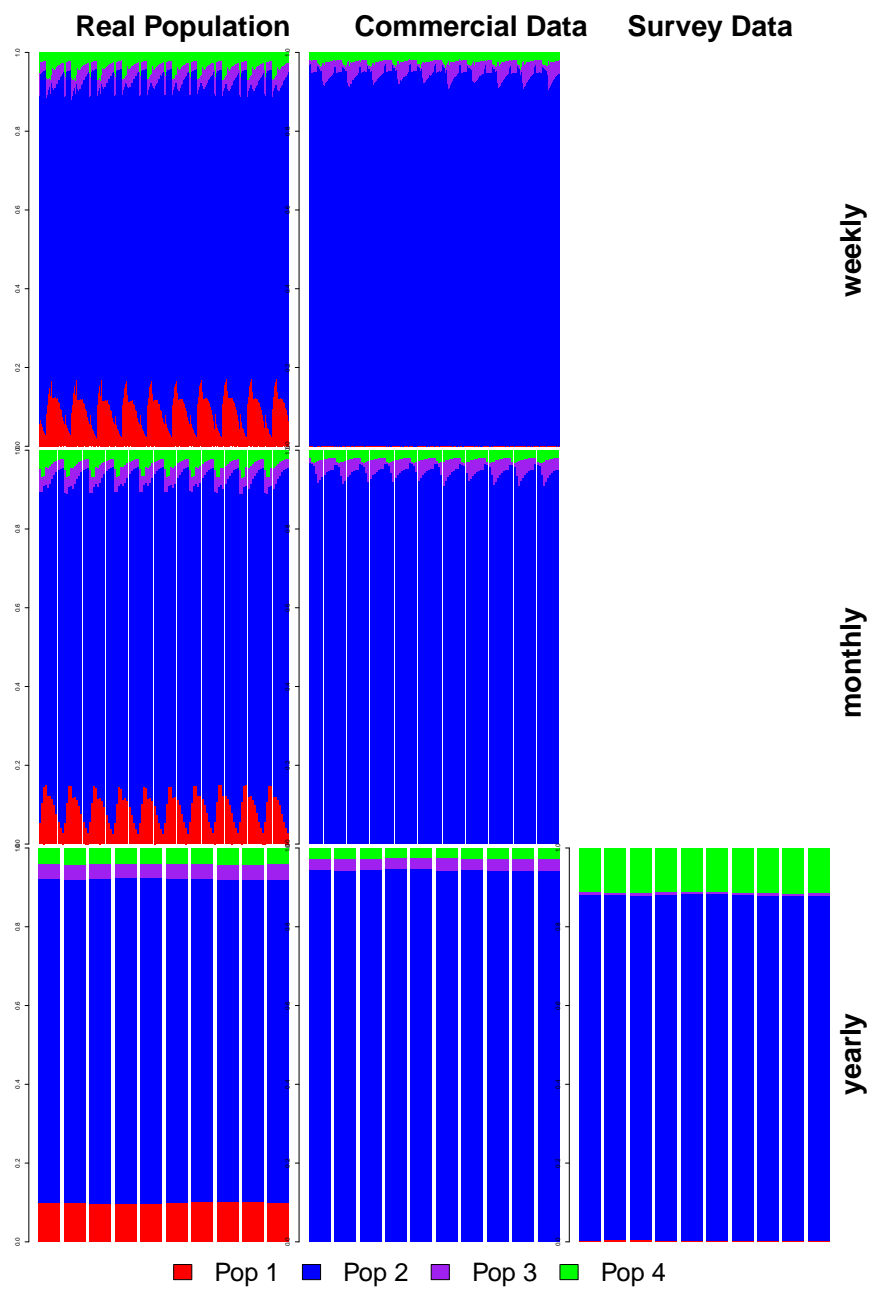


Figure 3: Data aggregation at different temporal resolutions over a ten-year period

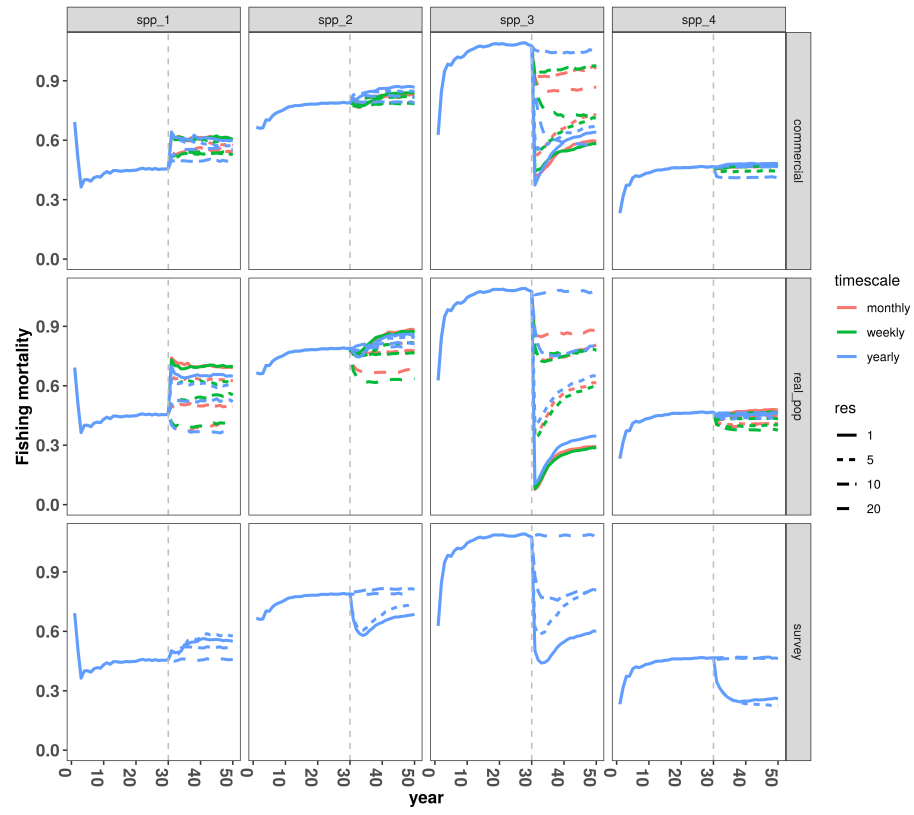


Figure 4: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes the timescale, while linestyle denotes the spatial resolution.

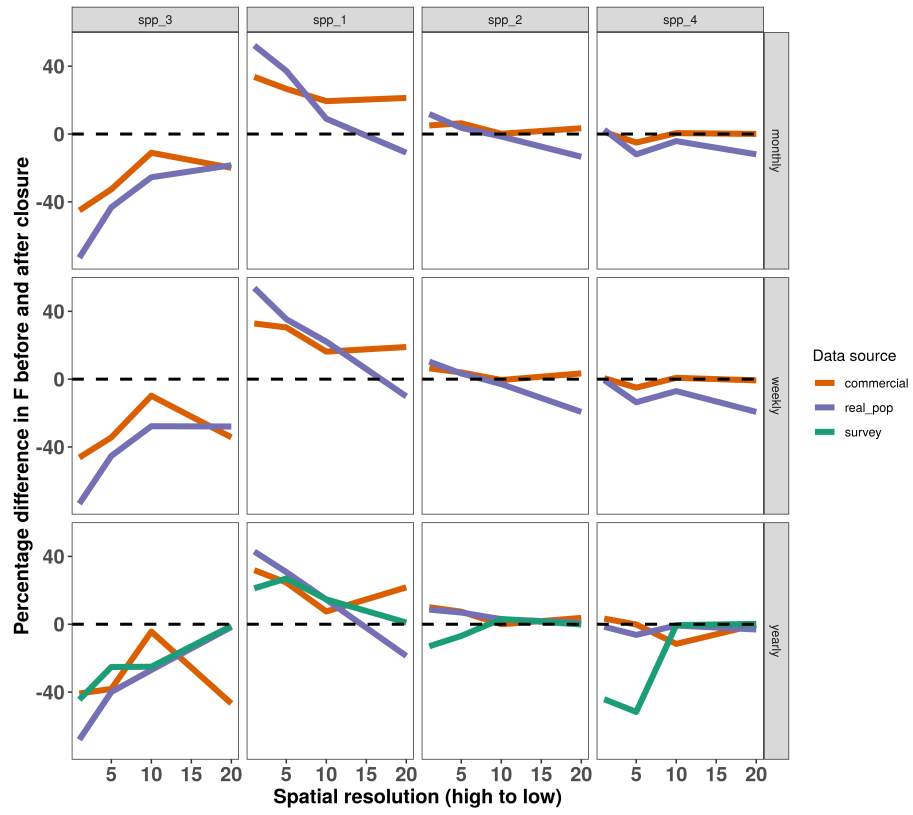


Figure 5: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.



## 502 References

- 503 Alverson, D.L., Freeberg, M.H., Murawski, S.A., Pope, J., 1994. A global assessment of  
504 fisheries bycatch and discards.
- 505 Bailey, R.M., Carrella, E., Axtell, R., Burgess, M.G., Cabral, R.B., Drexler, M., Dorsett, C.,  
506 Madsen, J.K., Merkl, A., Saul, S., 2018. A computational approach to managing coupled  
507 human–environmental systems: the POSEIDON model of ocean fisheries.
- 508 Bartumeus, F., Da Luz, M.G.E., Viswanatham, G.M., Catalan, J., 2005. Animal Search  
509 Strategies: A Quantitative Random Walk Analysis. *Ecological Society of America* 86,  
510 3078–3087.
- 511 Bastardie, F., Nielsen, J.R., Ulrich, C., Egekvist, J., Degel, H., 2010. Detailed mapping  
512 of fishing effort and landings by coupling fishing logbooks with satellite-recorded vessel  
513 geo-location. *Fisheries Research* 106, 41–53.
- 514 Batsleer, J., Hamon, K.G., Overzee, H.M.J., Rijnsdorp, A.D., Poos, J.J., 2015. High-grading  
515 and over-quota discarding in mixed fisheries. *Reviews in Fish Biology and Fisheries* 25,  
516 715–736.
- 517 Bellido, J.M., Santos, M.B., Pennino, M.G., Valeiras, X., Pierce, G.J., 2011. Fishery discards  
518 and bycatch: Solutions for an ecosystem approach to fisheries management? *Hydrobiologia*  
519 670, 317–333.
- 520 Bertrand, S., Bertrand, A., Guevara-Carrasco, R., Gerlotto, F., 2007. Scale-invariant move-  
521 ments of fishermen: The same foraging strategy as natural predators. *Ecological Applica-*  
522 *tions* 17, 331–337.
- 523 Beverton, R.J., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations , 533.
- 524 Catchpole, T.L., Revill, A.S., 2008. Gear technology in Nephrops trawl fisheries. *Reviews in*  
525 *Fish Biology and Fisheries* 18, 17–31.
- 526 Codling, E.A., Plank, M.J., Benhamou, S., Interface, J.R.S., 2008. Random walk models in  
527 biology. *Journal of the Royal Society, Interface / the Royal Society* 5, 813–34.
- 528 Crowder, B.L.B., Murawski, S.a., Crowder, L.B., Murawski, S.a., 1998. Fisheries Bycatch:  
529 Implications for Management. *Fisheries* 23, 8–17.
- 530 Deriso, R.B., 1980. Harvesting Strategies and Parameter Estimation for an Age-Structured  
531 Model. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 268–282. **arXiv:1410.**  
532 **7455v3.**

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

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

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

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

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

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

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

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

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

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

563 Holmes, S.J., Bailey, N., Campbell, N., Catarino, R., Barratt, K., Gibb, A., Fernandes, P.G.,  
564 2011. Using fishery-dependent data to inform the development and operation of a co-  
565 management initiative to reduce cod mortality and cut discards. *ICES Journal of Marine  
566 Science* 68, 1679–1688.

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

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

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

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

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

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

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

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

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

590 Ricker, W.E., 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*  
591 11, 559 – 623.

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

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

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

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

601 Schlater, M., Malinowski, A., Menck, P.J., 2015. Analysis, Simulation and Prediction of  
602 Multivariate Random Fields with Package RandomFields. *Journal of Statistical Software*  
603 63, 1–25. [arXiv:1501.0228](#).

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

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

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

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

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

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

620 Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Da Luz, M.G.E., Raposo, E.P., Stanley, H.E.,  
621 1999. Optimizing the success of random searches. *Nature* 401, 911–914.