

# Highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

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## Abstract

To understand how data resolution impacts inference on mixed fisheries interactions we developed a highly resolved spatiotemporal discrete-event simulation model (‘MixFishSim’)[CM: I think *MixFishSim* is more effective] incorporating: i) delay-difference population dynamics, ii) population movement using Gaussian Random Fields to simulate patchy, heterogeneously distributed and moving fish populations, and iii) fishery dynamics for multiple fleet characteristics based on population targeting under an explore-exploit strategy. ~~This is implemented via a mix of correlated random walk movement (for exploration) and learned behaviour (for exploitation) phases of the fisheries.~~ Fifty years of sub-daily fishing activity was simulated and used to draw inference on the underlying community structures. ~~We applied ‘MixFishSim’ to draw compared inferences on community structure when using data generated from: based on commercial catch, a simulated fixed-site sampling survey design and the true (simulated) underlying populations. We thereby i) establish the potential limitations of fishery-dependent data in providing a robust characterisation picture of spatiotemporal distributions; and then ii) simulated an area closure based on~~

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areas defined from the different data sources at a range of temporal and spatial resolutions. Our framework allows users to explore the assumptions in modelling observational data and evaluate the underlying dynamics of such approaches at a fine spatial and temporal scale. In application to a mixed fishery exploiting four different populations ~~w~~ We found ~~d~~ Different spatial patterns were evident and ~~that~~ the effectiveness of the spatial closure reduced when data were aggregated across larger spatial areas. ~~;~~ and then ii) We then simulated an area closure based on areas defined from the different data sources. A simulated area closure showed that ~~a~~ Aggregation across time periods has less of a negative impact on the closure success than aggregation over space. ~~and~~ While not as effective as when based on on the true population, closures based on high catch rates observed in commercial data were still able to reduce fishing on a protected species.

MixFishSim ~~Our framework~~ allows users to explore the assumptions in modelling ~~====~~ resolutions. Aggregation across time periods has less of a negative impact on the closure success than over space. ~~and~~ While not as effective as when based on on the true population, closures based on high catch rates observed in commercial data were still able to reduce fishing on a protected species.

Our framework allows users to explore the assumptions in modelling ~~~~~~~~~ ~~f5e5489e3bc3778abecffc1d0c3d90fdb3592e8b~~ observational data and evaluate the underlying dynamics of such approaches at a fine spatial and temporal scale. From our application ~~w~~ We conclude that commercial data, while containing bias, provide a useful tool for managing catches in mixed fisheries if applied at the correct spatiotemporal scale.

*Keywords:* spatiotemporal, mixed fisheries, individual based, spatial management, heterogeneity, bycatch avoidance

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## 1. Introduction

Fishers exploit a variety of fish populations that are heterogeneously distributed in space and time with varying knowledge of species distributions. As fishers do not have full control over what species they select when fishing in ‘mixed fisheries’ it can result in catch of low quota or protected species. If over-quota catch of a species for which they have no quota is discarded without being accounted for it limits our ability to control fishing mortality (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp et al., 2007) and the ability to manage fisheries for the biological and economic sustainability (Ulrich et al., 2011; Bat-sleer et al., 2015).

There is increasing interest in technical solutions such as gear and spatial closures as measures to reduce unwanted catch [which is often discarded](#) (Kennelly and Broadhurst, 2002; Catchpole and Reville, 2008; Bellido et al., 2011; Cosgrove et al., 2019). ~~A-and-a~~adaptive spatial management strategies have been proposed as a way of reducing over-quota discards (Holmes et al., 2011; Little et al., 2015; Dunn et al., 2014). However, if fisheries are to reduce unwanted catch through spatial avoidance, an in-depth understanding of spatiotemporal fishery dynamics is required.

Understanding the correct scale for spatial management measures to be effective is crucial as it enables implementation of effective solutions which minimise economic impact (Dunn et al., 2016). For example, the problem can be to identify a scale that promotes species avoidance for vulnerable or low quota species while allowing continuance of sustainable fisheries for available quota species. Identifying the correct spatial scale remains a challenge because data on fish location at high temporal and spatial resolutions is expensive and difficult to collect and proxies are usually inferred from scientific surveys or commercial catches with limited spatial and temporal resolution. Thus, implementation of spatial measures is hampered by a lack of knowledge of fish and fishery spa-

31 spatiotemporal dynamics and understanding of the scale at which these processes  
32 become important for management.

33

34

35 Identifying appropriate spatial scales for fisheries closures ~~has been a highlighted~~  
36 ~~ais~~ is crucial to their success (Costello et al., 2010; Dunn et al., 2016). Inference on  
37 fisheries spatial dynamics is hampered where spatial information is coarse due to  
38 low resolution reporting of fisheries catch which is aggregated across larger grid-  
39 ded areas (Branch et al., 2005). Further, if data does not allow identification of  
40 spatial features it may lead to poorly sited closures ~~that~~~~which~~ are ineffectual or  
41 have unintended consequences. For example, increased benthic impact on pre-  
42 viously unexploited areas from the cod closure in the North Sea were observed  
43 without the intended effect of reducing cod exploitation (Rijnsdorp et al., 2001;  
44 Dinmore et al., 2003)).

45

46 More refined spatiotemporal information has since become available through  
47 the combination of logbook and Vessel Monitoring System (VMS) data (Lee  
48 et al., 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al., 2017)  
49 and more real-time spatial management has been possible (e.g. Holmes et al.,  
50 2011). However, fishers establish favoured fishing grounds through an explore-  
51 exploit strategy (Rijnsdorp et al., 2011; Bailey et al., 2019) where they search  
52 for areas with high catches and then use experience to return to areas where  
53 they have experienced high catch in the past. This leads to an inherently biased  
54 sampling where target species are over-represented in the catch as fishers exploit  
55 areas of high abundance. There is a need to understand the influence of these  
56 biases on any spatial management measures which are implemented based on  
57 inference from commercial landings or catch data.

58

59 To understand the effect of spatiotemporal aggregation of data and fishery  
60 targeting on our perception of spatial abundance of different fish populations we  
61 ask two fundamental questions regarding inference derived from observational

62 data:

- 63 1. Do different sources of sampling-derived fisheries data reflect the under-  
64 lying community structure?
- 65 2. How does data aggregation and data source impact on the success of spa-  
66 tial fisheries management measures?

67 To answer these questions we i) develop a simulation model where popula-  
68 tion dynamics are highly-resolved in space and time, using a Gaussian spatial  
69 process to define suitable habitat for different populations. As the precise lo-  
70 cations of the fish are known directly rather than inferred from sampling or  
71 commercial catch, we can use the population model to validate how inference  
72 from fisheries-dependent and fisheries independent sampling relates to the real  
73 community structure in a way we could not with real data. We ii) compare, at  
74 different spatial and temporal aggregations, the real (simulated) population dis-  
75 tributions to samples from fisheries-dependent and fisheries independent [CM:  
76 hyphenate or don't both, i.e., fishery-independent] catches to test if these are a  
77 true reflection of the relative density of the populations. We then iii) simulate a  
78 fishery closure to protect a species based on different spatial and temporal data  
79 aggregations.

80

81 We use these evaluations to draw inference on the utility of commercial data  
82 in supporting management decisions.

## 83 2. Materials and Methods

84 A Discrete-event simulation (DES) model of a hypothetical fishery was de-  
85 veloped as a software package (*MixFishSim*). The modular approach enabled  
86 efficient computation by allowing for sub-modules implemented on time-scales  
87 appropriate to capture the characteristic of the different processes (Figure 1).  
88 The following sub-modules were included to capture the full system: 1) Popu-  
89 lation dynamics, 2) Recruitment dynamics, 3) Population movement, 4) fishery

90 dynamics.

91

92 Population dynamics for any number of species, as chosen by the user oper-  
 93 ate on a daily time-step (with recruitment occurring only during defined seasons  
 94 for each population), while population movement occurs on a weekly time-step,  
 95 with the fishing module operating on a tow-by-tow basis (i.e. multiple events a  
 96 day).

97

## 98 2.1. Population dynamics

99 The basic population level processes were simulated using a modified two-  
 100 stage Deriso-Schnute delay difference model which models the fish populations in  
 101 terms of aggregate biomass of recruits and mature components rather than keep-  
 102 ing track of individuals (Deriso, 1980; Schnute, 1985; Dichmont et al., 2003). A  
 103 daily time-step was chosen to discretise continuous population processes on a bi-  
 104 ologically relevant and computationally tractable timescale. Population biomass  
 105 growth was modelled as a function of previous recruited biomass, intrinsic pop-  
 106 ulation growth and recruitment functionally linked to the adult population size.  
 107 Biomass for each cell  $c$  was incremented each day  $d$  as follows (the full parameter  
 108 list is detailed in Table 1):

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

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

114

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

$$C_{c,d} = \frac{F_{c,d}}{F_{c,d} + M_{c,d}} \cdot \left(1 - e^{-(F_{c,d} + M_{c,d})}\right) \cdot B_{c,d} \quad (2)$$

119 where  $C_{c,d}$  is the summed catch from the fishing model across all fleets and ves-  
 120 sels in cell  $c$  for the population during the day  $d$ , and  $B_{c,d}$  the daily biomass for  
 121 the population in the cell. Here, catch is the sum of those across all fleets and  
 122 vessels,  $C_{c,d} = \sum_{fl=1}^{FL} \sum_{v=1}^V E_{fl,v,c,d} \cdot Q_{fl} \cdot D_{c,d}$  with  $fl$  and  $FL$  the fleet and total  
 123 number of fleets,  $v$  and  $V$  the vessel and total number of vessels respectively  
 124 and  $E_{fl,v,c,d}$  and  $Q_{fl}$  fishing effort and catchability of the gear, and  $D_{c,d}$  is the  
 125 density of the population at the location fished.

126

## 127 2.2. Recruitment dynamics

128 Recruitment is modelled as a function of adult biomass. In *MixFishSim*, it  
 129 can either take the form of a stochastic Beverton-Holt stock recruitment relation-  
 130 ship, or a stochastic Ricker stock recruitment relationship. The Beverton-Holt  
 131 relationship is defined as (Beverton and Holt, 1957):

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

132 where  $\alpha$  is the maximum recruitment rate,  $\beta$  the spawning stock biomass (SSB)  
 133 required to produce half the maximum stock size,  $S$  current stock size and  $\sigma^2$   
 134 the variability in the recruitment due to stochastic processes. The stochastic  
 135 Ricker form (Ricker, 1954) is:

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

136 where  $\alpha$  is the maximum productivity per spawner and  $\beta$  the density dependent  
 137 reduction in productivity as the SSB increases.

### 138 2.3. Population movement dynamics

139 Population movement is a combination of directed (advective) movement  
140 where at certain times of year the population moves towards spawning grounds  
141 by increasing the probabilities of moving into the spawning grounds from adja-  
142 cent cells, and random (diffusive) movement, governed by a stochastic process  
143 where movement between adjacent cells is described by a set of probabilities  
144 which are affected by the suitability of habitat, temperature in a cell and the  
145 thermal tolerance of a population to that temperature.

146  
147 The combined process results in a population structure and movement pat-  
148 tern unique to each population, with population movement occurring on a  
149 weekly basis. The decision to model population movement on a weekly timescale  
150 was to reflect that fish tend to aggregate in species specific locations that have  
151 been observed to last around one to two weeks (Poos and Rijnsdorp, 2007b).  
152 Therefore this process approximated the demographic shifts in fish populations  
153 throughout a year with seasonal spawning patterns (Figure S7).

154 To simulate fish population distribution in space and time a Gaussian spa-  
155 tial process was employed to model habitat suitability for each of the popula-  
156 tions on a 2d grid. We first defined a Gaussian random field process,  $\{S(c) :$   
157  $c \in \mathbb{R}^2\}$ , where for any set of cells  $c_1, \dots, c_n$ , the joint distribution of  $S =$   
158  $\{S(c_1), \dots, S(c_n)\}$  is multivariate Gaussian with a *Matérn* covariance structure,  
159 where the correlation strength weakens with distance controlled by two param-  
160 eters, with  $\nu$  a scale parameter in the units of distance and  $\kappa$  a shape parameter  
161 which determines the smoothness of the process. We use the most commonly  
162 used Matérn covariance structure as it is a flexible form that under certain  
163 conditions is of the same form as an exponential function and itThis enables  
164 us to model the spatial autocorrelation observed in animal populations where  
165 density is more similar in nearby locations, but that correlation decreases non-  
166 linearly (Tobler, 1970; F. Dormann et al., 2007; Poos and Rijnsdorp, 2007b).  
167 We change the parameters to implement different spatial structures for the dif-  
168 ferent populations using the *RandomFields* R package (Schlather et al., 2015).



169 We define a stationary habitat field with an anisotropic pattern (to simulate a  
 170 depth gradient) and combine it with a temporally dynamic thermal tolerance  
 171 field to imitate two key drivers of population dynamics without modelling the  
 172 processes explicitly. Each population was initialised at a single location, and  
 173 subsequently moved across the entire space according to a probabilistic distri-  
 174 bution based on habitat suitability (represented by the normalised values from  
 175 the GRFs), temperature tolerance and distance from current cell:

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

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

180

181 During pre-defined weeks of the year the habitat suitability is modified with  
 182 user-defined spawning habitat locations, resulting in each population having  
 183 concentrated areas where spawning takes place. The populations then move to-  
 184 wards these cells in the weeks prior to spawning, resulting in directional move-  
 185 ment towards the spawning grounds.

186

187 A time-varying temperature covariate changes the interaction between time  
 188 and suitable habitat on a weekly time-step. Each population  $p$  was assigned a  
 189 thermal tolerance with mean,  $\mu_p$  and standard deviation,  $\sigma_p$  so that each cell  
 190 and population temperature tolerance is defined that:

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

191 Where  $Tol_{c,p,wk}$  is the tolerance of population  $p$  for cell  $c$  in week  $wk$ ,  $T_{c,wk}$  is  
 192 the temperature in the cell given the week and  $\mu_p$  and  $\sigma_p$  the mean and stan-  
 193 dard deviation of the population temperature tolerance. The variables, their  
 194 meaning and units for population movement is provided in Table 2.

195

196     The final combined process results in a population structure and movement  
 197 pattern unique to each population, with population movement occurring on a  
 198 weekly basis. The decision to model population movement on a weekly timescale  
 199 was to reflect that fish tend to aggregate in species specific locations that have  
 200 been observed to last around one to two weeks (Poos et al 2007). Therefore this  
 201 process approximated the demographic shifts in fish populations throughout a  
 202 year with seasonal spawning patterns (Figure S7).

#### 203 2.4. Fleet dynamics

204     Fleet dynamics ~~were can be~~ broadly categorised into three components. *Fleet*  
 205 *targeting* ~~determined~~*determines* the fleet catch efficiency and preference to-  
 206 wards a particular population; *trip-level decisions* ~~determined that~~*determines*  
 207 the initial location to be fished at the beginning of a trip; and *within-trip deci-*  
 208 *sions* ~~determined fishing locations, that determines movement from one fishing~~  
 209 ~~spot to another~~ within a trip. This results in an explore-exploit strategy ~~was~~  
 210 ~~implemented in the model that combined these three components~~ for individual  
 211 vessels to maximise their catch from an unknown resource distribution (Bailey  
 212 et al., 2019). The decision to use an individual based model for fishing vessels  
 213 was taken because fishers are heterogeneous in their location choice behaviour  
 214 due to different objectives, risk preference and targeting preference (Van Putten  
 215 et al., 2012; Boonstra and Hentati-Sundberg, 2016). Therefore fleet dynamics  
 216 are emergent from individual dynamics rather than pre-defined group dynamics.

##### 217 2.4.1. Fleet targeting

218     Each fleet of  $n$  vessels was characterised by both a general efficiency,  $Q_{fl}$ ,  
 219 and a population specific efficiency,  $Q_{fl,p}$  which are each bound by  $[0,1]$ . The  
 220 product of these parameters  $[Q_{fl} \cdot Q_{fl,p}]$  affects the overall catch rates for the fleet  
 221 and the preferential targeting of one species over another. This, in combination  
 222 with the parameter choice for the step-function defined below (as well as some

223 randomness from the exploratory fishing process) determined the preference of  
224 fishing locations for the fleet.

#### 225 *2.4.2. Decision about where to fish at the start of a trip*

226 Several studies (for a review see Girardin et al., 2017) have confirmed past  
227 activity and past catch rates are strong predictors of fishing location choice.  
228 For this reason, the fleet dynamics sub-model included a learning component,  
229 where a vessel’s initial fishing location in a trip was based on selecting from  
230 previously successful fishing locations. This was achieved by calculating an  
231 expected revenue based on the catches from locations fished in the preceding  
232 trip as well as the same month periods in previous years and the travel costs  
233 from the port to the fishing grounds. Then a vessel chooses randomly from the  
234 top 70 % of fishing events (defined as the ‘threshold’) in terms of expected profit  
235 within that season.

#### 236 *2.4.3. Decision about where to fish within a trip*

237 Fishing locations within a trip are initially determined by a modified ran-  
238 dom walk process. As the simulation progresses the within-trip decision become  
239 gradually more influenced by experience gained from past fishing locations (as  
240 per the initial trip-level location choice), moving location choice towards areas  
241 of higher perceived profit. A random walk was chosen for the exploratory fishing  
242 process as it is the simplest assumption commonly used in ecology to describe  
243 optimal animal search strategy for exploiting heterogeneously distributed prey  
244 about which there is uncertain knowledge (Viswanathan et al., 1999). In a ran-  
245 dom walk, movement is a stochastic process through a series of steps. These  
246 steps have a length, and a direction that can either be equal in length or take  
247 some other functional form. The direction of the random walk was also cor-  
248 related (known as ‘persistence’) providing some overall directional movement  
249 (Codling et al., 2008).

250

251 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 relating recent fishing success, measured as the summed value of fish caught (revenue,  $Rev$ );

$$Rev_{c,d} = \sum_{p=1}^P L_{c,d,p} \cdot Pr_p \quad (7)$$

where  $L_{c,d,p}$  is landings of a population  $p$ , and  $Pr_p$  price of a population. All population prices were kept the same across fleets and seasons. 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, that can be controlled separately, but is determined by the relationship:

$$Le = e^{\log(\beta_1) + \log(\beta_2) - \left(\log\left(\frac{\beta_1}{\beta_3}\right)\right) \cdot Rev} \quad (8)$$

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  $(x_t, y_t)$  to  $(x_{t+1}, y_{t+1})$  is defined by:

$$\begin{aligned} (x_{t+1}, y_{t+1}) &= x_t + Le \cdot \cos\left(\frac{\pi \cdot Br_{t+1}}{180}\right), \\ y_t + Le \cdot \sin\left(\frac{\pi \cdot Br_{t+1}}{180}\right) \end{aligned} \quad (9)$$

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

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

where  $Le$  is the step length,  $Br_t$  is the bearing at time  $t$ ,  $k$  the concentration parameter from the von Mises distribution that we correlate with the revenue so that  $k = (Rev + 1/RefRev) \cdot max_k$ , where  $max_k$  is the maximum concentration value,  $k$ , and  $RefRev$  is parametrised as for  $\beta_3$  in the step length function. Details of the variables, meaning and units for fleet dynamics are provided in Table 3.

#### 273 2.4.4. Local population depletion

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

#### 283 2.5. Fisheries independent survey

284 A fisheries-independent survey is simulated where fishing on a regular grid  
285 begins each year at the same time for a given number of stations (a fixed station  
286 survey design). Catches of the populations at each station are recorded but not  
287 removed from the population (catches are assumed to have negligible impact  
288 on population dynamics). This provides a fishery independent snapshot of the  
289 populations at a regular spatial intervals each year, similar to scientific surveys  
290 undertaken by fisheries research agencies.

291

#### 292 2.6. Software: R-package development

293 The simulation framework is implemented in the statistical software package  
294 R (R Core Team, 2017) and available as an R package from the author’s github  
295 site ([www.github.com/pdolder/MixFishSim](http://www.github.com/pdolder/MixFishSim)).

296

### 297 3. Model calibration

298 We calibrate *MixFishSim* to investigate the influence of data aggregation on  
299 spatial inference.

### 300 3.1. Population models

301 We calibrated the simulation model for four example populations with dif-  
302 ferent demographics, growth rates, natural mortality and recruitment (Table 4).  
303 Habitat preference (Figure S3) and temperature (Figures S5, with temperature  
304 tolerance S6) defined to be unique to each population resulting in differently  
305 weekly distribution patterns (Figures S7-S9). In addition, each of the pop-  
306 ulations was assumed to have two defined spawning areas that result in the  
307 populations moving towards these areas in pre-defined weeks (Figure S4) with  
308 population-specific movement rates (Table 4). The population demographics  
309 were defined to broadly represent three mobile low-medium value groundfish  
310 species and one high value species with low mobility, with the dynamics hypo-  
311 thetical but as you might expect to find in a typical demersal fishery.

### 312 3.2. Fleet calibration

313 The fleets were calibrated to reflect five different characteristic fisheries with  
314 unique exploitation dynamics (Table 5). By setting different catchability coef-  
315 ficients ( $Q_{fl,p}$ ) we create different targeting preferences between the fleets and  
316 hence spatial dynamics. The learned random walk process implies that within  
317 a fleet different vessels have different spatial distributions based on individual  
318 experience. The step function was calibrated dynamically within the simula-  
319 tions as the maximum revenue obtainable was not known beforehand. This was  
320 implemented so that vessels take smaller steps when fishing at a location that  
321 yields landings value in the top 90th percentile of the value experienced in that  
322 year so far (as defined per fleet in Table 5).

323  
324 Fishing locations were chosen based on random search and, with increasing  
325 proportion as time progressed, experience of profitable catches built up in the  
326 same month from previous years and from the previous trip. ‘Profitable’ in  
327 this context was defined as the locations where the top 70 % of expected profit  
328 would be found given revenue from previous trips and cost of movement to the  
329 new fishing location. This probability was based on a logistic sigmoid function

330 with a lower asymptote of 0 and upper asymptote of 0.95, and a growth rate  
331 that ensures the upper asymptote (where decisions are mainly based on past  
332 knowledge) is reached approximately halfway through the simulation.

333

### 334 3.3. Survey settings

335 The survey simulation was set up with a fixed gridded station design with  
336 100 stations fished each year, starting on day 92 and ending on day 112 (5  
337 stations per day) with same catchability parameter ( $Q_p = 1$ ) for all populations  
338  $p$ . This approximates a real world survey design with limited seasonal and  
339 spatial coverage.

### 340 3.4. Example research question

341 To illustrate the capabilities of *MixFishSim*, we investigate the influence of  
342 the temporal and spatial resolution of different data sources on the reduction in  
343 catches of a population given spatial closures. To do so, we set up a simulation  
344 to run for 50 years based on a  $100 \times 100$  square grid (undetermined units), with  
345 five fleets of 20 vessels each and four fish populations. Fishing takes place four  
346 times a day per vessel and five days a week, while population movement is every  
347 week.

348

349 *How does sampling-derived fisheries data reflect the underlying population*  
350 *structure?*

351

352 To answer this question we compare different spatial and temporal aggrega-  
353 tions of the true population distributions to:

- 354 a) **fisheries-independent data:** the inferred population density from a  
355 fixed-site sampling survey design as commonly used for fisheries monitor-  
356 ing purposes;
- 357 b) **fisheries-dependent data:** the inferred population density from our  
358 fleet model that includes fishery-induced sampling dynamics.

359 We allow the simulation to run unrestricted for 30 years, then implement  
360 spatial closed areas for the last 20 years of the simulation based on data (either  
361 derived from the commercial catches, fisheries-independent survey or the true  
362 population) used at different spatial and temporal scales.

363

364 The following steps are undertaken to determine closures:

- 365 1. Extract data source (true population, commercial or survey),
- 366 2. Aggregate according to desired spatial and temporal resolution,
- 367 3. Interpolate across entire area at desired resolution using simple bivariate  
368 interpolation using the *interp* function from the R package *akima* (Akima  
369 and Gebhardt, 2016). This is intended to represent a naive spatial model  
370 of catch rates, without knowledge of the spatial population dynamics.
- 371 4. Close area covering top 5 % of catch rates

372 In total 28 closure scenarios were run that represent combinations of:

- 373 • **data types:** commercial logbook data, survey data and true population,
- 374 • **temporal resolutions:** weekly, monthly and yearly closures,
- 375 • **spatial resolutions:** 1 x 1 grid, 5 x 5 grid, 10 x 10 grid and 20 x 20 grid,
- 376 • **closure basis:** highest 5 % of catch rates for the protected population

377 We implemented a series of spatial closures targeted at reducing fishing mor-  
378 tality on population 3, given the different data sources and spatial and temporal  
379 resolutions above. We use the effectiveness of these closures in reducing fishing  
380 mortality as a way of evaluating the trade-offs in data sources and resolution.  
381 Survey closures were on an annual basis only, as this was the most temporally  
382 resolved survey data available. We evaluated the factors contributing to the suc-  
383 cess of the closures through a regression tree (using the R package REEMtree  
384 (Sela and Simonoff, 2011)) to identify the factor most contributing to differences  
385 in fishing mortality before and after the closure.



## 386 4. Results

### 387 4.1. Emergent simulation dynamics

388 Individual habitat preferences and thermal tolerances result in different spa-  
389 tial habitat use for each population (Figure S1) and consequently different sea-  
390 sonal exploitation patterns (Figure S2).

It can be seen from a single vessels movements during a trip that the ves-  
sel exploits three different fishing grounds, each of them multiple times (Figure  
2(A)), while across several trips fishing grounds that are further apart are fished  
(Figure 2 (B)). These different locations relate to areas where the highest rev-  
enue were experienced, as shown by Figure 2 (D), where several vessels tracks  
are overlaid on the revenue field, i.e.

$$Rev_c = \sum_{p=1}^P B_{c,p} \cdot Q_{fl,p} \cdot Pr_p$$

391 Vessels from the same fleet (and therefore targeting preference) may exploit  
392 some shared and some different fishing grounds depending on their own personal  
393 experience during the exploratory phase of the fishery (Figure 2 (C)). This  
394 results from the randomness in the correlated random walk step function, with  
395 distance moved during the exploitation phase and the direction stochastically  
396 related to the revenue experienced on the fishing ground (Figure 2 (D)).

### 397 4.2. How does sampling-derived fisheries data reflect the underlying population 398 structure?

399 The ~~aggregated~~ catch composition ~~aggregated at different spatial resolutions~~  
400 from each of the data sources (~~which shows~~ average seasonal patterns over a  
401 ten-year period) highlights different patterns in perceived community structure  
402 depending on the data source and aggregation level (Figure 3). The finer spatial  
403 grid for the true population (top left) and commercial data (top middle) show  
404 visually similar patterns, though there are large unsampled areas in the com-  
405 mercial data from a lack of fishing activity (particularly in the lower left part  
406 of the sampling domain). The survey data at this spatial resolution displays

407 very sparse information about the spatial distributions of the populations. The  
 408 slightly aggregated data on a 5 x 5 grid shows similar patterns and, while los-  
 409 ing some of the spatial detail, there remains good consistency between the true  
 410 population and the commercial data. Survey data starts to pick out some of the  
 411 similar patterns as the other data sources, but lacks spatiotemporal coverage.  
 412 The spatial catch information on a 10 x 10 and 20 x 20 grid lose a signifi-  
 413 cant amount of information about the spatial resolutions for all data sources,  
 414 and some differences between the survey, commercial and true population data  
 415 emerge.

416

417 Different perceptions of the proportion of each stock in an area are seen when  
 418 we aggregate the data at different timescales, with weekly (top), monthly (mid-  
 419 dle) and yearly (bottom) catch compositions from across an aggregated 20 x 20  
 420 area showing different patterns (Figure 4). In the true population, the monthly  
 421 aggregation captures the major patterns of composition seen in the weekly data  
 422 with the percentage of different populations in the catch having similar mean  
 423 and standard deviations (Table 7). In the weekly and monthly data population  
 424 2 dominates. However, some of the variation was lost when aggregated to an  
 425 annual level, as indicated from the lower standard deviations (Table 7).

426

427 The commercial data on a weekly basis shows some of the same patterns as  
 428 the true population, though the population 1 (in red) is less well represented  
 429 and some weeks are missing catches from the area. Here, weekly and monthly  
 430 compositions were nearly identical (Figure 4; Table 7). Again, yearly values  
 431 head a similar mean but smaller standard deviation.

432

433 The survey data was only available on an annual basis, and showed again  
 434 a slightly different composition from the true population and the commercial  
 435 data; in particular a greater proportion of population 4 (Figure 4).

436 4.3. How does data aggregation and source impact on spatial fisheries manage-  
437 ment measures?

438 ~~We implemented a spatial closure using the different data sources and spatial~~  
439 ~~and temporal aggregations as outlined in the protocol in Section 3.4. We used~~  
440 ~~this to assess the efficacy of a closure in reducing fishing mortality on population~~  
441 ~~3, given availability of data and its use at different resolutions in order to~~  
442 ~~evaluate the trade-offs in data sources.~~

443 In most cases the fishery closure was successful in reducing fishing mortality  
444 on the species of interest (population 3; Figure 5). Interestingly the largest re-  
445 ductions in fishing mortality happened immediately after the closures, following  
446 which the fisheries “adapted” to the closures ~~by finding new areas of high abun-~~  
447 ~~dance to fish. This led to~~ fishing mortality increasing again, though not to past  
448 levels (Figure 5). The exception to the success was the closures implemented  
449 based on the coarsest spatial (20 x 20) and temporal resolution (yearly) that  
450 was ineffective (i.e. failed to reduce fishing mortality) with all data sources.  
451 As expected, closures based on the “known” population distribution were most  
452 effective, with differing degrees of success using the commercial data. Fishing  
453 mortality rates on the other species changed in different proportions, depending  
454 on whether the displaced fishing effort moved to areas where the populations  
455 were found in greater or lesser density.

456  
457 The factor most contributing to differences in fishing mortality before and  
458 after the closure was the population (72 % showing that the closures were ef-  
459 fective for population 3), followed by data resolution (21 %), data type (7 %)  
460 with the least important factor the timescale (< 1 %). In general the finer the  
461 spatial resolution of the data used the greater reduction in fishing mortality for  
462 population 3 after the closures (Figure 6). The notable outliers are the com-  
463 mercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly  
464 timescale, where closures were nearly as effective as the fine-scale resolution. In  
465 this case the closures were sufficiently large to protect a core area of the habitat  
466 for the population, but this was achieved in a fairly crude manner by closing a

large area - including area where the species was not found (Figure 7) that may have consequences in terms of restricting the fishery in a much larger area than necessary. We found that these trade-offs existed, with high catches maintained with an effective closure when the highest resolution data was used, with the effect being linear when the true population distribution was known and also persisting for closures based on commercial information (Figure 8).

## 5. Discussion

Our study presents a new highly resolved fisheries simulation framework to evaluate the importance of data scaling and considers potential bias introduced through data aggregation when using fisheries data to infer spatiotemporal dynamics of fish populations. 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 species targeting in fisheries resulting in preferential sampling (Martínez-Minaya et al., 2018). Often data are 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 increasingly employing more nuanced spatiotemporal approaches to maximise productivity while taking account of both the biological and human processes operating on different time-frames (Dunn et al., 2016), understanding assumptions behind the data used - increasingly a combination of logbook and positional information from vessel monitoring systems - is vital to ensure measures are effective.

### 5.1. Simulation dynamics

We employ a simulation approach to model each of the population and fishery dynamics in a hypothetical ‘mixed fishery’, allowing us to i) evaluate the

consequences of different aggregation assumptions on our understanding of the spatiotemporal distribution of the underlying fish populations, and ii) evaluate the effectiveness of a spatial closure given those assumptions.

Our approach is unique in that it captures fine scale population and fishery dynamics and their interaction in a way not usually possible with real data and thus not usually considered in fisheries simulations. While other simulation frameworks seek to model individual vessel dynamics based on inferred dynamics from VMS and logbook records (Bastardie et al., 2010), or as a system to identify measures to meet particular management goals (Bailey et al., 2019), our framework allows users to explore the assumptions in modelling observational data and to evaluate the underlying dynamics of such approaches at a fine spatial and temporal scales. This offers the advantage that larger scale fishery patterns are emergent properties of the system and results can be compared to those obtained under a statistical modelling framework.

Typically, simulation models that treat fish as individuals are focussed on exploring the inter- and intra- specific interactions among fish populations (e.g. OSMOSE; Shin et al. (2004)) in order to understand how they vary over space and time. Our focus was on understanding the strengths and limitations of inference from catch data obtained through commercial fishing activity with fleets exploiting multiple fish populations. This shows how-and realised catch distributions that may differ from the underlying populations, as identified by Gillis et al. (2008). As such, we favoured a minimum realistic model of the fish populations (Plagányi et al., 2014) taking account of environmental but not demographic stochasticity, while incorporating detailed fishing dynamics that take account of different drivers in a mechanistic way.

Demographic stochasticity arises due to individual-level variability in time to reproduction and death. This form of stochasticity is often modelled by drawing random time intervals from a given distribution (Gillespie, 1977). The impact

527 of demographic stochasticity depends on the population size, with the effects  
528 expected to decrease with increasing population size (Lande et al., 2010). This  
529 contrasts with environmental stochasticity, which affects all population sizes  
530 and is present at the population level in our model by variability in recruitment.

531

532 We take account of heterogeneity in fleet dynamics due to different prefer-  
533 ences and drivers similarly to other approaches (Fulton et al., 2011), but at an  
534 individual vessel rather than fleet level. We do not explicitly define fleets as  
535 rational profit maximisers at the outset, but consider there are several stages  
536 to development of the fishery; information gathering through search where the  
537 resource location is not known, followed by individual learnt behaviour of prof-  
538 itable locations. This provides a realistic model of how fishing patterns are  
539 established and maintained to exploit an uncertain resource through an explore-  
540 exploit strategy (Mangel and Clark, 1983; Bailey et al., 2019).

## 541 *5.2. How does sampling-derived fisheries data reflect the underlying population* 542 *structure?*

543 Our results demonstrate the importance of considering data scale and resolu-  
544 tion when using observational data to support management measures. We find  
545 that understanding of the community composition dynamics will depend on the  
546 level of data aggregation and its important to consider the scale of processes;  
547 including population movement rates, habitat uniformity and fishing targeting  
548 practices if potential biases in data are to be understood and taken into account  
549 (Figures S1, 2).

550

551 Our simulation shows that, despite biases introduced through the fishing  
552 process, the commercially derived data could still inform on the key spatial  
553 patterns in the community structures where the fisheries occurred, which was  
554 spatially limited due to the “hotspots” of commercially valuable species be-  
555 ing fished. Similarly, despite the even spatial coverage the survey was able to  
556 capture some of the same spatial patterns as the true population, but missed

557 others due to gaps between survey stations limiting spatial and temporal cov-  
 558 erage (Figure 3). This provides a challenge when modelling unsampled areas in  
 559 inferring species distribution maps, though these limitations may be overcome  
 560 by understanding the relationship between the species and habitat covariates  
 561 where these are known at unsampled locations (Robinson et al., 2011).

562

### 563 *5.3. How does data aggregation and source impact on spatial fisheries manage-* 564 *ment measures?*

565 From our simulations spatial disaggregation was more important than the  
 566 temporal disaggregation of the commercial data. This reflects the fact that there  
 567 was greater spatial heterogeneity over the spatial domain than experienced in  
 568 individual locations over the course of the year (Figure S1).

569

570 The yearly data assumes the same proportion of each population caught at  
 571 any time of the year due to the data aggregation. This assumption introduces  
 572 ‘aggregation bias’ as the data may only be representative of some point (or no  
 573 point) in time. The monthly data shows some consistency between the real pop-  
 574 ulation and commercial data for population 2 - 4, though population 1 remains  
 575 under-represented. On an annual basis, interestingly the commercial data un-  
 576 der represents the first species (in red) while the survey over represents species  
 577 1. This is likely due to the biases in commercial sampling, with the fisheries  
 578 not targeting the areas where population 1 are present and the survey sampling  
 579 areas where population 1 is more abundant than on average. This indicates that  
 580 fixed closures, at the right resolution, when based on commercially derived data  
 581 have the potential to reduce fishing mortality. The likely cost of poor spatial  
 582 and temporal resolution is associated with reduced effectiveness and potentially  
 583 closing fishing opportunities for other fisheries (Figure 8).

584

585 Two contrasting real world approaches in this respect were the spatial clo-  
 586 sures to protect cod in the North Sea. In one example, large scale spatial closures

were implemented with little success due to effort displacement to previously unfished areas (Dinmore et al., 2003), while in another small scale targeted spatiotemporal closures were considered to have some effect in reducing cod mortality without having to disrupt other fisheries substantially (Needle and Catarino, 2011). These examples emphasise the importance of considering the right scale and aggregation of data when identifying area closures and the need to consider changing dynamics in the fisheries in response to such closures.

Our study showed that fishing rates on other populations also changed (both up and down) as a side-effect of closures to protect one species. This indicates the importance in considering fishing effort reallocation following spatial closures, and our simulation allows us to consider the spatiotemporal reasons for these changes.

#### 5.4. Model assumptions and caveats

We modelled the population and fleet dynamic processes to draw inference on the importance of data scale and aggregation in understanding and managing mixed fisheries and their impact on multiple fish populations. In doing so, we necessarily had to make a number of simplifying assumptions.

Fish populations in our simulations move in pre-defined timescales and according to fixed habitat preferences and temperature gradients (Figures S3, S5). Our assumptions in calibrating the model (movement rates, temperature tolerances) will have a direct impact on our conclusions on the relative importance of spatial and temporal processes. These assumptions could be explored in a future study by varying the parameters and assessing the robustness of our conclusions. For our example application we have chosen movement rates to reflect aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

In addition, we have assumed that fishing vessels are not restricted by quota and therefore discarding of species for which vessels have no quota or that are



unwanted is not taken into account. This is likely to be a significant source of bias in any inference using commercial data and should also be explored. For example, *MixFishSim* could be altered to allow for spatiotemporal appraisal of the impact of discarding on fisher behaviour and underlying populations via inclusion as discarding behaviour, or through move-on rules or cessation of fishing activity when quota is exhausted.

### 5.5. Future applications of *MixFishSim*

We consider that the increased availability of high resolution catch and locational information from commercial fisheries will require it to be a key source of data for ensuring management is implemented at the right scale in future. For example, identifying hot-spots for bycatch reduction or identifying spatial overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al., 2015; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the potential to test some of the assumptions behind the modelling approaches in identifying such hotspots and indeed behind spatiotemporal modelling in general, (e.g. comparing GAMs, GLMMs, Random Forests and geostatistical models under different data generation processes as exemplified by Stock et al. (2019)).

Other novel applications of our framework could be: testing different survey designs given multiple species and data generating assumptions (Xu et al., 2015); commercial index standardisation methods and approaches and understanding of appropriate scales and data aggregations and non-proportionality in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004); exploring assumptions about the distribution of natural mortality and fishing mortality throughout the year and importance of capturing in-year dynamics in estimating stock status (Liu and Heino, 2014); at sea sampling scheme designs to deliver unbiased estimates of population parameters (Cotter and Pilling, 2007; Kimura and Somerton, 2006); adaptive management (Walters, 2007; Dunn et al., 2016); testing the ability of commonly employed fleet dynamics models

such as Random Utility Models to capture fine scale dynamics and understand their importance (Girardin et al., 2017); and as a detailed operating model in a management strategy evaluation (Mahévas and Pelletier, 2004).

## 6. Conclusions

*MixFishSim* provides a detailed simulation framework to explore the interaction of multiple fisheries exploiting different fish populations. The framework enables users to evaluate assumptions in modelling commercially derived data through comparison to the true underlying dynamics at a fine spatial and temporal scale. Understanding these dynamics, the limitations of the data and any potential biases that may be introduced when making inference on spatiotemporal interactions will enable users to identify weaknesses in modelling approaches and identify where data collection is needed to strengthen inference.

Our application shows that inference on community dynamics may change depending on the scale of data aggregation. There is an important balance in ensuring that the data are sufficiently spatially and temporally disaggregated that the main features of the data are captured, yet maintaining enough data coverage that the features can be distinguished. We found in our application that there was greater spatial heterogeneity than temporal heterogeneity and that when using aggregated data to define spatial closures coarser temporal resolution (months instead of weeks) could still achieve the same results in reducing exploitation rates of a vulnerable species at the highest temporal resolution data. Conversely, reducing the spatial resolution had a negative effect on the effectiveness of the measures (though importantly, there was still some benefit even with coarse spatial resolution).

While any findings are likely to be case specific, our findings emphasise the need to understand population demographics, habitat use and movement rates

676 in designing any closure scenario based on observational sampling. This infor-  
677 mation can then be used to set the bounds on data aggregation used in modelling  
678 studies aimed at informing the management measures.

679

680 *MixFishSim* has numerous potential additional applications as it enables  
681 the user to apply methods to a fisheries system where there is detailed under-  
682 standing of underlying spatiotemporal dynamics. This enables identification of  
683 weaknesses or limitations which would not be possible otherwise. In future, we  
684 recommend use of the framework to test hypotheses that are otherwise unable  
685 to be analysed using real world data due to limitations of data collection. That  
686 way the knowledge gained through simulation can inform the future design of  
687 management measures.

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## 694 **Appendices**

Table 1: Description of variables for population and recruitment dynamics sub-modules.

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 $d$	$d^{-1}$
$B_{c,d}$	biomass in cell $c$ for day $d$	$d^{-1}$
$\alpha$	the maximum recruitment rate (Beverton Holt) or maximum productivity per spawner (Ricker)	kg
$\beta$	the stock size required to produce half the maximum rate of recruitment (Beverton Holt) or density dependent reduction in productivity per capita of SSB	kg

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

Variable	Meaning	Units
<i>Thermal tolerance</i>		
$T_{c,wk}$	Temperature for cell $c$ in week $wk$	$^{\circ}\text{C}$
$\mu_p$	Mean of the thermal tolerance for population $p$	$^{\circ}\text{C}$
$\sigma_p$	Standard deviation of thermal tolerance for population $p$	$^{\circ}\text{C}$
<i>Population movement model</i>		
$\lambda$	Decay rate for population movement	-
$Hab_{c,p}$	Habitat suitability for cell $c$ and population $p$	-
$Tol_{c,wk,p}$	Thermal tolerance for in cell $c$ at week $wk$ for population $p$	-
$d_{I,J}$	Euclidean distance between cell $I$ and cell $J$	-

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

Variable	Meaning	Units
$Rev$	Revenue from fishing tow	$\text{€}$
$L_p$	Landings of population $p$	kg
$Pr_p$	Average price of population $p$	$\text{€ kg}^{-1}$
$Le$	Step length for vessel	-
$Br$	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 settings.

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				
Movement $\lambda = 0.1$				
Population dynamics				
Starting Biomass	1e5	2e5	1e5	1e4
Beverton-Holt Recruit $\alpha$	6	27	18	0.3
Beverton-Holt Recruit $\beta$	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
$K = 0.3$				
$wt = 1$				
$wt_{d-1} = 0.1$				
M (annual)	0.2	0.1	0.2	0.1
Movement dynamics				
$\mu_p$	12	15	17	14
$\sigma_p^2$	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 $Pr_p1 = 100$					
Price $Pr_p2 = 200$					
Price $Pr_p3 = 350$					
Price $Pr_p4 = 600$					
$Q_p$	0.01	0.02	0.02	0.01	0.01
$Q_p$	0.02	0.01	0.02	0.01	0.03
$Q_p$	0.01	0.02	0.02	0.01	0.02
$Q_p$	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 $\beta_3$ , the land- ings value $n$ th quantile	90	90	85	90	80
step function $rate$	20	30	25	35	20
Past Knowledge = TRUE					
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 on population 3 (ordered by most effective first). The fishing mortality rate before the closure was 1.08.

Scenario No	F after closure	% F change	data type	timescale	resolution
9	0.29	-73.47	true Population	weekly	1.00
10	0.29	-72.94	true Population	monthly	1.00
11	0.35	-68.04	true Population	yearly	1.00
45	0.58	-46.70	commercial	yearly	20.00
1	0.58	-46.21	commercial	weekly	1.00
23	0.59	-45.27	true Population	weekly	5.00
2	0.59	-45.06	commercial	monthly	1.00
7	0.60	-44.48	survey	yearly	1.00
24	0.61	-43.20	true Population	monthly	5.00
3	0.64	-40.82	commercial	yearly	1.00
25	0.65	-39.94	true Population	yearly	5.00
17	0.67	-38.11	commercial	yearly	5.00
15	0.71	-34.38	commercial	weekly	5.00
43	0.71	-34.31	commercial	weekly	20.00
16	0.73	-32.58	commercial	monthly	5.00
51	0.78	-27.92	true Population	weekly	20.00
37	0.78	-27.76	true Population	weekly	10.00
39	0.79	-26.98	true Population	yearly	10.00
38	0.81	-25.47	true Population	monthly	10.00
21	0.81	-25.21	survey	yearly	5.00
35	0.81	-25.05	survey	yearly	10.00
44	0.87	-19.91	commercial	monthly	20.00
52	0.88	-18.39	true Population	monthly	20.00
30	0.96	-11.06	commercial	monthly	10.00
29	0.98	-9.80	commercial	weekly	10.00
31	1.03	-4.36	commercial	yearly	10.00



53	1.06	-1.64	true Population	yearly	20.00
49	1.07	-1.01	survey	yearly	20.00

Table 7: Mean and standard deviation of proportions of each species at different levels of temporal aggregation

Data type	Timescale	Population 1	Population 2	Population 3	Population 4
commercial	monthly	0.047(0.014)	94.435(1.47)	3.122(1.468)	2.396(0.444)
commercial	weekly	0.047(0.016)	94.426(1.514)	3.117(1.563)	2.411(0.498)
commercial	yearly	0.051(0.001)	94.388(0.205)	3.021(0.175)	2.539(0.046)
True Population	monthly	9.225(3.872)	83.287(5.522)	3.624(1.151)	3.864(1.519)
True Population	weekly	9.358(3.992)	83.165(5.596)	3.567(1.233)	3.91(1.592)
True Population	yearly	9.899(0.173)	82.25(0.308)	3.821(0.119)	4.031(0.05)
survey	yearly	0.372(0.005)	87.667(0.193)	0.729(0.02)	11.232(0.172)

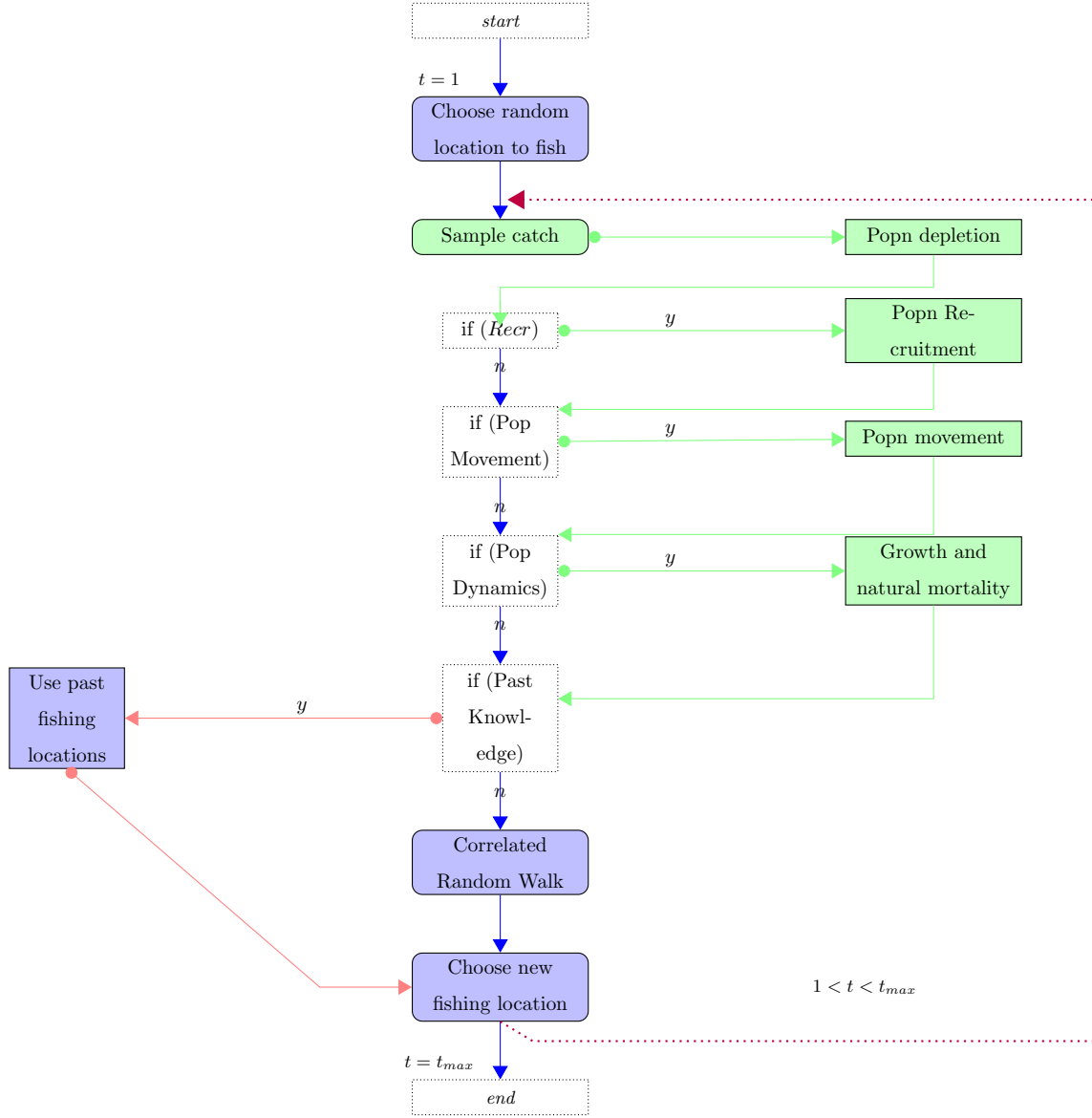


Figure 1: Schematic overview of the simulation model. Blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur;  $t = \text{tow}$ ,  $t_{max}$  is the total number of tows; (Recr), (Pop Movement), (Pop 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.

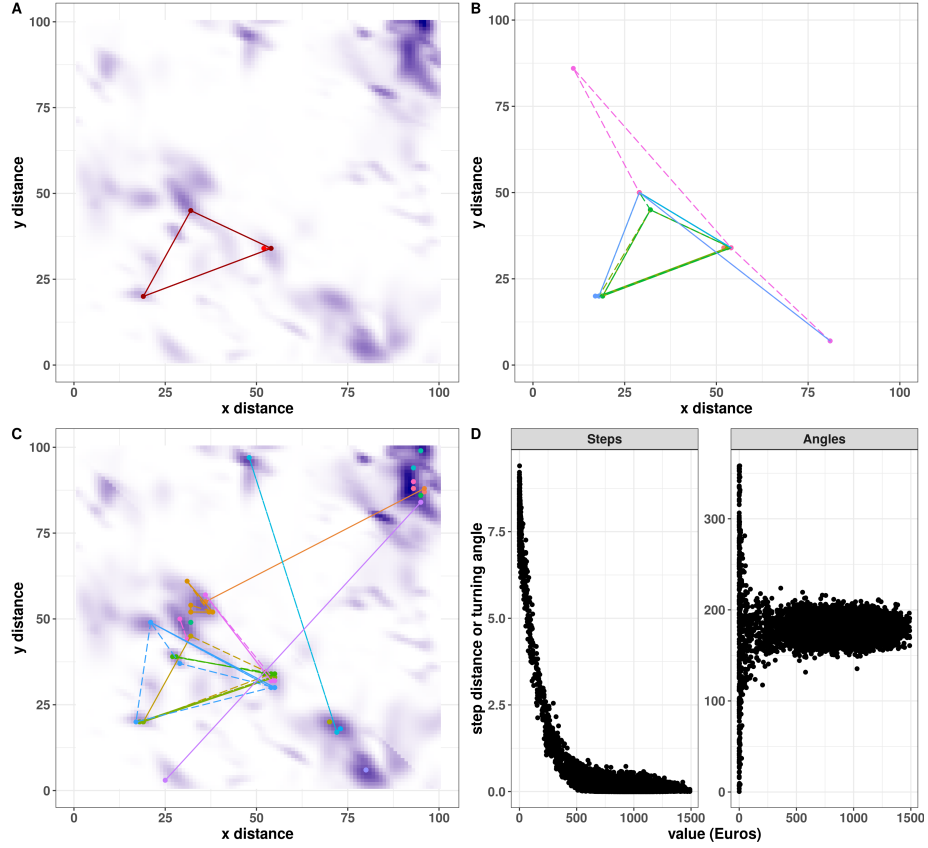


Figure 2: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the revenue of a fishing site (landings  $\times$  price; darker purple = higher revenue); (B) the fishing locations of the vessel over several trips (value field changes over the period so not shown). Note that movements are a mixture of correlated random walk (solid lines) and experience-based (dashed lines), and that the field is wrapped on a torus so that opposite sides of the spatial domain are considered spatially close; (C) the locations of multiple vessels from the same fleet overlaid on the value field, (D) the realised step distance and turning angles for a single vessel over the simulation.

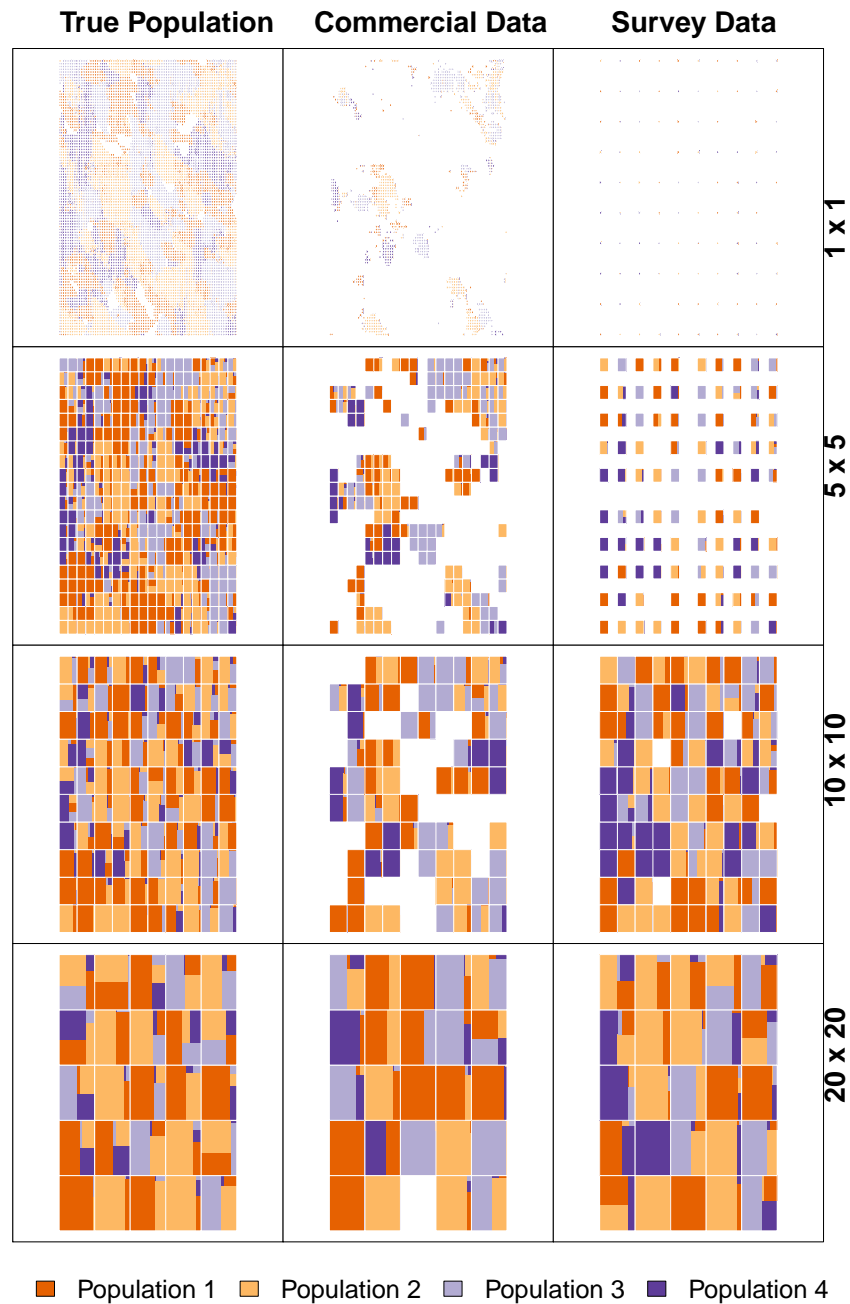


Figure 3: [Colour] Data aggregation at different spatial resolutions over a ten year period. The figure shows catch composition at each spatial unit represented by a square pie chart of the four populations. The area of each colour is proportional to the weight of each population caught in that unit. Figure produced using the R package ‘mapplots’ (Gerritsen (2014)).

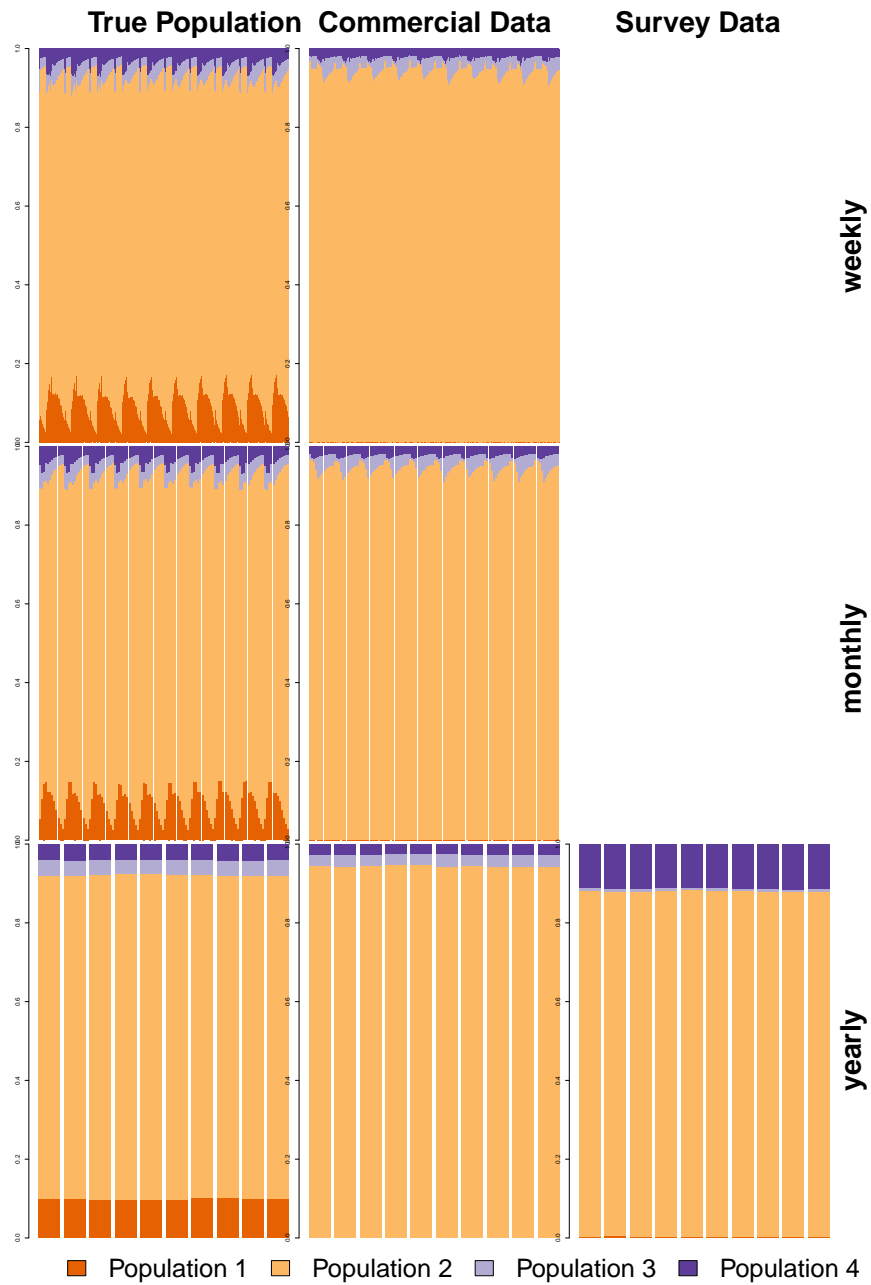


Figure 4: [Colour]Proportion of each population (y axis) for data aggregated at different temporal resolutions. Data is aggregated over a ten-year period for an area 20 x 20. Each bar represents either a week, month or year respectively.

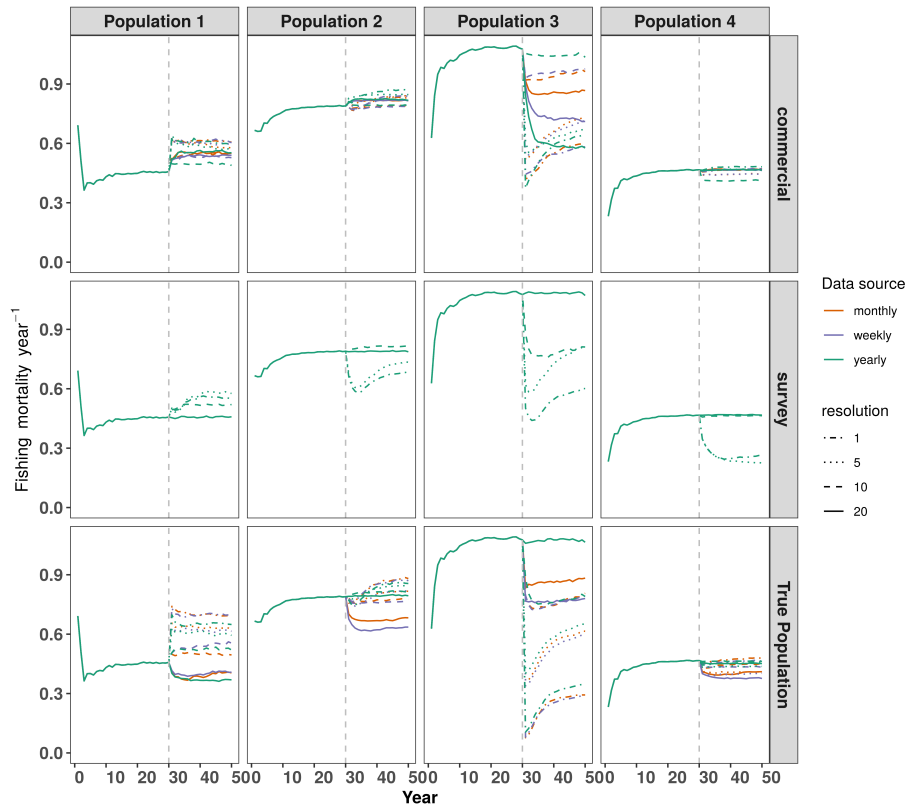


Figure 5: [Colour]Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes timescale, while linestyle denotes spatial resolution. The vertical dashed line indicates the onset of the spatial closures.

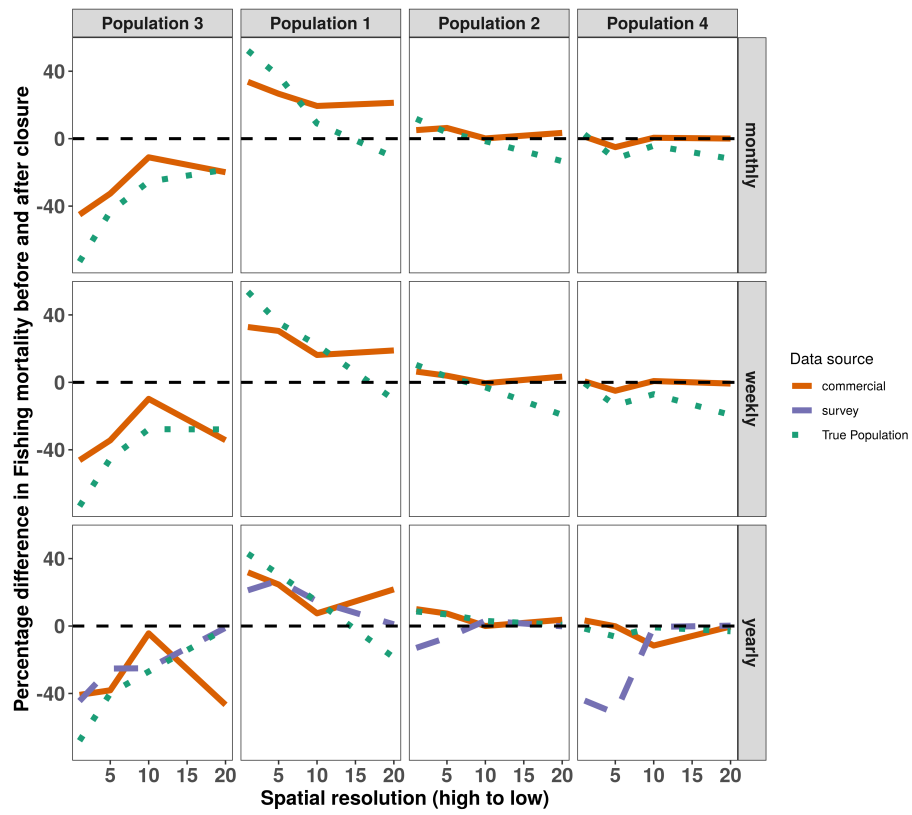


Figure 6: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.



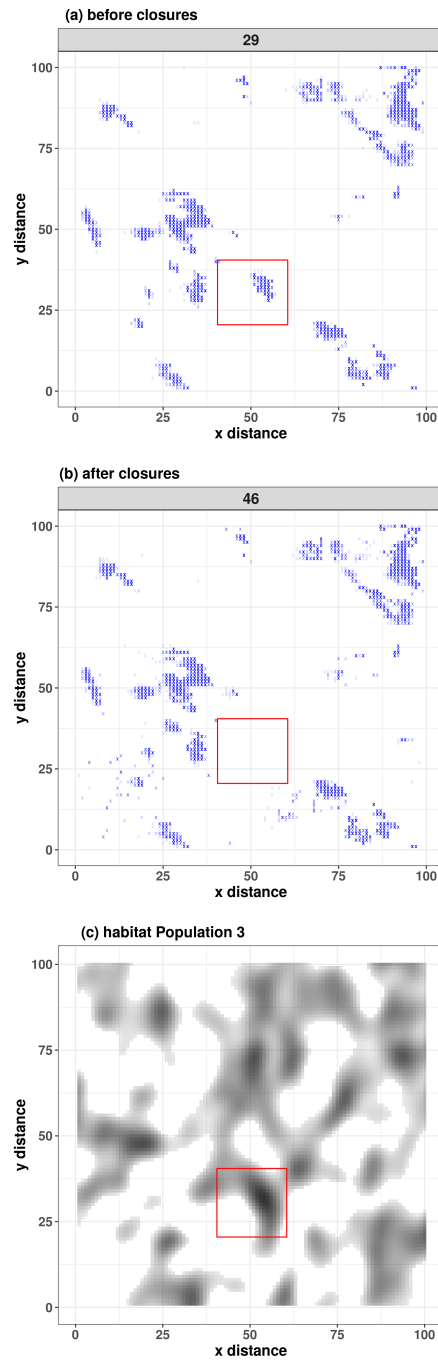


Figure 7: The location of fishing effort, (a) before the spatial closure and (b) after the spatial closure (years in panel), and (c) the suitable habitat for population 3. The site of the closure can be seen in the red box on all three panels.

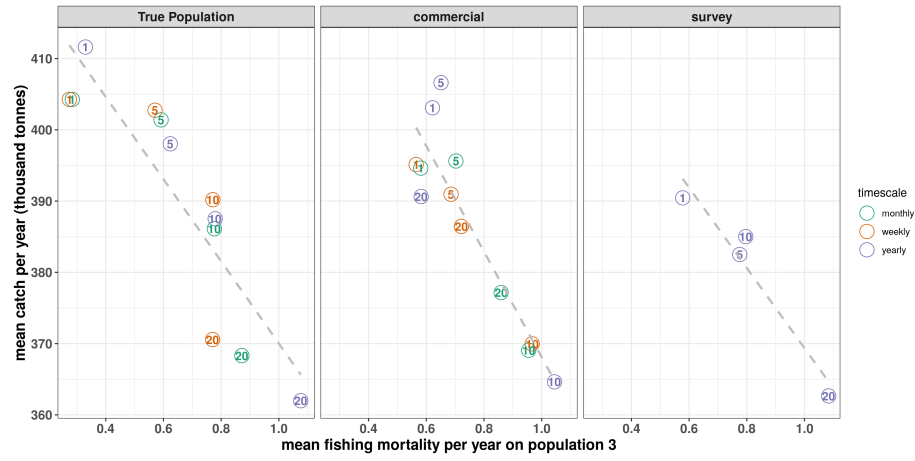


Figure 8: [Colour]Effectiveness of closure with regards to reducing fishing mortality on protected population (further left on x-axis is best) and maintaining high catches in the fishery (highest on y-axis is best). The numbers indicate the spatial resolution of the data, while grey lines indicate the direction of the trade-off between reducing fishing mortality and overall catches.

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